Assessing the density and distribution of spotted hyaenas (*Crocuta crocuta*) in Hluhluwe–iMfolozi Park, KwaZulu-Natal, South Africa

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ABSTRACT

Protected areas are becoming increasingly isolated refugia for large carnivores and are critical for their survival. Spotted hyaenas (*Crocuta crocuta*) have, for centuries, been ‘managed’ as problem causing animals and their conservation has been largely overlooked. To preserve a population, it is paramount to understand its distribution and abundance through reliable and cost-effective monitoring techniques. My study estimated the density of spotted hyaenas and their use of space in Hluhluwe–iMfolozi Park (HiP), South Africa. I compared camera trap by-catch data and call-up surveys between 2013–2018 to assess spotted hyaena densities. The camera trap data estimated an average of 16.72 (SD: ±2.22) hyaenas per 100 km^2 between 2013–2018, with an annual estimated high of 19.01 in 2018 and a low of 12.77 in 2015. The call-up surveys consistently produced lower estimates than those obtained from the camera trap data. These results highlight the importance of calibrating the response probability factor for call-up surveys to maintain precision. The space use of spotted hyaenas was analysed using the photo-capture data obtained during the same six-year period, to produce individual 100% Minimum Convex Polygon’s (MCPs). Seven clan territories were identified from individual female home ranges that overlapped by more than 66% of their MCPs. Territory sizes were similar to historical estimates for the park, with averages of 13.96 (SD: ±6.48) km^2 in Hluhluwe and 34.61 (SD: ±23.87) km^2 in iMfolozi. My study successfully used by-catch camera data to calculate annual density estimates and investigate the spatial use patterns for spotted hyaenas in HiP. I demonstrate that this approach is cost-effective and reliable for calculating density estimates. Conservation practitioners should take heed of the advancements in technology and analytical capacity now available to them to improve monitoring efforts. My study specifically calls for collaborative efforts to use existing camera trap data to improve regional estimates and population trends of spotted hyaenas across their range.

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CHAPTER 1 – GENERAL INTRODUCTION

An estimated 27,000 to 47,000 spotted hyaenas (*Crocuta crocuta*, Erxleben 1777; hereafter hyaenas) exist on the African continent, and although they are regarded as the most abundant large carnivore in Africa, their numbers are in decline (Bohm & Höner, 2015). Furthermore, there is a significant void in our understanding of their population trends, and density estimates are limited (Hofer & Mills, 1998b; Hunnicutt et al., 2016). It has been noted that due to decreasing prey numbers and increasing human settlement, hyaena populations outside of protected areas are decreasing (Bohm & Höner, 2015) and only some sub-populations within protected areas are stable (Bohm & Höner, 2015). As these sub-populations continue to be isolated within remaining protected areas, this species must be carefully monitored (Kruuk, 1998; Bohm & Höner, 2015) and effective conservation management strategies are implemented to ensure the species' continued survival.

Against this backdrop, the Kruger National Park (KNP) in South Africa has a hyaena population that has increased in numbers in recent years, possibly from an increase in prey abundance (Ferreira & Funston, 2020). However, despite this increase, a recent Red List assessment by the South African National Biodiversity Institute and the Endangered Wildlife Trust categorised hyaenas as regionally near threatened (Hunnicutt et al., 2016). The justification for such a categorisation was a nationwide decrease in most sub-populations outside of the KNP. One such population, believed to be showing a negative trend in abundance, is the third biggest in South Africa: Hluhluwe–iMfolozi Park (HiP), KwaZulu-Natal. According to call-up surveys from 2003, 2004, 2010, 2013 and 2015, the HiP population decreased by 66% over those 12 years (Graf et al., 2009; Ezemvelo KwaZulu-Natal Wildlife (EKZNW) unpublished data). It is believed that this decrease could be related to a decrease in the density of prey animals in the preferred size class for hyaenas (Hayward, O'Brien et al., 2007; Somers et al., 2017).

Data deficiency for the assessment of hyaena abundance, and trends thereof, has also been identified as a conservation concern (Hofer & Mills, 1998a, 1998b). Additionally, protected area managers need to find innovative and cost-effective ways to manage and monitor their wildlife, as public funding is limited (Motau & Wale, 2018). Thus, finding the means to effectively monitor hyaenas across protected areas, particularly those representing strongholds for the regional population, such as HiP, is essential.

The use of camera trapping in ecology has been around for more than half a century (Pearson, 1959) and its use as an animal surveillance tool has been readily available to the public for over 30 years (Kays & Slauson, 2008). Over the last 20 years, the use of and subsequent literature on camera trapping as a tool for surveying elusive carnivores has grown significantly (McCallum, 2013). Specifically, the analytic techniques that have developed over this period have further allowed camera trapping to become a powerful, non-invasive tool for establishing density and abundance estimates (Efford et al., 2009; Royle, Nichols et al., 2009), and determining population demographic parameters (Karanth et al., 2006; Gardner et al., 2010).

Since 2013, an annual camera trapping survey for leopards (*Panthera pardus*) has been conducted in HiP (Mann et al., 2019). Using the abundant hyaena by-catch data from this survey, I aim to investigate hyaena density and space use between 2013 and 2018. More specifically, I have chosen to use the spatially explicit capture-recapture (SECR) analytical framework (Gopalaswamy et al., 2012) as a robust means of estimating hyaena density trends from these data (Gopalaswamy et al., 2012; de Blocq, 2014).

Given their ecological importance as a keystone species (Paine, 1969), and the recent concern regarding their declining numbers (Bohm & Höner, 2015; Hunnicutt et al., 2016), understanding hyaena spatial ecology in HiP is vitally important for managing the species, as well as the park as a whole. Hyaenas are spatially influenced by numerous ecological and anthropomorphic factors (Hofer & Mills, 1998a, 1998b; Boydston, Kapheim, Watts et al., 2003; Kolowski et al., 2007; Kolowski & Holekamp, 2009; Périquet, Fritz et al., 2015). By using six years' worth of camera trapping data, I also aim to estimate the space use patterns of hyaenas within the park for the first time in 40 years (Whateley, 1981). As this species is often involved in human–wildlife conflict incidences (Hofer & Mills, 1998a; Parker et al., 2014; Megaze et al., 2017), understanding space use is vital for understanding and managing such conflict (Woodroffe & Ginsberg, 1998).

CHAPTER 2 – STUDY ANIMALS AND STUDY SITE

2.1 Spotted hyaenas

2.1.1 Global distribution and status

Hyaenas are widespread throughout Sub-Saharan Africa and occupy a wide range of habitats (Holekamp & Dloniak, 2010), from open deserts (Mills, 1990) to dense forests (Sillero-Zubiri & Gottelli, 1992). Throughout their range, density varies significantly, with the prey-rich savanna plains of East Africa (Kruuk, 1972; Watts & Holekamp, 2008, 2009) hosting the greatest density. More specifically, the Ngorongoro Crater in Tanzania has had the highest population density on record, with an estimated 170 hyaenas per 100 km^2 (Kruuk, 1972). The Serengeti system has the largest population in Africa, with over 8,000 individuals across Tanzania and Kenya (Bohm & Höner, 2015). A second significantly large population is that of the KNP in South Africa, which is believed to have between 6,998 and 7,680 sub-adult and adult individuals (Ferreira & Funston, 2020). However, density varies substantially between habitat types, ranging from 2.6 hyaenas per 100 km^2 in the Malelane Mountain bushveld to 21.1 in the Acacia-dominated lowlands (Mills et al., 2001).

Hyaenas occupy a wide range of habitats and a range of climatic and ecological conditions (Holekamp & Dloniak, 2010). The species occurs at a range of altitudes, from sea level (Tilson & Henschel, 1986) up to altitudes of 4,100 m (Young & Evans, 1993). Most noteworthy temperature changes are those in the semi-deserts of southern Kalahari, where hyaenas deal with a change in temperature from as low as −10° to as high as 40°C (Mills, 1990). Similarly, the animal is adapted to both arid and thick woodland environments (Tilson & Henschel, 1986; Creel & Creel, 2002, p. 249).

Although density estimates are limited in many parts of this species' range, global and regional status reports confirm a decreasing trend in most sub-populations throughout Africa (Hofer & Mills, 1998a; Bohm & Höner, 2015; Hunnicutt et al., 2016). The two greatest threats to hyaenas are habitat loss and human persecution (Hofer & Mills, 1998a; Cardillo et al., 2004). As the human population expands and prey numbers outside of protected areas decrease, hyaenas are placed under increased pressure (Hofer & Mills, 1998a). Hyaena populations have become highly fragmented with most viable populations limited to protected areas (Hofer & Mills, 1998a; Hunnicutt et al., 2016).

2.1.2 Social and reproductive ecology

The behaviour of hyaenas has been well researched over the last 60 years (Holekamp & Dloniak, 2010). Through reviewing the vast behavioural literature available on this species, Holekamp and Dloniak (2010) identified “fixed” behaviours true to most, if not all, studied populations of hyaenas. In contrast, they also noticed much behavioural plasticity between sub-populations, throughout their diverse range of habitats (Holekamp & Dloniak, 2010).

Hyaenas are structured into a matriarchal social clan with single or multiple matrilineal kin groups at its core (Frank, 1986b; Kruuk, 1972). All females within the clan can mate – and do so – with multiple males, as do males with multiple females (Henschel & Skinner, 1987; East et al., 2003). This sexual behaviour can result in single litters with multiple fathers (East et al., 2003). Hyaenas are sexually mature after two years (Matthews, 1939), and it is from this age that nearly all males disperse from their natal clan with the aim of being accepted by a new clan and mating with numerous females (East et al., 2003), preferably those of higher rank (Szykman et al., 2001). Males may immigrate to more than one clan throughout their lifetime (Van Horn et al., 2003), and can move across four to five different clan territories in pursuit of a suitable clan (Smale et al., 1997).

In the wild, hyaenas have been recorded to live to be older than 19 years (Drea & Frank, 2003). In a fission-fusion, highly structured and ranked society, the manner in which individuals experience these 19 years varies greatly (Holekamp & Dloniak, 2010). Those of higher rank are more likely to live longer (Watts & Holekamp, 2009) and reproduce more (Holekamp et al., 1996), although cub survival in some systems is not correlated with maternal rank (White, 2005). Nevertheless, in most systems, low-ranked individuals continue to battle for nutrients and calories throughout their existence (Holekamp et al., 1996; Smith et al., 2008). Ranking within the clan is based on maternal rank inheritance and is not achieved through size or fighting (Holekamp & Dloniak, 2010). After a 110-day gestation period (Jaarsveld et al., 1988), the modal litter size is two (Holekamp & Dloniak, 2010). The offspring that survive are ranked directly below their mothers and males subsequently lose this ranking and become subordinates when they emigrate (East & Hofer, 2001).

The natal den is a hole or cave with a very small entrance to prevent lions (*Panthera leo*) from making their way inside (Kruuk, 1972). These natal dens are usually occupied just for the first few weeks of the cub’s life before their mother moves them to the communal den (Cooper, 1993; White, 2006). The distances of a female’s natal den from the communal den have been shown to be positively correlated with decreasing rank (Boydston et al., 2006).

The length of time a cub is reared at the communal den varies between clans and habitat types (Holekamp & Dloniak, 2010). In more ecologically challenging areas with sparser prey, cubs remain at the den for between 12 and 15 months (Mills, 1990), but in the higher prey-density plains of Masai Mara National Reserve in Kenya, cubs leave the den by the age of nine months (Watts et al., 2009).

Maternal investment in cub rearing is long and intense in comparison to other carnivores (Estes, 2012; Jaarsveld et al., 1988; Watts et al., 2009). Females provide cubs with a rich milk for as long as 11–16 months (Mills, 1990; Watts et al., 2009; Watts & Holekamp, 2008). Similar to independence from the den, the time of weaning has been suggested to correlate with prevailing conditions (Holekamp & Dloniak, 2010), with the arid Kalahari hyaenas having a late weaning age of 16 months (Mills, 1990) and the prey-rich plains of Amboseli, Kenya resulting in a weaning age of 11 months (Watts & Holekamp, 2008). Once weaned, these cubs still have another two years before their skull and jaw muscles are fully developed to bite through bones and eat with as much efficiency as the adults (Watts et al., 2009). It is believed that this prolonged maternal investment has evolved to ensure greater cub survival (Watts et al., 2009).

The age at which females have their first litter varies between systems (Holekamp & Dloniak, 2010). In Holekamp and Dloniak's (2010) meta-analysis, the study population with the youngest mothers was noted to be in the Kalahari with a mean average age of 37 months at first parturition (Mills, 1990). The Serengeti population had an average age of 46 months at first parturition (Hofer & East, 2003) and is regarded as the study population with the latest birthing age (Holekamp & Dloniak, 2010). Once sexual maturity is reached, the interval between successful litters again varies between study populations. Serengeti hyaenas have been shown to have the longest intervals between litters, with an average of 19–21 months (Mills, 1990; Hofer & East, 1995). In Amboseli and the Masai Mara of Kenya, the inter-litter intervals are, on average, roughly 25% shorter, at 14–15 months (Holekamp & Dloniak, 2010).

The reproductive status, social rank and sex of an individual influence the amount of time, and the distance, the individual will need to cover to obtain their required energetic intake (Hofer & East, 1993c; Boydston, Kapheim, Szykman et al., 2003; Kolowski et al., 2007). The Serengeti represents a good example of how the reproductive state of hyaenas can influence spatial behaviour (Hofer & East, 1993c). Here, female hyaenas without denning cubs commuted 15–18 times a year, with an average of 6–10 days spent away from the den at a time (Hofer & East, 1993c). This situation is contrasted against females with cubs that returned more frequently to the communal den and their cubs, and only spent 3–4 days away at a time. These frequent returns to the den may have energy-related consequences for females with cubs, as the increased frequency of return trips can result in average yearly commutes more than 2.6 times further than those without cubs (Hofer & East, 1993c). Boydston Kapheim, Szykman et al. (2003) found that despite further distances being covered by den-bound females, their home ranges were smaller and closer to the den than those females without cubs.

Higher-ranked females, who have greater access to food (Holekamp, Smale et al., 1997), are more likely to breed younger, more regularly and more successfully than lower-ranking females (Holekamp et al., 1996). Lower-ranking females are more inclined to hunt alone (Holekamp & Dloniak, 2010) and need to cover greater distances to acquire their nutritional intake (Boydston, Kapheim, Szykman et al., 2003; Höner et al., 2005). This greater movement away from communal dens, and out of clan territory, can in turn have consequences for their survival because it increases the chances of encountering intra- and inter-specific competitors (Boydston, Kapheim, Szykman et al., 2003; Woodroffe & Ginsberg, 1998).

Excluding the dispersal events of males (Smale et al., 1997), males on average cover a greater distance and are more spatially active than females within a clan (Henschel, 1986; Kolowski et al., 2007). The greater activity observed in males is likely due to their monitoring of multiple females (Kolowski et al., 2007), as it is believed that the greater time a male spends with a receptive female, the greater chance they have of successfully reproducing (East et al., 2003).

It is believed that clan size is influenced by food availability (Macdonald & Johnson, 2015; Mills, 1990). This hypothesis is supported when comparing differences in clan sizes across 19 study sites (Holekamp & Dloniak, 2010). Clans ranged from 6 members in the deserts of Namibia (Tilson & Henschel, 1986) to 67 in the game rich plains of Ngorongoro Crater in Tanzania (Kruuk, 1972). The largest ever clan on record is the Talek West Clan of the Masai Mara which averaged 113 individuals in 2013 (Green et al., 2018).

2.1.3 Feeding ecology

Hyaenas have an average daily food intake of 3.8–4 kg per individual (Green et al., 1984; Henschel & Tilson, 1988; Henschel & Skinner, 1990), but they can consume up to 18 kg in one sitting (Bearder, 1977), devouring prey as quickly as 1.3 kg per minute (Kruuk, 1972). Hyaenas have been recorded feeding on a wide range of items, including fruits, insects (Mills, 1990) and anthropogenic organic waste (Yirga et al., 2012). Hyaenas have been recorded hunting prey items as large as hippopotamuses (*Hippopotamus amphibious*) (Henschel &

Skinner, 1990) and scavenging on giraffe carcasses (*Giraffa camelopardalis*) or elephants (*Loxodonta africana*) has been observed (Hayward, 2006; Périquet, Valeix et al., 2015). Hayward's (2006) meta-analysis of 15 study populations revealed that hyaenas show no preference for specific prey species but do prefer medium- to large-sized prey items (56–182 kg). Often, hyaenas preferentially hunt alone, with as much as 75% of hunts made in the Masai Mara done in this manner (Holekamp, Smale et al., 1997). Even antelope as large as blue wildebeest (*Connochaetes taurinus*) have been reported as being pursued by a single hyaena (Holekamp, Smale et al., 1997).

Although previously believed to be almost exclusively a scavenger, hyaenas in most regions obtain the majority of their food through hunting (Holekamp & Dloniak, 2010). In the Masai Mara, 95% of hyaena diet is attributed to their own kills (Holekamp et al., 1999). Nevertheless, in parts of northern Ethiopia, where hyaenas and humans live in proximity to one another, as little as 11% of their diet is through predation while the rest is through scavenging (Abay et al., 2011). The adaptability of hyaenas' dietary behaviour is well represented in accounts from Ngorongoro Crater, Kenya and Hwange National Park of Zimbabwe (Höner et al., 2002; Périquet, Valeix et al., 2015). In these systems, lion numbers are comparatively high, increasing the number of large carcasses available. Consequently, the hyaenas' scavenging behaviour increased, and Cape buffalo (*Syncerus caffer*) and elephant carcasses became a dominant part of their diet (Périquet, Valeix et al., 2015). This adaptability has also been shown in anthropogenic waste dependant populations (Abay et al., 2011), where the hyaena diet changes at the onset of religious fasting periods (Yirga et al., 2012).

The plasticity of hyaenas' foraging behaviour is believed to have had assisted in making it the most abundant large carnivore in Africa (Hayward, 2006; Holekamp & Dloniak, 2010; Bohm & Höner, 2015). Nevertheless, prey availability has continuously been identified as one of the most important ecological determinants for the perpetuation of the species (Kruuk, 1972; Höner et al., 2005; Watts & Holekamp, 2008, 2009).

2.1.4 Inter-specific competition

Interference and exploitative competition can both play a strong role in the dynamics that play out between lions and hyaenas (Périquet, Fritz et al., 2015). Generally, a strong level of vigilance is maintained by hyaenas when in the presence of lions (Watts et al., 2010), and both temporal and spatial avoidance has been documented (Hayward & Hayward, 2007; Sogbohossou et al., 2018; Périquet et al., 2021). However, despite high levels of vigilance, hyaenas still frequently succumb to predation from lions (Périquet, Fritz et al., 2015).

Hyaenas incur kleptoparasitism from lions in most systems in which they co-exist (Carbone et al., 1997; Périquet, Fritz et al., 2015) and some may adopt risk avoidance behaviour (Creel & Christianson, 2008), which may reduce optimal foraging and have consequences for population success. Kleptoparasitism occurs bidirectionally for lions and hyaenas, although lions steal more hyaena kills than vice versa (Périquet, Fritz et al., 2015). Nevertheless, it is prey availability (Périquet, Valeix et al., 2015) and the population structure of both species that influences what dynamic plays out in a specific system (Kruuk, 1972; Cooper, 1991; Watts & Holekamp, 2008). The number of hyaenas and lions at a specific carcass plays an important role in whether hyaenas will succeed in either staying on their own kill or displacing lions from theirs (Cooper, 1991; Höner et al., 2002). Cooper (1991) believed a ratio of at least four hyaenas to one lion was necessary for the successful acquisition of a carcass. At higher densities, hyaenas are more likely to recruit clan mates to defend kills than in lower-density systems (Trinkel & Kastberger, 2005; Périquet, Valeix et al., 2015) and thus have greater foraging success. Conversely, hyaenas are less likely to successfully steal kills when adult male lions are present at a carcass (Cooper, 1991; Höner et al., 2005; Périquet, Valeix et al., 2015). Interestingly, the scavenging behaviour of hyaenas increases with an increase in male lions within the system, as large prey items are killed more frequently and more unfinished carcasses remain (Höner et al., 2002; Périquet, Fritz et al., 2015). Thus, the presence of male lions within a system can both inhibit and facilitate the coexistence with hyaenas.

An added complexity to this interspecific dynamic is evident with the onset of anthropogenic disturbance. During Green et al.'s (2018) study of the hyaenas of the Masai Mara, it was noted that an increased level of human settlement bordering the reserve brought about more pastoralists encountering lions and hyaenas. Lions are more likely to be persecuted in retaliation killings by herders than hyaenas during the day (Kissui, 2008) and it is believed that this might be one of the causes of the lion population decreasing in the Masai Mara. With a lower lion population and an increased number of livestock on which to prey, the hyaena population increased.

2.1.5 Anthropogenic impacts

Anthropogenic disturbance can influence hyaena populations in three main ways: direct destruction (Hofer et al., 1996; Mills, 1998a; Kissui, 2008), changes in temporal and spatial behaviour (Boydston, Kapheim, Watts et al., 2003; Kolowski et al., 2007; Holekamp & Dloniak, 2010) and impact on diet (Abay et al., 2011; Yirga et al., 2012). The lethal persecution of hyaenas has been shown to directly influence the species' population demographics

(Holekamp & Smale, 1992; Hofer, 1998). The latter two mechanisms through which humans may influence hyaena populations play out more indirectly. The most notable example is the global land use changes outside of protected areas that have been identified as a cause of global wildlife decline (Virani et al., 2011). The decreasing trend in hyaenas numbers globally has been largely attributed to the human-induced reduction in prey numbers outside of protected areas (Hofer & Mills, 1998b; Bohm & Höner, 2015).

The direct killing of hyaenas through poisoning, snaring and hunting continues to put pressure on most populations outside of protected areas, as well as some of those inside (Hofer & Mills, 1998b). Hyaenas are killed for five main reasons. Firstly, for the utilisation of body parts for traditional beliefs or, secondly, for food (Hofer & Mills, 1998b). Thirdly, in certain regions there has been an increased demand for hyaenas by trophy hunters (Pers. Comm. EKZNW Animal Scientist – Brent Coverdale, 2021). Fourthly, they may be destroyed in retaliation as potentially problem-causing animals (Hofer & Mills, 1998b). Finally, through untargeted snaring, the incidental killing of these animals plagues many populations, including those of the Serengeti (Hofer et al., 1996) and Zululand (Hunnicutt et al., 2016). It is believed that 50% of adult hyaena deaths in the Serengeti are caused by these traps (Hofer & Mills, 1998a). In South Africa, a strong belief in the supernatural properties of hyaena body parts has placed additional pressure on hyaena populations (Majova, 2005).

Large predators are susceptible to retaliatory killings by livestock owners (Kissui, 2008), with hyaenas being commonly targeted through poisoning (Kissui, 2008). The devastating and unselective nature of poisoning can result in entire clans being killed (Holekamp & Smale, 1992). These events can influence social, demographic and spatial dynamics (Holekamp & Dloniak, 2010). For example, the Talek Clan of the Masai Mara has gone through two fission events because of human disturbance (Holekamp & Dloniak, 2010). The first fission event took place in the late 1980s, where an entire territory was vacated after a poisoning event of a clan (Holekamp & Smale, 1992). Mid- to low-ranking females dispersed from the neighbouring clan and colonised the vacant land (Holekamp et al., 1993). The second fission event, in the late 1990s, resulted from indirect human disturbance (Holekamp & Dloniak, 2010). An increased level of cattle grazing through the centre of the Talek home range began to divide the clan (Holekamp & Dloniak, 2010), as hyaenas avoided the pastoralists (Boydston, Kapheim, Watts et al., 2003). This spatial division subsequently created two clans, the Talek West and Talek East (Holekamp & Dloniak, 2010).

Although highly adaptable, hyaenas may be incurring a fitness cost when adapting their behaviour in response to humans (Boydston, Kapheim, Watts et al., 2003; Kolowski et al., 2007; Kolowski & Holekamp, 2009), which is known as the risk effect (Creel & Christianson, 2008). Kolowski et al. (2007) suggest that there is a trade-off between successful nocturnal foraging (Kruuk, 1972) and increased risk to predation of hyaena cubs by lions. It has been shown in female wolves (*Canis lupus signatus*) with young, that their increased diurnal activity may be a response to high predatory activity at night (Vilà et al., 1995). Kolowski et al. (2007) believe that should the foraging times available to a weaning mother be limited, and daytime foraging be reduced due to anthropogenic disturbance, cubs may be more at risk of predation.

It should also be noted that not all hyaena populations show a negative response to increased human disturbance, and a positive relationship between hyaenas and humans can take place. Yirga et al. (2017) found that hyaena density in parts of northern Ethiopia was at its highest closest to villages. These areas had a low natural prey density, but refuse waste and livestock were an important part of hyaena diet (Yirga et al., 2012). Furthermore, in areas where the human population has increased, and lion populations have been depleted through persecution, hyaena survivorship has improved and subsequent population growth has been recorded (Green et al., 2018).

2.1.6 Disease

Disease is seldom reported as a major ecological determinant for hyaenas. Even a high prevalence of tuberculosis, a major zoonotic disease in the KNP and HiP (Michel et al., 2006), in prey species has not been shown to influence hyaena populations (Ferreira & Funston, 2016). Nevertheless, rabies, canine distemper virus (CDV) and *Streptococcus equi* subsp. *ruminatorum* have impacted some populations (Mills, 1990; Haas, 1996; Watts & Holekamp, 2009; Höner et al., 2012). The death of almost an entire clan in the Kalahari has been attributed to rabies (Mills, 1990). Furthermore, it is believed that because of the social behaviour of hyaenas, older adults are more susceptible to contracting the disease as they come into contact with the most hyaenas (Mills, 1990). For this reason, it may be possible for rabies to cause a demographic shift within some populations (Mills, 1990). In the Serengeti, the death of multiple cubs below the age of six months was caused by CDV (Haas, 1996). Interestingly, the strain discovered in these animals was closer to that observed in lions than domestic dogs (Haas, 1996). However, it should also be noted that although both of these diseases have been recorded in several populations, their prevalence and impact on hyaena populations is substantially lower than in other large carnivores (Watts & Holekamp, 2009). It has been hypothesised that this resistance to disease is an evolutionary adaptation due to their high scavenging and carrion content diet (Watts & Holekamp, 2009).

The pathogenic bacterium *Streptococcus equi* subsp. *ruminatorum* outbreak in the Ngorongoro Crater in 2002 and 2003 coincided with increased mortality within the hyaena population (Höner et al., 2012). Of the individuals infected with the bacteria, 12.5% died. During the outbreak, the mortality increase throughout the population was predominantly in relation to yearlings and adult males. It is believed that this disparity between adult male and female mortality rates is because males are of lower rank than females in hyaena society, which translates to poorer nutritional intake overall (Henschel & Skinner, 1990), possibly making them more vulnerable to pathogenic bacterium-induced death (Höner et al., 2012). The increased level of mortality during the outbreak and decreased sub-adult survivorship resulted in a slower population growth over the subsequent three years (Höner et al., 2012).

2.2 Hluhluwe–iMfolozi Park

2.2.1 Landscape and vegetation

Situated between 28°00’ and 28°26’S and 31°43’ and 32°09’E, HiP in northern KwaZulu-Natal, South Africa (Figure 2.2-1), is the oldest proclaimed protected area in Africa. The Park is also one of the largest fully fenced protected areas in South Africa, covering 900 km^2 (Howison et al., 2017). Being situated between the coast and interior plateau, HiP has a mosaic of different soils, geology and vegetation types (Howison et al., 2017; Waldram, 2005). Topographically, the park lies at 45 m above sea level, at its lowest point, at the confluence of the Black and White Umfolozi rivers in the iMfolozi section and climbs to 750 m in the north-west of the Hluhluwe section. Hluhluwe is typified by hilly terrain with steep valleys. Moving south, these hills gradually shallow out into iMfolozi (Howison et al., 2017).

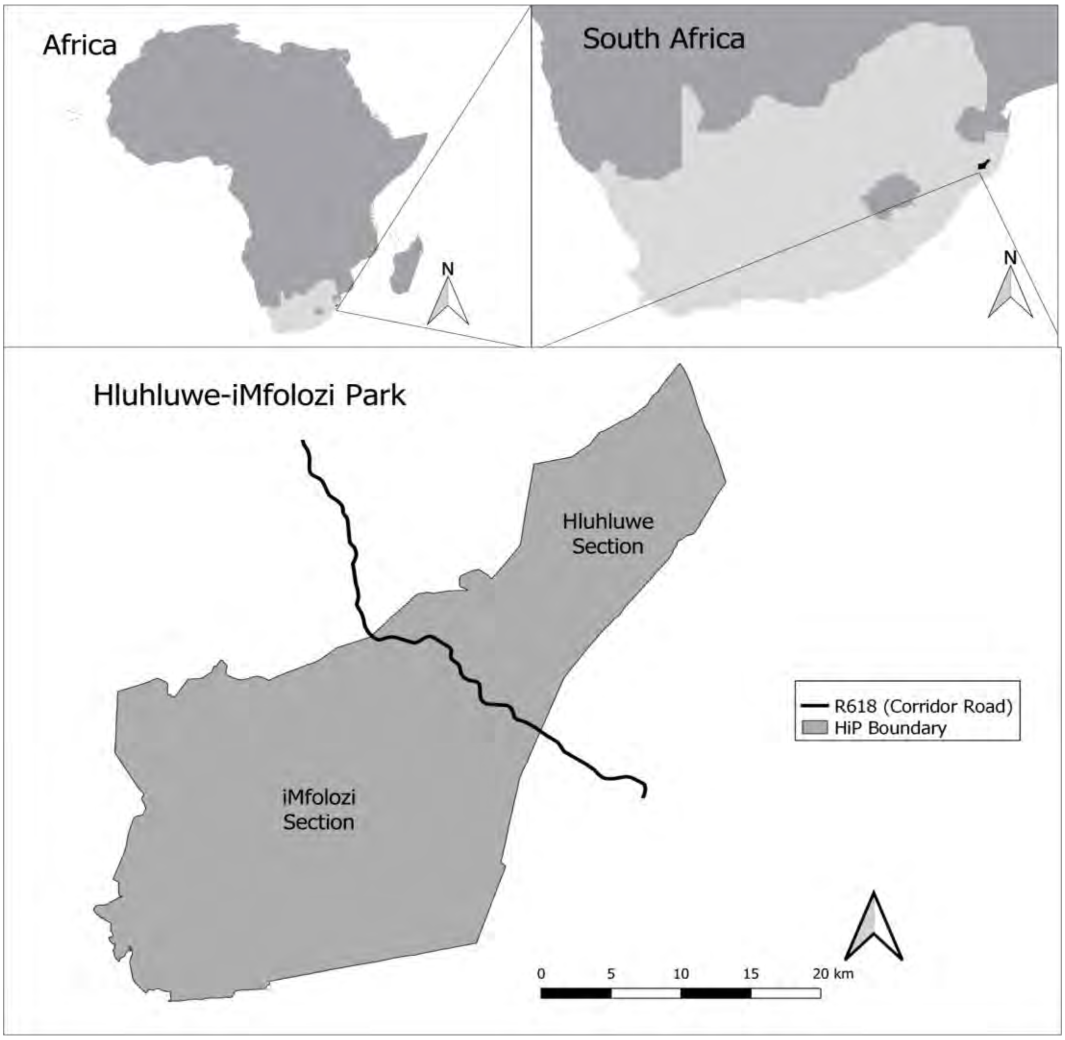


Figure 2.2-1: HiP's geographic position within South Africa. The Park is separated into two sections, Hluhluwe and iMfolozi. These sections are separated by a tarred road known as the Corridor Road.

HiP's landscape has been likened to the Serengeti ecosystem of Tanzania (Howison et al., 2017): fertile soils, concentrated summer rainfall and a vegetation mosaic of Acacia woodland and grassland, interspersed with patches of forests (Howison et al., 2017). The most notable difference between the two systems is the size, with the Serengeti covering an open area more than 16 times that of the fenced HiP. Nevertheless, the fertile soils and palatable vegetation of both systems result in a high abundance of both browsers and grazers (Howison et al., 2017).

HiP has tropical characteristics in its flora and fauna due to its westerly position in the Indian Ocean Coastal Belt Biome (Acocks, 1975; Waldram, 2005; Howison et al., 2017). However, its position at a transition point between the tropical coastal belt and Lowveld savanna (Whateley & Porter, 1983; Howison et al., 2017) gives rise to a diverse array of vegetation types, broadly categorised as Tropical Bush, Savanna and Zululand Thornveld (Acocks, 1975;

Whateley & Porter, 1983). More than 20 vegetation communities have been identified within HiP (Whateley & Porter, 1983; Howison et al., 2017; Figure 2.2-2).

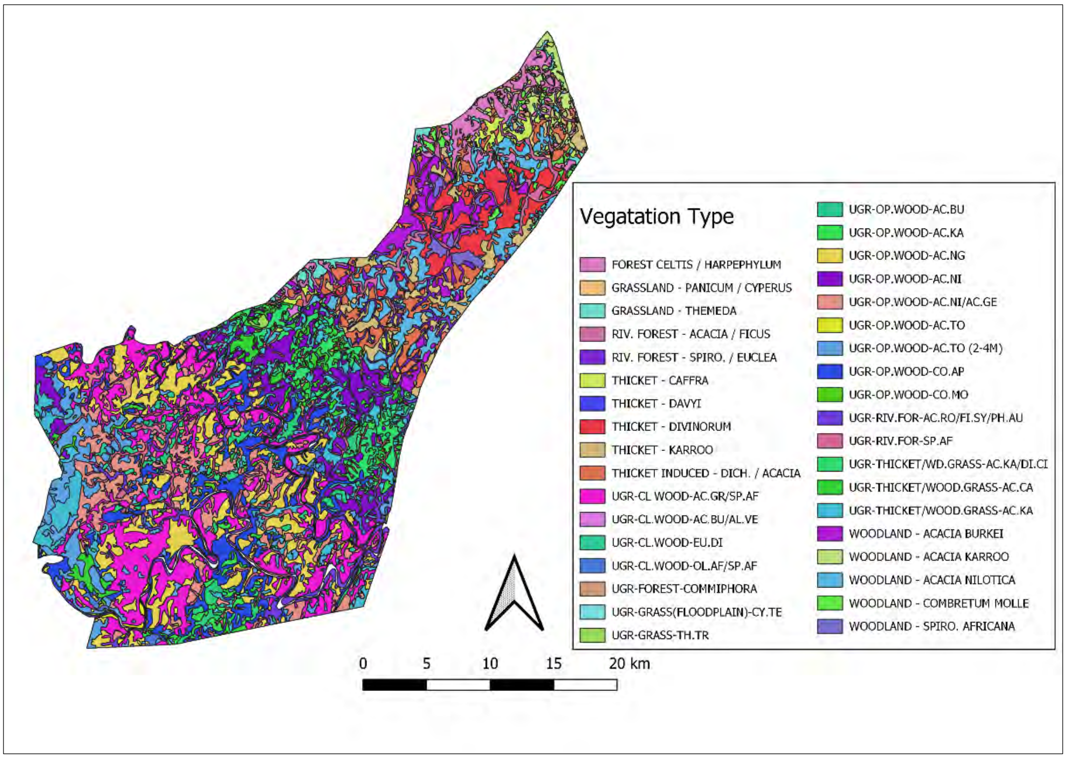


Figure 2.2-2: HiP's diverse array of vegetation types, based on Whateley and Porter's (1983) vegetation assessment.

The most common woody vegetation types present in the savanna landscape of HiP are the *Acacia* woodland and *Acacia* thicket (Whateley & Porter, 1983; Howison et al., 2017). These occur on hillsides with dolerite substrates, shallow shale-based hills, steep slopes in Hluhluwe and Corridor sections and many east facing slopes in iMfolozi. The single most prevalent vegetation type is tambotie (*Spirostachys africana*) woodland. This habitat is most noticeable in the catchment areas of the low-lying sections of iMfolozi (Whateley & Porter, 1983; Howison et al., 2017). Forests also cover nearly 10% of HiP's woody vegetation, namely white stinkwood – African wild plum (*Celtis africana - Harpephyllum caffrum*) and sycamore fig – weeping boer-bean (*Ficus sycomorus – Schotia brachypetala*) forests. The former occurs on the highest section of the park, the north-west of Hluhluwe; the latter characterises many banks of the major rivers and tributaries (Whateley & Porter, 1983; Howison et al., 2017).

The herbaceous layer of HiP is comprised of both bunch grasslands and grazing lawns (Howison et al., 2017). The most common species making up the latter is guinea grass (*Panicum maximum*), needle grass (*Enteropogon monostachyus*) and LM grass (*Dactyloctenium australe*). Grazing lawns extend throughout HiP, covering 10–15% of the park, which is an important source of food for grazers (Cromsigt et al., 2017). Fragmenting these lawns are the bunch grasslands which comprise mostly of red grass (*Themeda triandra*) on the clay soils, dropseed (*Sporobolus africanus* and *Sporobolus pyramidalis*), and love grass (*Eragrostic curvula* and *Eragrotis superba*) on the sandier soils (Whateley & Porter, 1983; Howison et al., 2017).

2.2.2 Rainfall and temperature

Falling within the summer rainfall region of South Africa, the seasonal variation in water availability in HiP is pronounced (Howison et al., 2017). Across the park, rainfall strongly correlates with elevation (Balfour & Howison, 2002; Howison et al., 2017) and mean annual rainfall ranges from less than 550 mm in the low-lying areas of iMfolozi to around 1,000 mm in the hills of Hluhluwe (Howison et al., 2017). Annual variation in rainfall in HiP has revealed alternating dry and wet phases that last between 4 and 10 years at a time (Balfour & Howison, 2002).

Between 2012 and 2019, HiP experienced a severe drought. The average monthly rainfall dropped from 70.68 mm per month in the 2012/2013 season, to 33.49 mm per month in 2015/2016, before recovering to 67.92 mm in the 2018/2019 season (EKZNW unpublished data; Figure 2.2-1).

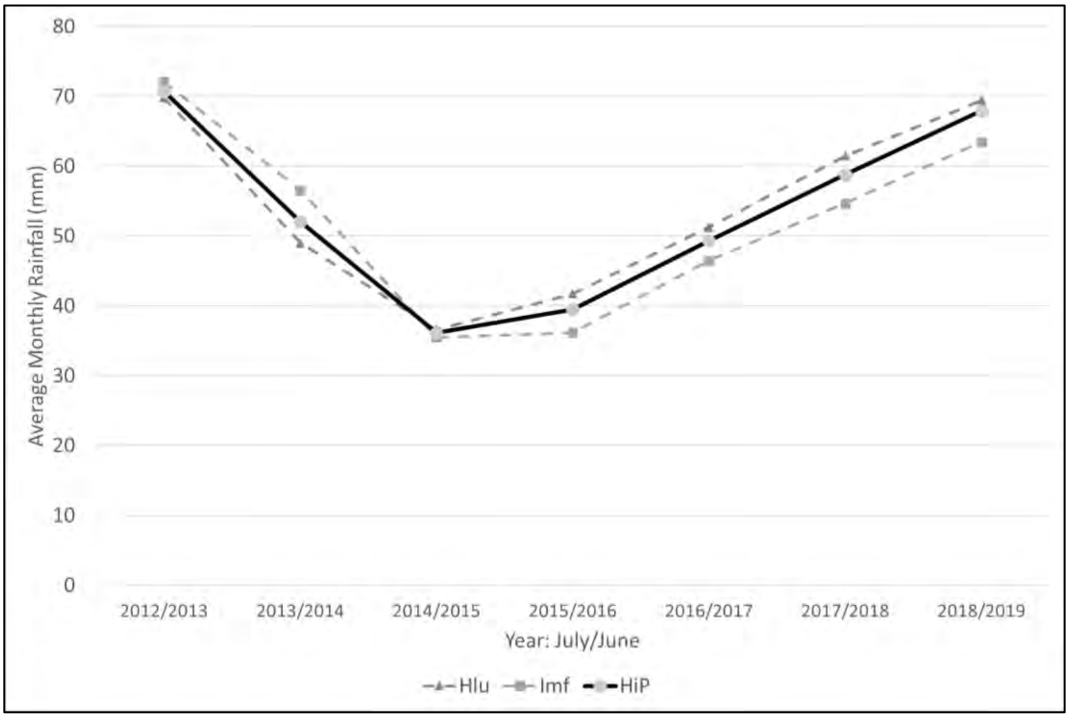


Figure 2.2-2: Average monthly rain across HiP between 2012 and 2019. Years ran from July through to June to include the full rainy season each year. Averages for Hluhluwe ("Hlu") and iMfolozi ("Imf") sections of the park are shown.

All three large rivers running through HiP, the Hluhluwe, Black Mfolozi and White Mfolozi, which used to flow all year round, have now stopped flowing seasonally (Howison et al., 2017). There are, however, places within the park where water remains throughout the year. Most noteworthy of these is the 2 km backlog of water in the Hluhluwe River due to the construction of the Hluhluwe Dam outside the park. It should be noted that there are many pans and wallows within the park that can hold water for months after rain (Graf, 2008). The iMfolozi section has the greatest area without a perennial water source, spanning 10 km in the west (Howison et al., 2017).

Temperature records in HiP show further heterogeneity throughout the park (Howison et al., 2017). The average summer daily high temperatures recorded from Hilltop Camp in Hluhluwe and the low-lying western region of iMfolozi are 24.8°C and 32.8°C, respectively (Howison et al., 2017); average daily low winter temperatures have been recorded as 11.7°C and 10.7°C, respectively (Howison et al., 2017).

2.2.3 Prey density

Herbivore composition and abundance in HiP have fluctuated dramatically both prior to and throughout its history as a protected area (Le Roux et al., 2017). The population trends of many of these species have coincided with changes in management strategies. After intensive exploitation of game throughout Zululand in the 1800s, the Hluhluwe and iMfolozi Game Reserves were founded in 1895, to conserve dwindling animal numbers, in particular the white rhinoceros (*Ceratotherium simum simum*) (Brooks & Macdonald, 1983; Le Roux et al., 2017; Te Beest et al., 2017). Within 30 years of its declaration, the reserves were placed under new management (Veterinary Department), to deal with the Nagana epidemic (Brooks & Macdonald, 1983; Le Roux et al., 2017). At the turn of the century, Nagana had begun to influence livestock management in Zululand, causing reduced cattle fertility, limited growth and increased mortality (Connor, 1994; Kluge, 1945). Wildlife was identified as being carriers of the disease (Kluge, 1945) and the Veterinary Department implemented large-scale culling programmes to reduce its spread (Brooks & Macdonald, 1983; Le Roux et al., 2017). In just 20 years, 70,000 animals were destroyed in and around HiP (Brooks & Macdonald, 1983; Le Roux et al., 2017). This strategy was identified as futile and stopped before the introduction of DDT aerial sprays in 1950–1951 (Te Beest et al., 2017). The Nagana epidemic was concluded to be under control by 1953, and the provincial conservation governing body took back responsibility of HiP (Te Beest et al., 2017).

In the 1950s, game numbers began to increase in HiP once more (Le Roux et al., 2017), and a veld preservation approach to management in the 1960s, 70s and 80s saw the continued culling of nyala (*Tragelaphus angasii*), warthog (*Phacochoerus africanus*), wildebeest and common zebra (*Equus quagga*) (Brooks & Macdonald, 1983; Le Roux et al., 2017). In the 1980s, a change in management strategy resulted in a process-based management approach being implemented that used veld burning, live removals and other management tools to maintain game numbers (Le Roux et al., 2017). Zebra, wildebeest and warthog numbers all recovered over this period. However, from 1972 to 2016 the number of common waterbuck (*Kobus ellipsiprymnus*) and common reedbuck (*Redunca arundinum*) plummeted from 1,700 and 623, respectively, to 120 and almost nothing (Brooks & Macdonald, 1983; Le Roux et al., 2017).

An ungulate census has been conducted every two years across HiP since 1994 (Grange et al., 2012). Distance sampling is done at 34 line transects throughout HiP and each transect is generally sampled 16 times during the 3-month long census. Over the past 10 years, herbivore density in HiP has undergone substantial changes, with the start of a dramatic decline in small to intermediate (<400 kg) species in 2008 (Le Roux et al., 2017). Trends in the prey population abundance between 2010 and 2016 in HiP have predominantly been decreasing. Nyala, warthog, giraffe, wildebeest and zebra have all reduced in number, with only buffalo, impala (*Aepyceros melampus*) and greater kudu (*Tragelaphus strepsiceros*) having shown some stability. Increased predator populations in the early 2000s have been speculated as the possible cause for the negative trend in many prey species over this period (Le Roux et al., 2017).

2.2.4 Predators

HiP has an almost full complement of large carnivores (Rowe-Rowe, 1992; Somers et al., 2017), and both hyaenas and leopards have persisted through time without reintroduction (Rowe-Rowe, 1992; Somers et al., 2017). The reintroduction of wild dogs (*Lycaon pictus*), lions and cheetahs (*Acinonyx jubatus*) have all had varying levels of success within the park (Somers et al., 2017; Trinkel et al., 2008). Estimates for these species in 2018 were 36, 70 and 8 individuals, respectively (EKZNW unpublished data; KZN-WAG minutes).

After the extirpation of lions in the first half of the 20th century, a founder population was established by 1965 through reintroduction and natural dispersal (Anderson, 1981). The initial group of lions consisted of three adult females, one adult male, two female cubs and one male cub (Anderson, 1981; Somers et al., 2017). Despite the culling of sub-adults to reduce predation on neighbouring community livestock in the 1970s and 80s (Somers et al., 2017), by 1974, the population had grown to 114 individuals (Anderson, 1981) and around 140 by 1987 (Maddock et al., 1996) but then decreased to 80 by 1999. It was identified that inbreeding was impacting the lion population of HiP during this time (Trinkel et al., 2008). Genetic restoration of the population took place with the reintroduction of a further 16 lions between 1999 and 2001 (Trinkel et al., 2008). However, annual abundance estimates dropped in the early 2000s after this supplementation (Trinkel et al., 2008). From 2004 to 2008, the population recovered to a high of 12.7 lions per 100 km^2. The population remained above 11.8 per 100 km^2 until 2017, but then dropped down to 7.8 per 100 km^2 (EKZNW unpublished data). The most commonly observed kills made by lions in HiP are buffalo, wildebeest, nyala, zebra, impala and kudu (Somers et al., 2017). More recently, impala and buffalo have been observed being consumed most frequently (Somers et al., 2017).

Wild dogs are the most endangered carnivore in southern Africa and have been persecuted intensively by landowners and conservation managers alike (Vaughan-Kirby, 1917; Woodroffe & Sillero-Zubiri, 2012; Somers et al., 2017). This species was likely extirpated from the Zululand region by 1944 (Somers et al., 2017). In the early 1980s, the first reintroduction into

HiP took place (Whateley & Brooks, 1985). Multiple supplementations and live removals have taken place since 1997 as part of the wild dog metapopulation management strategy for South Africa (KZN-WAG minutes; Mills et al., 1998; Somers et al., 2017). The population has fluctuated amidst these supplementations and removals. However, the wild dog population in HiP gradually increased through the early 2000s from only 5 individuals in 2000, up to a high of 13.4 dogs per 100 km^2 in 2011. Density remained above 10 per 100 km^2 up until 2017, when it dropped to 7.8 per 100 km^2 (EKZNW unpublished data; KZN-WAG minutes). Research in the 1990s noted HiP wild dog diet consisted mostly of nyala and impala (Krüger et al., 1999). Wild dog packs within the park have historically been large enough to defend kills from hyaenas (Darnell et al., 2014).

After being considered extirpated from the park, the mass reintroduction of 64 cheetahs took place between 1966 and 1969 (Whateley & Brooks, 1985; Rowe-Rowe, 1992). However, by 1992, the entire park was believed to only have 15 cheetahs left (Rowe-Rowe, 1992). A number of further reintroductions have taken place since, but numbers remain low (Somers et al., 2017). Nyala and impala have been recorded as the most commonly observed kills made by cheetahs in HiP (Whateley & Brooks, 1985; Somers et al., 2017).

In 2011, estimates placed the density of leopards at roughly 11 leopards per 100 km^2. This estimate dropped to 6 per 100 km^2 in 2013, and by 2017 it was believed to be as low as 2.6 (± 0.6) leopards per 100 km^2 (Mann et al., 2017). One of the possible causes for the reduced density over the past seven years in HiP has been speculated to be illegal killing both inside and outside the park for the skin trade (Mann et al., 2017) and retaliation killings (Pers. observations). The diet of leopards in HiP is believed to consist predominantly of impala and nyala (Somers et al., 2017).

Although once regarded as common in the region (Somers et al., 2017), brown hyaenas (*Parahyaena brunnea*) have not been seen in HiP for decades, and their demise is believed to have coincided with an increase in spotted hyaena numbers (Rowe-Rowe, 1992; Somers et al., 2017). A reintroduction of four brown hyaenas took place in HiP in the late 1970s, but this was unsuccessful (Rowe-Rowe, 1992).

There have been 6 notable pieces of hyaena literature coming out of HiP over the past 60 years (Deane, 1962; Whateley & Brooks, 1978; Whateley, 1981; Skinner et al., 1992; Graf, 2008; Graf et al., 2009). Four of these studies focussed on density estimates (Whateley & Brooks, 1978; Whateley, 1981; Graf, 2008; Graf et al., 2009), one on general ecology (Deane, 1962) and the other on feeding ecology (Skinner et al., 1992). The first scientifically-based density estimate of hyaenas in the park was for Hluhluwe in the late 1970s (Whateley & Brooks, 1978) and used the call-up technique (with mark-recapture) to get an estimate of 46 hyaenas per 100 km^2. Adopting the same method for iMfolozi, estimates of 36 hyaenas per 100 km^2 were established for this part of the park (Whateley, 1981). Over 20 years later, Graf et al. (2009) re-estimated the density of hyaenas and the spatial heterogeneity of this density, using the call-up method with a response probability factor. Their density estimates for between 2003 and 2004 of 35 hyaenas per 100 km^2 were consistent with the estimates of Whateley and Brooks (1978) and Whateley (1981). Furthermore, Graf et al. (2009) found that there was a great deal of short-term spatial heterogeneity in densities, and this was hypothesised to be due to the spatial distribution of prey species (Cromsigt, 2006).

Skinner et al. (1992) used scat analysis to establish the diet composition of hyaenas in iMfolozi and uMkhuze Game Reserves in 1989. From 162 scat samples, impala and nyala were identified as the most common species consumed in iMfolozi. This study of diet was unable to distinguish between what was acquired through hunting or through scavenging, however.

The most commonly observed kills over the past 30 years for hyaenas from field observations have been nyala, impala, greater kudu and buffalo, although kill observations have been very low for this species (Somers et al., 2017). At the time of Graf et al.'s (2009) 2003–2004 density estimates, the most abundant prey animals were impala, nyala, zebra, wildebeest, buffalo and warthog.

2.2.5 Anthropogenic setting

People have been utilising natural resources in and around the HiP region since the stone age and may even have initiated unintentional ecological change by introducing fire (Te Beest et al., 2017). The first Europeans set foot in the region 500 years ago (Bulpin, 2013) but featured very little in the subsequent 300 years. The Zulu Kingdom came to prominence in early 1819 under the leadership of King Shaka Zulu (Bulpin, 2013; Te Beest et al., 2017), prior to which the region was inhabited by smaller chiefdoms, most notably the Ndwandwe and Mthethwa peoples. The Ndwandwe occupied north of the Umfolozi Rivers and Mthethwa to the south (Te Beest et al., 2017). Between the two rivers, the land was largely vacant. After the rise of the Zulu Kingdom, this area became important hunting grounds for Shaka, but hunts were limited to seasonal and ceremonial purposes (Te Beest et al., 2017). Although wildlife trade and export were already underway by the early 1800s in Zululand (Bulpin, 2013; Te Beest et al., 2017), wildlife was still abundant between the Umfolozi Rivers. By the 1870s, firearm use became more common within Zululand and wildlife was decimated (Bulpin, 2013; Te Beest et al., 2017).

After the British took over in 1887, the Zulu people had to adapt to regular changes in wildlife protection laws and management strategies (Brooks, 2001; Te Beest et al., 2017). In 1890, game laws were introduced to protect wildlife from perceived over-harvesting (Brooks, 2001). These laws were adjusted three years later in response to concerns over the spread of Nagana, and residents were allowed once again to destroy game (Te Beest et al., 2017). The destruction allowed under these new laws were part of the rationale for the founding of the first reserves of Hluhluwe and iMfolozi in 1895 (Brooks, 2001; Te Beest et al., 2017). There was good support from the local inhabitants for the protection of wildlife at this time (Te Beest et al., 2017), and human density was low surrounding the reserves, at roughly 2.5 people per km^2 (McCracken, 2008). Eighty-eight years after the proclamation of these protected areas, they were finally linked through the formal declaration of the Corridor Game Reserve as a protected area in 1989 (Le Roux et al., 2017). In 1997, these three areas were unified to form one protected area that is now known as HiP (Te Beest et al., 2017).

In the first half of the 20th century, Nagana continued to influence much of the operations within and around the park (Te Beest et al., 2017). After the successful management of Nagana, the destruction of wildlife once again became illegal inside iMfolozi Game Reserve from 1953 and this caused great tension between field rangers and locals, who were now being arrested for poaching in an area wherein they were previously allowed to hunt (Te Beest et al., 2017).

The local peoples that surround HiP have continuously battled for land occupancy both inside and outside the park (Vincent, 1970; Brooks, 2001; Te Beest et al., 2017). This conflict continues to worsen as populations surrounding the park expand and fencing that was once in place to keep animals in, increasingly serves to keep people out (Brooks, 2001). Furthermore, the increasingly sprawling nature of the scattered homesteads and transformed land (Jewitt et al., 2015) leave HiP largely isolated from other protected areas (Te Beest et al., 2017).

Farmers and pastoralists have had to deal with the killing of livestock by predators for as long as both have coexisted. In South Africa, livestock predation worth more than R1 billion is believed to take place annually (Van Niekerk, 2010). Negative responses from livestock owners to carnivore conservation can often be attributed to livestock predation (Oli et al., 1994; Schumann et al., 2012). However, this is not always the case (Bruskotter et al., 2007), and wild dog conservation in HiP has been met with a generally positive response from neighbouring communities (Parker et al., 2014). Nevertheless, compensation pay-outs for livestock predation in communities neighbouring protected areas cost EKZNW substantial amounts of money each year (EKZNW unpublished data). Hyaenas are most frequently being blamed for this predation (Gusset et al., 2008; Parker et al., 2014).

CHAPTER 3 – SPOTTED HYAENA DENSITY ESTIMATES

3.1 Introduction

Large carnivores (>12 kg) are decreasing in abundance throughout the world (Ray et al., 2005); the risk of their extinction is driven largely by the expansion in the human population (Cardillo et al., 2004) and decreasing prey populations (Wolf & Ripple, 2016). Furthermore, these carnivores are becoming increasingly isolated to protected areas (Bohm & Höner, 2015), which are often small, fenced, and intensively managed (Lindsey et al., 2011; Miller et al., 2015). Carnivores in these isolated protected areas are prone to increased inbreeding (Trinkel et al., 2008) and limited emigration/immigration opportunities (Dolrenry et al., 2014). Thus, these populations may suffer reduced evolutionary potential and demographic stochasticity (Frankham et al., 2002; Miller et al., 2015), unless ongoing monitoring links directly into effective adaptive management strategies (Biggs & Slotow, 2008; Miller et al., 2013). In South Africa, like elsewhere in Africa (Woodroffe & Ginsberg, 1998), large carnivores are also under direct persecution pressure through both legal and illegal harvesting (Swanepoel et al., 2014; Hunnicutt et al., 2016). Regular and reliable density estimates are therefore integral to the conservation of these populations (Balme et al., 2009). Finding innovative and cost-effective ways of monitoring large carnivores, particularly cryptic species, will further serve to help protected areas achieve their conservation objectives.

Despite being the most abundant large carnivore in Africa, spotted hyaenas (“hyaenas” hereafter) populations are decreasing (Bohm & Höner, 2015). Poor monitoring of existing populations of hyaenas across Africa has been identified as a threat to the conservation of the species (Hofer & Mills, 1998a, 1998b; Hunnicutt et al., 2016). Furthermore, as a species under direct persecution from humans for the harvesting of body parts (Hofer & Mills, 1998a; Majova, 2005) and increased legal trophy hunting for the species (Hunnicutt et al., 2016), ongoing and rigorous population monitoring is necessary.

Hyaena monitoring techniques include call-ups, mark-recapture, and camera trapping. Mills (1998b) reviewed these approaches and elaborated on the mark-recapture method and the call-up technique. Notably, the use of remotely triggered camera traps to help estimate hyaena density was believed to have limited success and was not considered a worthwhile approach at the time (Mills, 1998b; Mills et al., 2001). However, over the past 20 years, technological advances allow for an SECR approach (Gopalaswamy et al., 2012; Efford, 2019) for analysing camera trap data to achieve robust density estimates for hyaenas (O'Brien & Kinnaird, 2011; de Blocq, 2014; Rich et al., 2019; Fouché et al., 2020).

3.1.1 Camera traps and the spatially explicit capture-recapture approach

Camera trapping technology has developed rapidly since the turn of the century (McCallum, 2013; Wearn & Glover-Kapfer, 2017), as have corresponding data analysis techniques (Borchers & Efford, 2008; Royle, Karanth et al., 2009; Gopalaswamy et al., 2012; Efford, 2019). For these reasons, camera traps are increasingly being used as a tool for estimating the density and abundance of nocturnal and elusive carnivores, such as hyaenas (O'Brien & Kinnaird, 2011; McCallum, 2013; Briers-Louw, 2017; Rich et al., 2019; Fouché et al., 2020) and have proven to be accurate and cost-effective (Wearn & Glover-Kapfer, 2017). Furthermore, using data from existing camera trap surveys to monitor non-target specific animals, such as hyaenas, is also possible (Harihar et al., 2010; de Blocq, 2014; Williams et al., 2020).

The traditional capture-recapture (CR) approach for camera trap data has been used for decades to produce abundance estimates for rare and elusive species, in particular (Karanth & Nichols, 1998; Kays & Slauson, 2008; McCallum, 2013). For individuals with distinct pelt patterns, using camera traps to identify an individual and record its capture history is an adapted, non-invasive method to the well-used statistical approach of mark-recapture sampling (Karanth & Nichols, 1998; Kays & Slauson, 2008). The fundamental parameter to these CR models is the capture probability of individuals within the population (Otis et al., 1978).

Abundance estimates derived from the CR approach are often reasonable, but to establish density estimates, the effective sampled area needs to be established. This area is calculated in an ad hoc manner and has been criticised by several authors (Efford, 2004; Royle, Karanth et al., 2009; Singh et al., 2010). Calculating this value is one of the greatest sources of error for the CR method (Soisalo & Cavalcanti, 2006). The effective sampled area is established by building a buffer around the trapping grid. This buffer is often produced through the mean maximum distance moved (MMDM) approach. It has been argued that, despite findings from Balme, Hunter et al. (2009) where the MMDM approach underestimated density in their study, this approach generally overestimates true density by underestimating the true area sampled (Soisalo & Cavalcanti, 2006; Sollmann et al., 2011).

The SECR approach for recapture data addresses the errors and shortfalls of the traditional CR models (Silver et al., 2004; Obbard et al., 2010; Blanc et al., 2013) by using the valuable spatial data available from trapping events (Efford et al., 2009; Royle, Nichols et al., 2009). At their core, these models use a combination of distance probability sampling and CR models to produce spatial density estimates that are not reliant on assumptions of geographical closure. SECR models try to link an animal's activity centres with the encounter observations from a camera trap survey. This linking is done by incorporating state (point process) models with observation models (Gardner et al., 2010; Efford, 2019). One of the most important factors influencing the catchability of individuals within a population is their movement relative to the detector (e.g. camera trap). Thus, camera traps that are closer to an animal's activity centre (or "home range centre") are expected to be more successful in capturing that individual. Therefore, detection probability is a decreasing function of distance from the animal's activity centre.

The SECR approach is conservative and has been preferred over the traditional CR models (Obbard et al., 2010; Sollmann et al., 2011; Noss et al., 2012). It provides good comparisons between studies because the methodology is largely standardised in comparison to the traditional CR approaches (Sollmann et al., 2011). The SECR method is split into two approaches, namely maximum likelihood (Efford, 2004; Borchers & Efford, 2008) and Bayesian inference (Royle & Young, 2008; Royle, Karanth et al., 2009). These differing approaches can be used by practitioners in the R programming language (R Core Team, 2020) with the "secr" (Efford, 2019) and "SPACECAP" (Gopalaswamy et al., 2012) packages, respectively.

Fundamentally, the maximum likelihood models maximise likelihood across a grid of possible activity centres to derive density (D). In this approach, the latent variables ("activity centres" (AC)) are integrated out of the likelihood models. The Bayesian approach uses data augmentation instead to make inference about unobserved activity centres and encounter histories. Although there is a fundamental difference in the approach taken by the two classes of models, both calculate the detection function in the same way and often give similar results (Marques et al., 2012).

3.1.2 Call-ups

Call-ups are a cost-effective and commonly used technique for population censuses of hyaenas (Kruuk, 1972; Whateley & Brooks, 1978; Whateley, 1981; Sillero-Zubiri & Gottelli, 1992; Mills et al., 2001; Ogutu et al., 2005; Graf et al., 2009; Cozzi et al., 2013). There are two approaches to call-up censuses for hyaenas. Firstly, using the mark-recapture approach and applying the Lincoln Index (Seber, 1973) allows for practitioners to estimate population size

(Kruuk, 1972; Whateley & Brooks, 1978; Sillero-Zubiri & Gottelli, 1992) but frequently without variance (Mills et al., 2001). The second, and more recent approach, uses probability models to estimate population density around call-up sites (Mills et al., 2001) and incorporates bootstrapping to produce confidence limits (Ogutu et al., 2005; Graf et al., 2009).

Call-up surveys based on response probability were standardised by Mills et al. (2001). These probability models rely on an estimate of maximum response distance to establish the sampled area at one call-up station (Mills et al., 2001). The length of time spent calling-up per sample station needs to be limited such that only hyaenas within the periphery of the sampled area have time to arrive at the call-up site and to be detected (Cozzi et al., 2013). Within the sampled area, a response probability needs to be established to calculate abundance across the area. Response probabilities are dependent on a number of factors and should be collaborated for habitat type and season (Cozzi et al., 2013). To maximise the “capture” of individuals who have responded, open call-up stations are selected (Graf et al., 2009). Independent experiments are required for establishing both above-mentioned parameters (Mills et al., 2001; Cozzi et al., 2013). This experimentation can be done through direct observation (Mills et al., 2001; Ogutu et al., 2005; Graf et al., 2009) or by using radio-telemetry (Graf et al., 2009; Cozzi et al., 2013). Although density estimates from call-ups are influenced by the respective parameters used, studies that have adopted the Mills et al. (2001) approach are comparable (Cozzi et al., 2013).

3.1.3 Ecological determinants

The ecological determinants for reproduction and survival of hyaenas have been shown, amongst others, to be prey availability (Höner et al., 2005; Hayward & Kerley, 2008; Watts & Holekamp, 2009), rainfall and water availability (Tilson & Henschel, 1986; Boydston et al., 2006), and inter-specific competition (Kruuk, 1972; Mills, 1990, Watts & Holekamp, 2009).

Prey availability has continuously been identified as one of the most important ecological determinants for the success of hyaenas (Kruuk, 1972; Höner et al., 2005; Watts & Holekamp, 2008, 2009), and their global demise outside of protected areas is largely attributed to a reduction in prey abundance (Bohm & Höner, 2015). Increased prey availability correlates positively with reproduction in hyaenas in some systems (Watts & Holekamp, 2009) and data presented from the Masai Mara show peaks in conception coincided with high energy availability in the form of migratory herds of zebra and blue wildebeest (Holekamp et al., 1999).

Water availability is an important determinant for hyaena presence, and dens are most frequently located near water sources (Tilson & Henschel, 1986; Mills, 1990; Boydston et al., 2006). If a water source dries up, females may be forced to relocate dens and even abandon cubs (Tilson & Henschel, 1986). Conversely, heavy rains have been attributed to the flooding of dens and subsequent mortality of cubs (Kruuk, 1972; Boydston et al., 2006), although such events are rare (Watts & Holekamp, 2009). In the arid Etosha National Park of Namibia, it was found that hyaenas increase their occupied territory two-fold from dry to wet season (Trinkel et al., 2004). This increase in territory was attributed to the wide dispersion of prey in response to increased water availability. Increased levels of movement away from den sites for foraging by mothers has been shown to reduce cub growth and survival rate within some populations (Hofer & East, 1993c).

Depredation (interference) (Kruuk, 1972; Mills, 1990; Palomares & Caro, 1999; Trinkel & Kastberger, 2005; Périquet, Fritz et al., 2015) and resource competition (exploitative) (Creel & Christianson, 2008; Watts & Holekamp, 2008, 2009; Périquet, Fritz et al., 2015) are two key mechanisms through which interspecific carnivore interactions can influence carnivore populations. The direction and magnitude through which these interactions take place is dependent on both prey availability and the density and demographics of the competing carnivores (Périquet, Fritz et al., 2015; Périquet, Fritz et al., 2021). The competitive relationship between hyaenas and lions is a complex one that can result in reduced population success for the former (Trinkel & Kastberger, 2005; Watts & Holekamp, 2008), but the dynamic is not exclusive, and increased lion density can facilitate the co-existence of these competitors through the provision of carcass remains (Périquet, Fritz et al., 2015).

The interference competition experienced by hyaenas from lions has been well-researched (Périquet, Fritz et al., 2015; Périquet et al., 2016). Three studies in the Masai Mara between 1979 and 2006 have all shown lions to be a notable cause of death for hyaenas in the region (Frank, 1986a; Frank et al., 1995; Watts & Holekamp, 2009). In Etosha National Park, as many as 71% of hyaena mortalities were attributed to lions (Trinkel & Kastberger, 2005). It is also worth noting that intraspecific competition can also induce hyaena mortalities, and infanticide by neighbouring clans does take place in some populations (Kruuk, 1972; Mills, 1990; Watts & Holekamp, 2009; Périquet, Fritz et al., 2015).

3.1.4 Aims and objectives

Early density estimates for hyaenas in HiP of South Africa estimated hyaena densities at 46 and 35 hyaenas per 100 km^2 in the Hluhluwe and iMfolozi sections, respectively (Whateley & Brooks, 1978; Whateley, 1981). Subsequently, Graf et al. (2009) found density to be consistent with the earlier 1970s records and, through call-ups, they estimated the population to be 35 hyaenas per 100 km^2. Continuing with the methods used by Graf et al. (2009), HiP management has performed three subsequent call-up surveys in 2010, 2013 and 2015. Results from these censuses have suggested a 66% decline in hyaena density for the park over this period (EKZNW unpublished data), and this was the catalyst for this chapter.

The poor monitoring of hyaena populations across the African continent has continued to be a conservation concern. HiP has historically had a strong population that was regarded as the third largest in South Africa (Hunnicutt et al., 2016). However, the recent decline in hyaena density at the turn of the 2010s has raised concern. To support HiP management, and to add to the existing literature with regards to monitoring techniques and their efficacy for cryptic species such as hyaenas, I assessed the density of hyaenas in HiP and how it has changed over time. My aims for this chapter were to:

1) Estimate the density of hyaenas through the SECR methodology from camera trapping data between 2013 and 2018. Here, I tested the hypothesis that hyaena abundance has declined significantly within HiP and is currently 33% of what it was in the early 2000s.

2) Run a call-up census in 2018 to have three years of overlapping estimate results from call-ups and camera trapping in 2013, 2015 and 2018. In doing so, I tested the hypothesis that call-up density estimates underestimated the hyaena population of HiP.

3) Identify the ecological factors that may be driving the observed population trends for hyaenas in HiP. I hypothesised that hyaena density in HiP is positively influenced by rainfall and prey availability, but negatively affected by lion density.

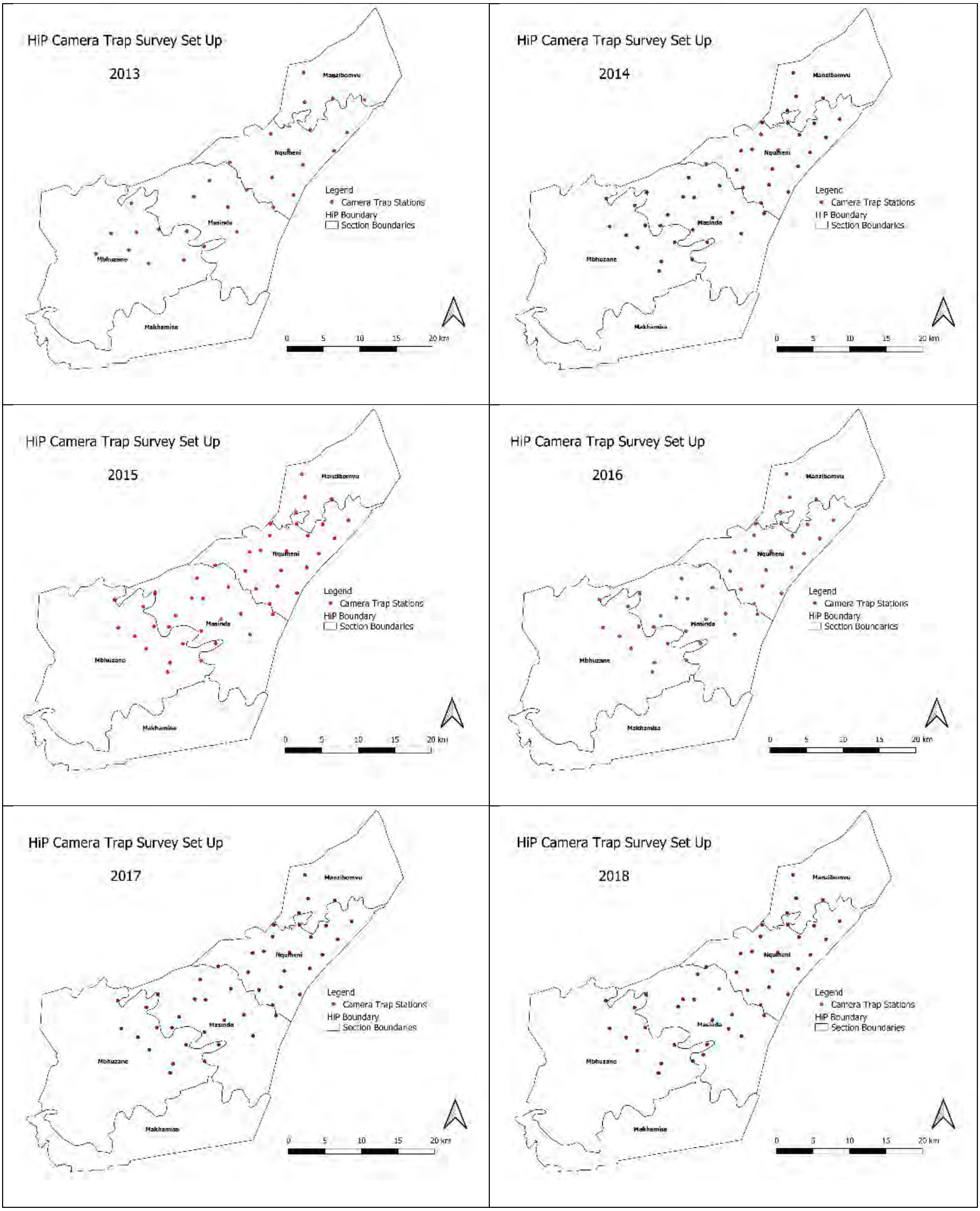
3.2 Methods

3.2.1 Camera trapping density estimates

In a collaborative monitoring effort between Ezemvelo KZN Wildlife, iSimangaliso Wetland Park Authority, Panthera and Wildlife ACT, the KwaZulu-Natal Leopard Monitoring Project was established in 2013 (Mann et al., 2017). As part of this initiative, annual camera trapping surveys have been conducted in HiP since the project started. The main aim of these surveys has been to establish density trends in the leopard population of HiP. I obtained permission to use the existing raw data collected from the surveys run in HiP between 2013 and 2018 to establish hyaena density. Using existing data to establish population statistics for non-target species has been done many times, with relevant examples found in Harihar et al. (2010), de Blocq (2014) and Williams et al. (2020).

Data collected from the annual surveys were limited to 45-day periods to support population closure assumptions made in the SECR analyses (Royle, Chandler, Sollmann et al., 2013). For all 6 surveys between 2013 and 2018, the bulk of the 45-day survey period fell within the autumn months of April and May, with start dates varying from 16th March to 1st May. For each year, except 2013, a total of 46 camera trap sites were active for the full length of the survey period. Two cameras were set up at these sampling sites, or “stations”, situated at opposite sides of the path or road. This arrangement was designed to photograph both flanks of a passing individual, to assist in building a comprehensive reference identikit of individuals. The 46 sites covered roughly a third of the park and were approximately 2–3 km apart. The locations of these sites were generally consistent across all years, with the exception of four sites in 2018 in the Masinda section of iMfolozi. These four sites were moved to new locations within the same section because of poor accessibility (Figure 3.2-1). In addition, the 2013 survey consisted of only 30 sites with an average spacing of 3,020 m but covered a similar area to subsequent surveys. The increase in total trapping sites from 2014 onwards was done to increase sampling resolution. The distance between sites was sufficient for SECR analysis, as mean home range sizes of hyaena clans in HiP have historically been recorded as 12 km^2 and 39 km^2, across Hluhluwe and iMfolozi sections respectively (Whateley & Brooks, 1978; Whateley, 1981). Although the former is believed to be an underestimate, the spacing of 2–3 km ensures at least two camera stations fell within any potential hyaena’s home range. During each survey, cameras were checked weekly to replace batteries and download images.

I built a draft identikit of individuals from the first survey in 2013. Subsequent years’ data were used to update and maintain the identikit. Images were processed using the program digiKam 5.9.0 (digiKam Developers Team, 2018). Using the identikit as a reference, individuals were identified through a combination of visual observations and pattern recognition software in the programme Hotspotter (Crall et al., 2013). The naming system for these animals included the name of the park, the species and their respective identification number (e.g. HiPSH1 = Hluhluwe–iMfolozi Park Spotted Hyaena 1). All individuals captured that could be identified were assigned their respective codes. For images where individuals could not be identified (e.g. oblique or right-angle view, poor lighting, wet pelt, etc) they were tagged as “Poor Quality”. Juveniles were also excluded from the SECR analyses, but images were labelled “Juvenile”, to maintain a record of these captures. Finally, identifying the sex of hyaenas is challenging and can be a source of error (Frank et al., 1990; Cunha et al., 2014). For this reason, I did not attempt to include sex into the analysis, as advocated by Sollmann et al. (2011).



HiP Camera Trap Survey Set Up 2013

HiP Camera Trap Survey Set Up 2014

HiP Camera Trap Survey Set Up 2015

HiP Camera Trap Survey Set Up 2016

HiP Camera Trap Survey Set Up 2017

HiP Camera Trap Survey Set Up 2018

Figure 3.2-1 Camera trapping grid design between 2013 and 2018 by the KwaZulu-Natal Leopard Monitoring Project. The camera trap array covered roughly an equal area across each year. The 2013 survey consisted of 30 camera sites and subsequent surveys included a total of 46 stations. Since 2014, most station site locations were consistent, except for four sites in the Masinda section in 2018.

Once image processing was complete, all available metadata of each image, which included date/time, geolocation (site number), pelt side used for identification (Right or Left) and individual identification, were exported to create a Capture History for each individual using the package “CamtrapR” (Niedballa et al., 2016) in the R statistical framework (R Core Team, 2020). Using the Capture Histories spreadsheet of all individuals, I removed all records of “Poor Quality” or “Juveniles”. I further separated all records into Right-Hand Side (RHS) and Left-Hand Side (LHS) Capture Histories. The respective dataset with the greatest number of individuals was then used to run SECR density estimates for that year. Lastly, sampling occasions were separated into 24-hour periods and captures of individuals at specific stations were binary per occasion. Capture events with the same individuals at the same station captured more than once within a 24-hour day period were collapsed into a single positive capture event. Once the Capture History sheet was completed, an additional Cameras Active sheet was created. This sheet represented both the location of the camera trap sites and their respective activity (i.e. 1 = active, 0 = inactive for respective trap nights). To run estimates on Hluhluwe and iMfolozi sections independently, I created separate Capture History spreadsheets for trap sites inside Hluhluwe and iMfolozi; that is, north and south of the Corridor Road, respectively.

For my study, I chose the likelihood approach to the SECR analysis because it runs faster than the Bayesian analysis and was more practical (Singh et al., 2010; Noss et al., 2012). I used the “secr” package (Efford, 2019) in the R platform (R Core Team, 2020) to compile a Capture Matrix for each site, individual and occasion from Capture Histories and Cameras Active datasheets. To produce an SECR analyses of this information, a map of suitable habitat must be completed for the camera trap data to be integrated over. This polygon is called the Effective Trapping Area (ETA), state space or habitat mask, and represents all possible Activity Centres (AC) for individuals captured during the survey. It is known that hyaenas move in and out of HiP’s fenced borders (Pers. Comm. Park Ecologist – Dave Druce, 2021) and, therefore, it is possible that hyaenas captured within the camera trap grid have ACs outside of the park boundary. To account for this and compare different habitat suitability approaches, I generated three habitat masks. All possible ACs within these ETAs were represented by pixels of 0.25 km^2 in size, which lie well below the suggested 1/64 of the total ETAs (Efford, 2019). I compared mean density estimate results between the different habitat mask approaches using a box and whisker analysis in R (R Core Team, 2020).

The first habitat mask created was a uniform polygon of 12,500 m buffer from the outer most camera traps. The SECR analysis that was projected on this ETA I called “12,500 m”. The 12,500 m buffer was utilised because telemetry data in the region, across a number of protected areas, show MMDM to be 12,419 m (Hunnicutt unpublished data). By selecting

12,500 m, I ensured that the probability of capturing individuals with ACs outside the ETA was near 0 (Efford, 2019). This decision was confirmed to be a conservative approach, as the suggested buffer of 4 times the Root Pooled Spatial Variance calculated from the capture histories (Efford, 2019) was never greater than 12,500 m for all 6 datasets. This habitat mask covered an average area of 1,806 km^2 across the 6 surveys.

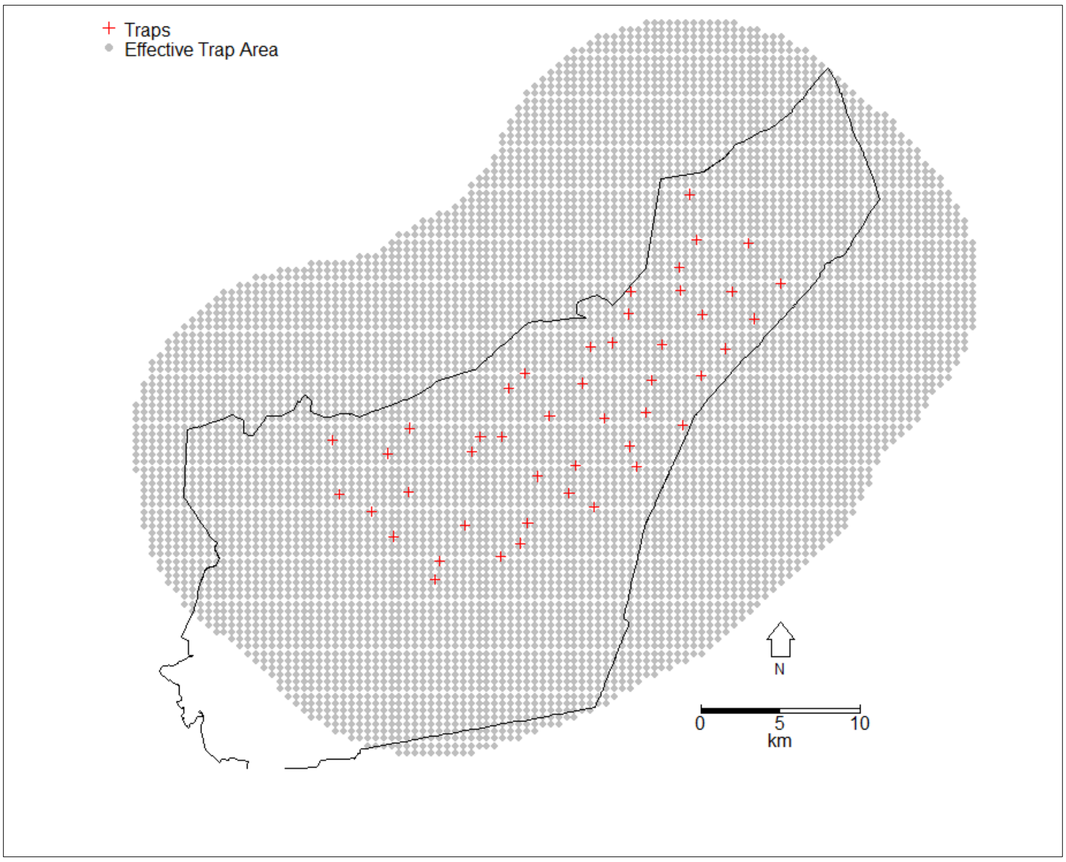


Figure 3.2-2: A visual representation of the 12,500 m Effective Trapping Area in 2018. Each grey dot represents a possible home range centre, 500 m equally spaced apart.

A second habitat mask was produced by projecting the 12,500 m mask and then using the park's fence as a hard boundary. By doing this, I excluded areas outside the park boundary as non-suitable habitat for hyaenas. This mask was referred to as the "Fenced" approach and covered an average area of 868 km^2 over the 6 years.

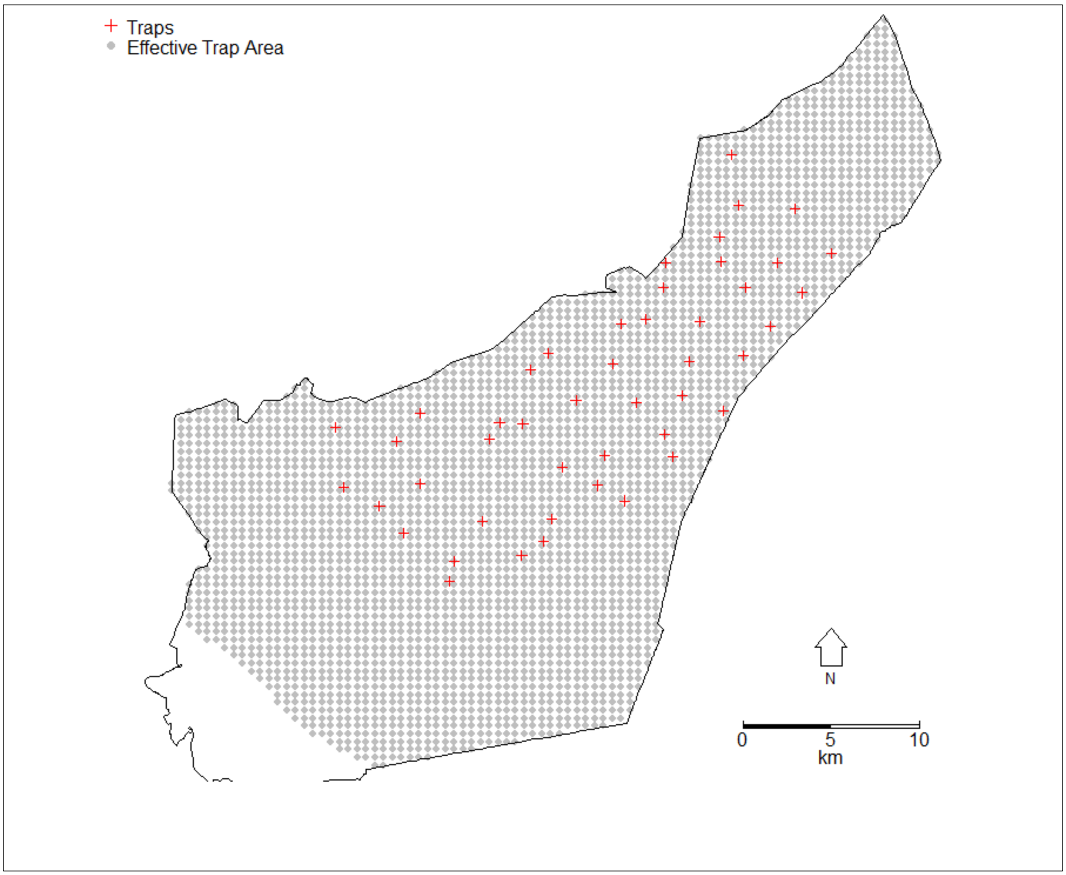


Figure 3.2-3: A visual representation of the Fenced Effective Trapping Area in 2018. Each grey dot represents a possible home range centre, 500 m equally spaced apart. Here, all habitats outside of the park's fence have been excluded from possible home range centres of hyaenas.

The final approach was an intermediate between the 12,500 m and Fenced approaches, which took into consideration the variability in porosity of the HiP fence and incorporated areas outside the park that are known to have hyaenas and which I termed "suitable habitat". To produce a map of "suitable habitat" within the uniform 12,500 m buffer polygon, I consulted Ezemvelo KZN Wildlife's Human Wildlife Conflict Officers working around HiP (Pers. Comm. Human Wildlife Conflict Manager for HiP – Sizwe Zulu, 2021). These officers were able to rank surrounding municipal wards from 1–5 in terms of reported hyaena conflict (1 being none, and 5 being weekly). Using these scores as a proxy for hyaena presence, and telemetry data from two hyaenas (EKZNW unpublished data), a "suitable habitat" map was produced using the park's boundary and high conflict ward boundaries in QGIS 3.16 (QGIS Development Team, 2020). This map was created to represent where hyaenas possibly occur; it was not necessarily a true reflection of hyaenas presents or absents in or around the park. There may be areas that have been excluded from this map that could have hyaenas present, but in the same way, some of these areas may not be suitable for these animals. Nevertheless, this patchy approach to habitat suitability is likely a more realistic representation of hyaena habitat use than a hard fence boundary or a uniform suitable habitat of 12,500 m around the trapping grid. I called this habitat mask “Clipped 12,500 m”. The Clipped 12,500 m ETA covered an average area of 1,360 km^2 across camera surveys.

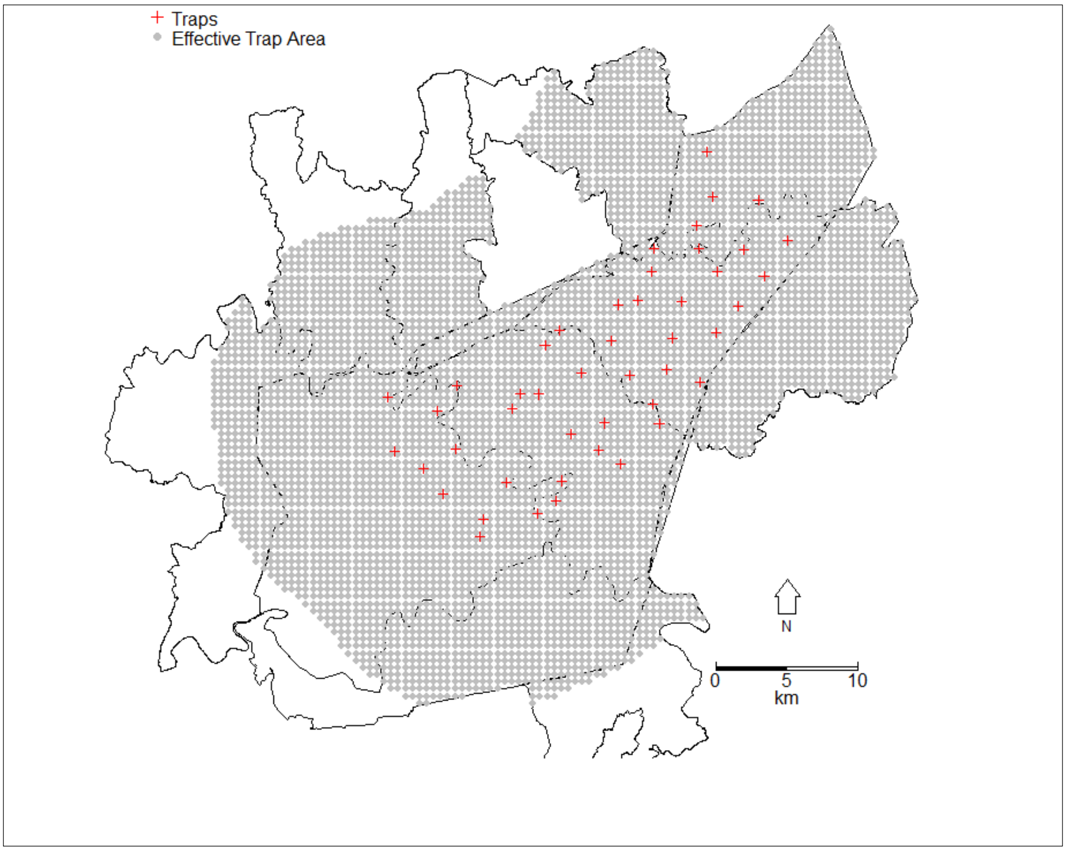


Figure 3.2-4: A visual representation of the Clipped 12,500 m Effective Trapping Area in 2018. Each grey dot represents a possible home range centre, 500 m equally spaced apart. Here municipal wards outside of the HiP which had low hyaena activity reported were excluded from possible home range centres for hyaenas.

Once the habitat masks were created, the maximum likelihood approach to SECR was used to estimate hyaena density for HiP in each year. I used the “secr” package (Efford, 2019) in the R platform (R Core Team, 2020) to analyse density across the three different ETA approaches. For each survey year, three model functions were compared using Akaike Information Criterion (AIC) scoring (Akaike, 1973; Symonds & Moussalli, 2011) adjusted for small sample sizes (AIC$_C$) (Burnham & Anderson, 2002). These model types were the exponential, hazard-rate and half-normal functions. Once the best fitting model was identified, the effective sample area was plotted for each function (Borchers & Efford, 2008). If the model continued to be sensitive to distances past the 12,500 m buffer width and did not plateau (Appendix 3.1), the models were excluded, and the next best model was chosen. If the AIC$_C$ score gave weight to multiple functions, the model averaging approach was used (Turek & Fletcher, 2012) as outlined by Efford (2019). Once the basic function had been chosen, the behavioural response of individuals was factored in uniformly across all detectors (b) and per detector (bk). These individual behaviour response models were run and AIC$_C$ weight scores compared against the null model. However, in all six years there was no support for behavioural response models (ie. b or bk). As such, the null model was selected in all cases.

3.2.2 Call-up density estimates

In November 2018, in collaboration with EKZNW and Wildlife ACT, I facilitated hyaena call-ups for HiP in accordance with the methodology adopted by Graf et al. (2009). The Park has maintained this census technique since Graf's work in 2003–2004 (Graf et al., 2009) and have subsequently run call ups in 2010, 2013 and 2015 (EKZNW unpublished data). The 2018 census was run over three nights between 14–16 November by two teams. The teams started each nights' sampling at sites neighbouring each other and then moved apart, to avoid double counting individuals. In total, the same 27 sites from 2015's survey were sampled (Figure 3.2-5). At each sampled site, an average of 30 minutes was spent sampling. This sampling consisted of playing six-minute-long recordings of sounds known to attract hyaenas (e.g. hyaenas fighting on a kill, mobbing lions and whooping) followed by five minute intervals of silence. Three minutes into the six-minute recording, the two 12 Ω horn speakers were rotated 90 degrees. The calling and silence intervals were repeated three times. If hyaenas were heard responding but not seen before the end of the third and final six-minute-long call, a fourth recording was played. Observers shone red filtered spotlights from the back of the vehicle to count the number of hyaenas observed at each station. If lions arrived, the call-up was abandoned.

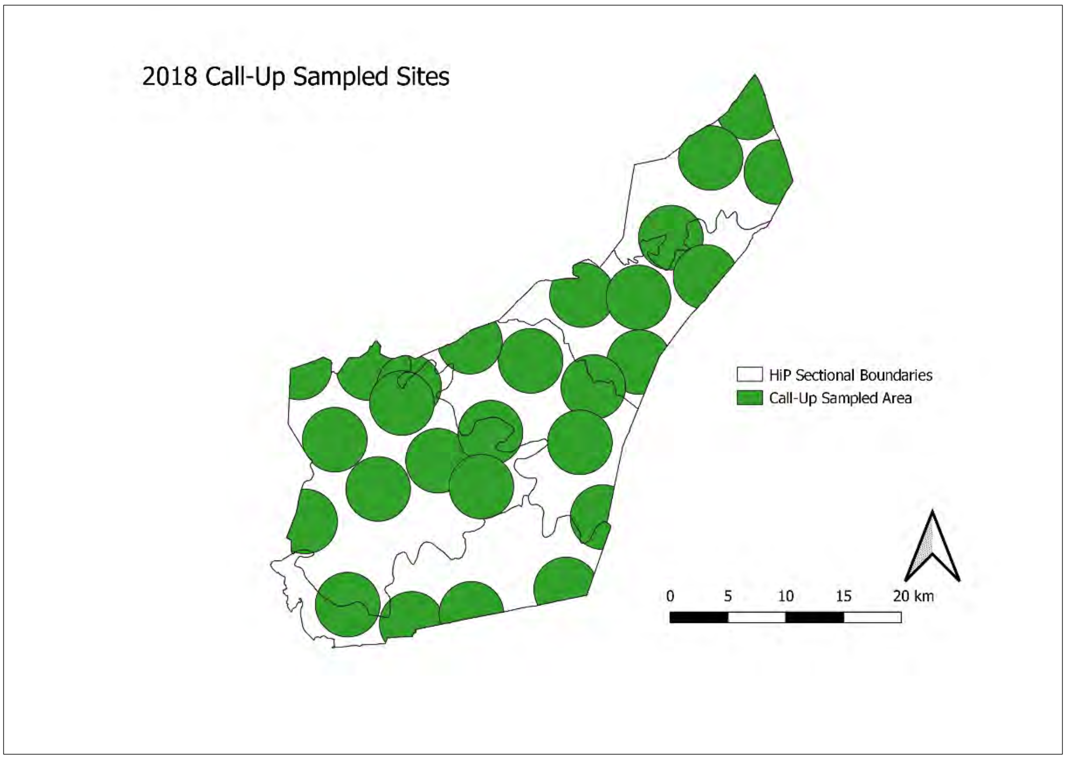


Figure 3.2-5: A depiction of the 531 km² area sampled during 2018 hyaena call-up census for HiP. A total of 27 call-up sites were sampled in 2018. The area sampled for each site is represented by the green circles and incorporates a 2.8 km radius around the respective sites.

I calculated a density estimate across the sampled area and then extrapolated this for the entire park (Graf et al., 2009). The sampled area per call-up site is the circular area surrounding the call-up site with a radius of the maximum response distance, which is 2.8 km (Graf et al., 2009; Figure 3.2-5). Thus, for each call-up site, the sampled area was 24.63 km^2, except for where a section of the circle area lay outside the park, in which case the portion was removed from the area sampled (Graf et al., 2009). It is noteworthy that the assumption that hyaenas outside of the park do not respond to call-ups may result in overestimates of density by underestimating sampled area, especially because the fencing of HiP is porous in some areas. Those sampled areas that overlapped were clipped and excluded, so as to not double sample. For the 2018 analysis, sample sites were largely the same as 2015. Thus, the sampled area per site from 2015 was maintained for 2018's analysis, except for including areas that were previously fenced out of the park but were now part of the park. Once the number of hyaenas observed per call-up site was established, and adjusted for response probability (p=0.6), an estimate of density (hyaenas/km^2) per call-up site was calculated using its respective sampled area. The mean hyaena density and confidence intervals per call-up site were then calculated using the non-parametric bootstrap method with 10,000 replications with replacement (Ogutu et al., 2005) in the R platform (R Core Team, 2020).

To compare my results from call-ups and camera trapping with an expected hyaena density for HiP, I ran predator-carrying capacity models (Hayward, O'Brien et al., 2007) between 2012 and 2018. The specific model tested was based on lion preferred weight class of prey species, as recommended by Hayward (Pers. Comm. Matthew Hayward, 2021).

3.2.3 Ecological determinants

Prey availability

A large herbivore census is run every two years across HiP and has been done since 1994 (Grange et al., 2012). Distance sampling is undertaken along 34 line transects throughout HiP, and each transect is generally sampled 16 times during the 3-month long census. Observations from these walked transect are analysed in the software package DISTANCE (Thomas et al., 2010). Density estimates were calculated for species that have more than 60 individuals sighted during the census (Grange et al., 2012), and these estimates were used to calculate hyaena prey availability (EKZNW unpublished data).

I used these data (between 2012 and 2018) to calculate changes in available prey biomass for hyaenas in HiP. All species that constituted more than 1% of total hyaena diet from Skinner et al.'s (1992) scat analysis, and that still occurred in HiP were included. As such, eight species were included, namely impala, nyala, Cape buffalo, common zebra, blue wildebeest, greater kudu, warthog and grey duiker (*Sylvicapra grimmia*). I summed the total biomass of these species, using 0.75 of adult male weight for average individual biomass for each species as recommended by Hayward, O'Brien and Kerley (2007; Appendix 3.4).

Rainfall

Rainfall records are collected monthly by EKZNW from section ranger outposts. I used these data to calculate the average monthly rainfall per year. To encompass a full rainy season, I ran my calculations from July to June of the following calendar year. Rainfall collection outposts were separated into Hluhluwe (3) and iMfolozi (2) sections to produce respective averages for each section.

Lion estimates

Lions are closely monitored through telemetry tracking, camera trapping and visual observations by EKZNW staff and the Wildlife ACT monitoring team (EKZNW unpublished data). Population estimates are based on known individuals and pride composition.

I used the existing data on lion densities between 2014 and 2018 (Appendix 3.4) to assess how they may influence hyaena densities.

General linear models

To establish how rainfall, prey availability and lion density influenced hyaena density in HiP, I ran a general linear model (GLM) in the R platform (R Core Team, 2020), using these three ecological determinants as predictors for hyaena density. Prey abundance was the total kg per km^2 of the eight most important prey species for hyaenas (Skinner et al., 1992). For estimates of abundance for years in which the herbivore census was not performed, I averaged abundance across the preceding and following years. Both lion estimates and prey abundance were taken from the previous year as determinants for hyaena density. The average mean rainfall (mm) from the year ending in June was used as a potential predictor of hyaena density in that specific year. Hyaena density estimates were extracted from the 12,500 m Clipped estimates (see results). In 2015, the density estimate lay outside of ecological logic compared with 2014 and 2016 estimates. For this reason, I averaged 2014 and 2016 estimates to calculate the 2015 estimate of hyaena density.

I ran a global GLM model with all three ecological variables included. I then compared these against a number of different combinations, which included Lion and Rainfall, Rainfall alone and Lion alone. I compared the AIC_c scores from these respective models to establish which model best predicted hyaena density (Burnham & Anderson, 2002). Models were considered to have some support relative to the best model if change in AIC_c score (ΔAIC_c) was less than 10 (Burnham & Anderson, 2002; Shipley, 2013).

3.3 Results

3.3.1 Hyaena density estimates from camera trapping

Across the 6 surveys between 2013 and 2018, a total effort of 11,336 camera trap nights was achieved. Trap nights did not vary significantly between surveys, except for 2013, which comprised only 30 trap sites and had a combined effort of 1,342 trap nights over the 45-day survey. Over the 6 surveys, 1,242 independent capture events were recorded, and a total of 230 individual identifications confirmed through RHS flank pelage recognition. The maximum number of individuals recorded for each survey varied from 59 in 2016 to 98 in 2018. Similarly, 2016 had the lowest number of independent capture events at 113, and 2018 had the highest, with 294.

Table 3.3-1: Summary of SECR model results from 12,500 m ETA and AIC scoring within each years' survey. Shaded grey items were the models selected for in respective years based on AIC_c weighting. EX = Exponential, HR = Hazard Rate and HN = Half-Normal.

Year	**Dataset**	**Function**	**Buffer**	**Density (100 km^2)**	**SE**	**LCL**	**UCL**	**AIC**	**AIC_C**	**$\Delta\text{AIC}_\text{C}$**	**AIC_C weight**	**Notes**
2013	RHS	Exponential	Uniform 12,500m	20.83	2.37	13.47	22.84	460.947	461.267	0	0.5106	
2013	RHS	Hazard Rate	Uniform 12,500m	19.98	2.5	15.64	25.51	461.43	461.97	0.703	0.3593	
2013	RHS	Half-Normal	Uniform 12,500m	17.94	2.32	13.94	23.08	463.682	464.002	2.735	0.1301	
2013	RHS	Model Average (HR, EX and HN)	Uniform 12,500m	18.43	2.65	13.93	24.39					Favoured Model
2014	RHS	Exponential	Uniform 12,500m	17.87	1.95	14.44	22.12	1,080.288	1,080.54	13.271	0	Favoured Model
2014	RHS	Hazard Rate	Uniform 12,500m	17.21	1.99	13.73	21.56	1,066.843	1,067.269	0	1	ETA Extends beyond 12,500m
2014	RHS	Half-Normal	Uniform 12,500m	16.58	1.8	13.4	20.5	1,145.326	1,145.579	78.31	0	
2015	RHS	Exponential	Uniform 12,500m	11.47	1.52	8.87	14.85	1,060.119	1,060.423	111.807	0	Favoured Model
2015	RHS	Hazard Rate	Uniform 12,500m	9.77	1.32	7.51	12.71	948.103	948.616	0	1	ETA Extends beyond 12,500m
2015	RHS	Half-Normal	Uniform 12,500m	11.25	1.42	8.79	14.4	1,163.789	1,164.093	215.477	0	
2016	LHS	Exponential	Uniform 12,500m	15.76	2.45	11.64	21.33	414.941	415.377	0	0.7981	
2016	LHS	Half-Normal	Uniform 12,500m	15.37	2.29	11.49	20.56	418.304	418.74	3.363	0.1485	
2016	LHS	Hazard Rate	Uniform 12,500m	14.88	2.39	10.88	20.34	420.049	420.789	5.412	0.0533	ETA Extends beyond 12,500m

2016	LHS	Model Average (EX and HN)	Uniform 12,500m	15.69	2.43	11.61	21.22					Favoured Model
2017	RHS	Hazard Rate	Uniform 12,500m	14.26	1.99	10.87	18.71	714.099	714.647	0	1	ETA Extends beyond 12,500m
2017	RHS	Exponential	Uniform 12,500m	14.96	1.94	11.62	19.26	727.843	728.167	13.52	0	Favoured Model
2017	RHS	Half-Normal	Uniform 12,500m	14.94	1.86	11.72	19.04	752.228	752.553	37.906	0	
2018	RHS	Exponential	Uniform 12,500m	18.26	2.01	14.73	22.63	973.263	973.518	0	0.9883	Favoured Model
2018	RHS	Hazard Rate	Uniform 12,500m	16.53	1.95	13.14	20.81	981.959	982.389	8.871	0.0117	ETA Extends beyond 12,500m
2018	RHS	Half-Normal	Uniform 12,500m	18.29	1.95	14.84	22.54	1,004.85	1,005.105	31.587	0	

Table 3.3-2: Summary of SECR model results from Clipped 12,500 m ETA and AIC scoring within each years' survey. Shaded grey items were the models selected for in respective years based on AIC$_c$ weighting. EX = Exponential, HR = Hazard Rate and HN = Half-Normal.

Year	**Dataset**	**Function**	**Buffer**	**Density (100 km^2)**	**SE**	**LCL**	**UCL**	**AIC**	**AICC**	**ΔAIC$_C$**	**AICC weight**	**Notes**
2013	RHS	Exponential	Clipped 12,500m	17.9	2.86	13.8	23.21	459.667	459.987	0	0.5917	
2013	RHS	Hazard Rate	Clipped 12,500m	20.19	2.53	15.81	25.78	461.003	461.544	1.557	0.2716	
2013	RHS	Half-Normal	Clipped 12,500m	18.17	2.33	14.14	23.35	462.597	462.917	2.93	0.1367	
2013	RHS	Model Average (HR, EX and HN)	Clipped 12,500m	18.53	2.61	14.08	24.39					Favoured Model
2014	RHS	Exponential	Clipped 12,500m	18.56	2	15.04	22.9	1,076.381	1,076.633	15.719	0	Favoured Model
2014	RHS	Hazard Rate	Clipped 12,500m	17.92	2.01	14.39	22.3	1,060.489	1,060.914	0	1	ETA Extends beyond 12,500m
2014	RHS	Half-Normal	Clipped 12,500m	17.35	1.86	14.07	21.38	1,141.528	1,141.781	80.867	0	
2015	RHS	Exponential	Clipped 12,500m	12.77	1.56	10.06	16.2	1,063.614	1,063.918	119.094	0	Favoured Model
2015	RHS	Hazard Rate	Clipped 12,500m	11.14	1.42	8.69	14.27	944.311	944.824	0	1	ETA Extends beyond 12,500m
2015	RHS	Half-Normal	Clipped 12,500m	12.47	1.49	9.88	15.73	1,166.12	1,166.423	221.599	0	
2016	LHS	Exponential	Clipped 12,500m	15.91	2.45	11.78	21.49	413.579	414.016	0	0.8044	
2016	LHS	Hazard Rate	Clipped 12,500m	15.16	2.37	11.78	20.57	418.696	419.436	5.42	0.0535	ETA Extends beyond 12,500m
2016	LHS	Half-Normal	Clipped 12,500m	15.5	2.3	11.6	20.71	417.047	417.483	3.467	0.1421	
2016	LHS	Model Average (EX and HN)	Clipped 12,500m	15.85	2.44	11.75	21.38					Favoured Model

2017	RHS	Exponential	Clipped 12,500m	15.61	1.97	12.21	19.96	726.776	727.1	12.391	0	Favoured Model
2017	RHS	Hazard Rate	Clipped 12,500m	15.23	2.02	11.76	19.72	714.161	714.709	0	1	ETA Extends beyond 12500m
2017	RHS	Half-Normal	Clipped 12,500m	15.45	1.89	12.17	19.62	750.663	750.988	36.279	0	
2018	RHS	Exponential	Clipped 12,500m	19.01	2.05	15.39	23.46	971.799	972.054	0	0.9866	Favoured Model
2018	RHS	Hazard Rate	Clipped 12,500m	17.53	1.99	14.04	21.88	980.217	980.647	8.593	0.0134	ETA Extends beyond 12500m
2018	RHS	Half-Normal	Clipped 12,500m	18.87	1.99	15.35	23.2	1,002.91	1,003.166	31.112	0	

Table 3.3-3: Summary of SECR model results from Fenced ETA and AIC scoring within each years' survey. Shaded grey items were the models selected for in respective years based on AIC_c weighting. EX = Exponential, HR = Hazard Rate and HN = Half-Normal.

Year	Dataset	Function	Buffer	Density (100 km^2)	SE	LCL	UCL	AIC	AICC	ΔAICC	AICC weight	Notes
2013	RHS	Exponential	Fenced	20.79	2.67	16.18	26.71	467.65	467.97	1.592	0.2863	
2013	RHS	Hazard Rate	Fenced	22.44	2.81	17.58	28.66	465.837	466.378	0	0.6345	
2013	RHS	Half-Normal	Fenced	20.75	2.6	16.24	26.5	470.22	470.54	4.162	0.0792	
2013	RHS	Model Average (HR, EX and HN)	Fenced	21.82	2.87	16.88	28.21					Favoured Model
2014	RHS	Exponential	Fenced	21.88	2.28	17.85	26.82	1,071.645	1,071.897	18.219	0	Favoured Model
2014	RHS	Hazard Rate	Fenced	21.21	2.26	17.22	26.12	1,053.253	1,053.678	0	1	ETA Extends beyond 12,500m
2014	RHS	Half-Normal	Fenced	20.99	2.18	17.13	25.71	1,136.499	1,136.752	83.074	0	
2015	RHS	Exponential	Fenced	16.81	1.92	13.44	21.01	1,083.507	1,083.811	138.94	0	Favoured Model
2015	RHS	Hazard Rate	Fenced	14.8	1.78	11.72	18.69	944.358	944.871	0	1	ETA Extends beyond 12,500m
2015	RHS	Half-Normal	Fenced	16.35	1.85	13.1	20.41	1180.537	1180.841	235.97	0	
2016	LHS	Exponential	Fenced	17.35	2.58	12.98	23.18	408.656	409.093	0	0.7968	
2016	LHS	Hazard Rate	Fenced	16.77	2.48	12.57	22.37	414.066	414.807	5.714	0.0458	ETA Extends beyond 12,500m
2016	LHS	Half-Normal	Fenced	16.9	2.45	12.74	22.42	411.9	412.337	3.244	0.1574	
2016	LHS	Model Average (EX and HN)	Fenced	17.28	2.56	12.94	23.07					Favoured Model
2017	RHS	Exponential	Fenced	18.53	2.23	14.66	23.43	728.74	729.064	11.246	0	
2017	RHS	Hazard Rate	Fenced	18.49	2.25	14.58	23.44	717.27	717.818	0	1	Favoured Model
2017	RHS	Half-Normal	Fenced	18.21	2.16	14.44	22.97	751.294	751.618	33.8	0	

2018	RHS	Exponential	Fenced	22.24	2.32	18.13	27.28	971.532	971.788	0	0.9899	Favoured Model
2018	RHS	Hazard Rate	Fenced	21.29	2.28	17.17	26.15	980.522	980.952	9.164	0.0101	ETA Extends beyond 12,500m
2018	RHS	Half-Normal	Fenced	21.92	2.27	17.9	26.83	1,001.251	1,001.506	29.718	0	

The MMDM by individuals captured more than once averaged 3,807 m (±932). The 2015 MMDM was substantially higher than all other years, at 5,453 m. Conversely, 2016 showed a lower-than-average MMDM.

Table 3.3-4: Summary of camera trapping parameters and density estimates. LCL = 95% lower confidence limit and UCL = 95% upper confidence limit.

		2013	***2014***	***2015***	***2016***	***2017***	***2018***	***Total***
Survey details	**View**	RHS	RHS	RHS	LHS	RHS	RHS	RHS
	Individuals	79	97	83	59	77	98	230
	Juvenile captures	2	2	1	0	10	19	
	Independent capture events	159	281	263	113	173	294	1242
	MMDM (m)	3047	4389	5453	2559	3651	3744	
	Trap nights	1342	2032	2085	2031	1917	1929	11336
Habitat mask		**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**Mean**
12500m	**Mean density per 100 km^2**	**18.43**	**17.87**	**11.47**	**15.69**	**14.96**	**18.26**	**16.11 (±2.45)**
	SE	*2.65*	*1.95*	*1.52*	*2.43*	*1.94*	*2.01*	
	LCL	*13.93*	*14.44*	*8.87*	*11.61*	*11.62*	*14.73*	
	UCL	*24.39*	*22.12*	*14.85*	*21.22*	*19.26*	*22.63*	
Fenced	**Mean density per 100 km^2**	**21.82**	**21.88**	**16.81**	**17.28**	**18.49**	**22.24**	**19.75 (±2.29)**
	SE	*2.87*	*2.28*	*1.92*	*2.56*	*2.25*	*2.32*	
	LCL	*16.88*	*17.85*	*13.44*	*12.94*	*14.58*	*18.13*	
	UCL	*28.21*	*26.82*	*21.01*	*23.07*	*23.44*	*27.28*	
Clipped 12500m	**Mean density per 100 km^2**	**18.53**	**18.56**	**12.77**	**15.85**	**15.61**	**19.01**	**16.72 (±2.22)**
	SE	*2.61*	*2.00*	*1.56*	*2.44*	*1.97*	*2.05*	
	LCL	*14.08*	*15.04*	*10.06*	*11.75*	*12.21*	*15.39*	
	UCL	*24.39*	*22.9*	*16.2*	*21.39*	*19.96*	*23.46*	

The three habitat masks revealed that the average mean Fenced estimates were higher than both 12,500 m and Clipped 12,500 m (Figure 3.3-1). The Fenced ETA average density estimate was 19.75 (±2.29) hyaenas per 100 km^2 across the 6 years. The 12,500 m ETA density average was lowest at 16.11 (±2.45) hyaenas per 100 km^2, and the Clipped 12,500 m gave results between the two, at 16.72 (±2.22).

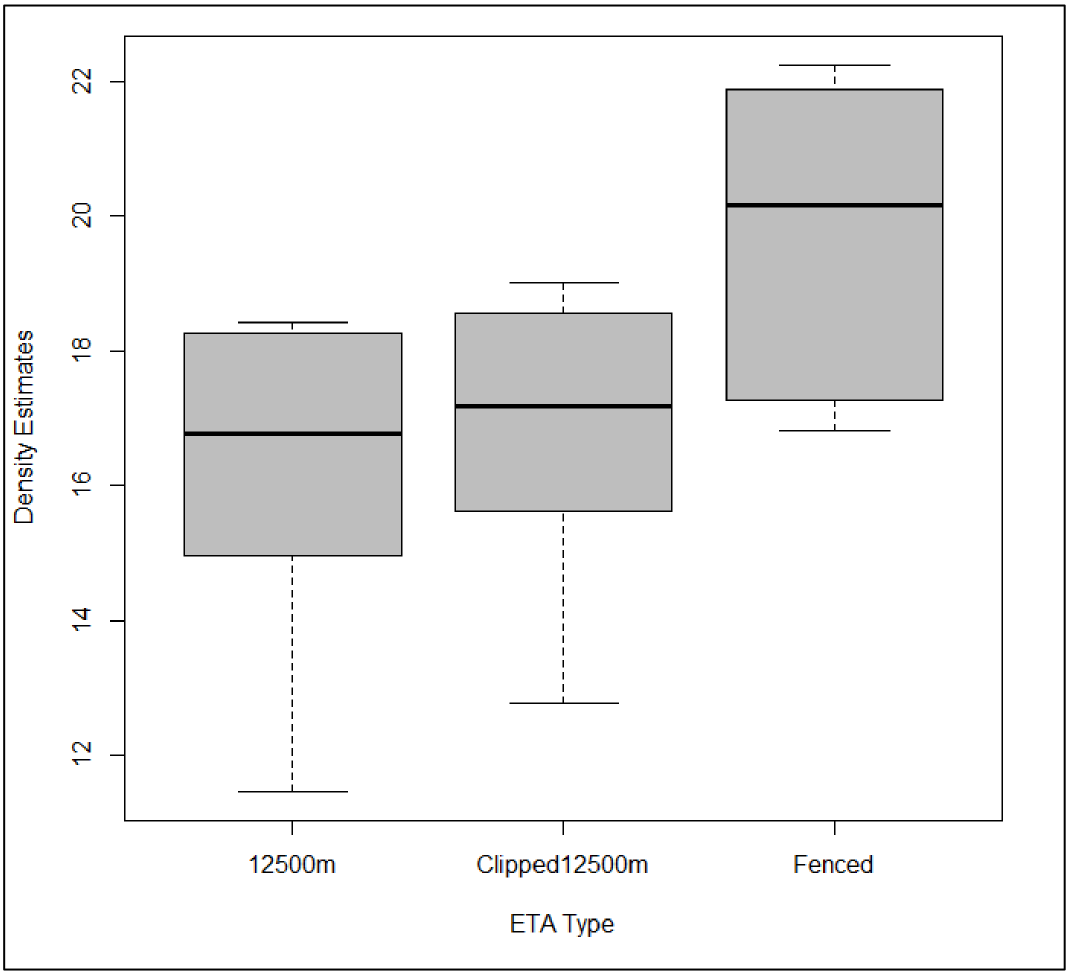


Figure 3.3-1: Box and Whisker analysis for mean density estimates for the three ETA approaches between 2013 and 2018.

The trend in density between 2013 and 2018 varied slightly between the different habitat suitability approaches. The Fenced approach had a lower relative decrease in density between 2014 and 2015 than the other two ETAs (Figure 3.3-2). Despite the Fenced approach consistently producing the highest density estimates and the 12,500 m mask producing the lowest, each mean estimate fell within the Clipped 12,500 m ETA 95% confidence interval limits. The only exception was for 2015, where the Fenced mean estimate lay outside the 95% CI. Hyaena density estimates were best represented by the SECR analysis projected on the Clipped 12,500 m habitat mask.

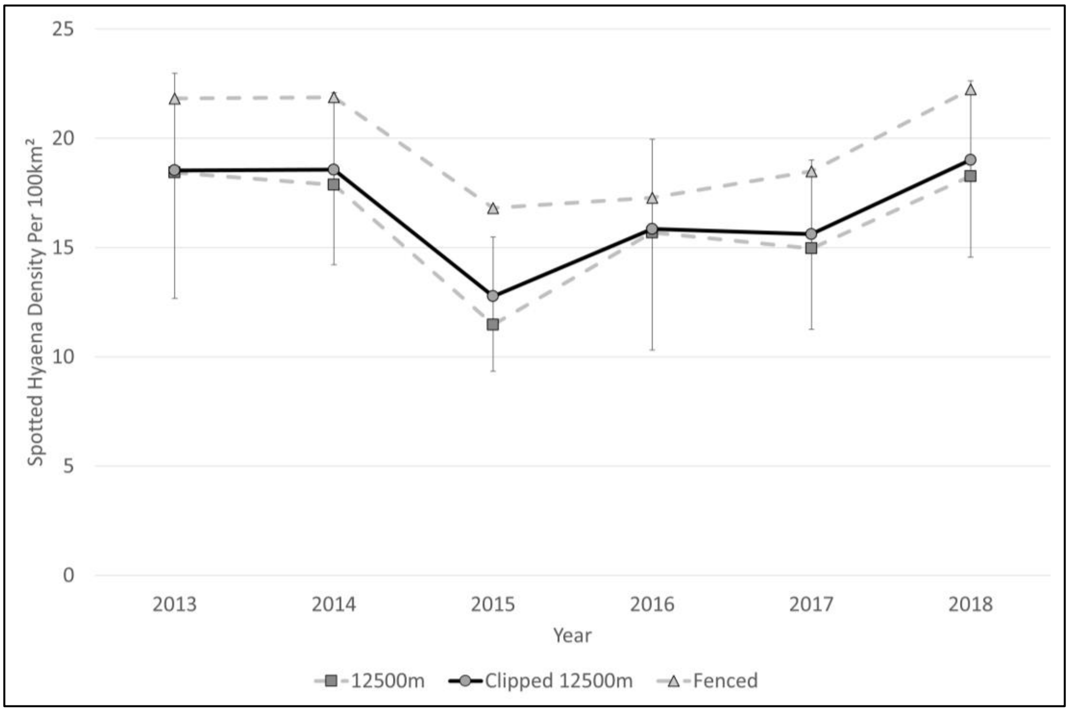


Figure 3.3-2: Trends in mean hyaena density estimates across three habitat masks between 2013 and 2018 with 95% CI bars shown for the Clipped 12,500 m estimates.

Spatial variation in hyaena density across the park was evident. The average density in the Hluhluwe section of HiP between 2013 and 2018 was 13.26 (±5.12) and iMfolozi was 20.05 (±5.54) hyaenas per 100 km^2 (Appendix 3.6).

3.3.2 Hyaena density estimates from call-ups

Results from the 2018 call-up survey produced a mean density of 11.41 hyaenas per 100 km^2 (95% CI: 5.61-16.88). Although not substantially different from the previous two call-ups in 2013 and 2015, the declining trend in density was maintained. Using the results from 2013, 2015 (EKZNW unpublished data) and 2018, the average mean density estimate from call-ups was 12.22 (±0.97) over my camera trap study period (Table 3.3-5).

Table 3.3-5: Hyaena call-up density estimates from 2013, 2015 and 2018.

		2013 ***(EKZNW unpublished data)***	***2015*** ***(EKZNW unpublished data)***	***2018*** ***(This study)***	***Mean***
Call-Up Estimates	**Mean Density per 100 km^2**	**13.47**	**12.07**	**11.41**	**12.22 (±0.97)**
	LCL	*6.57*	*6.45*	*5.61*	
	UCL	*20.59*	*17.74*	*16.88*	
	Area Sampled km^2	*506*	*522*	*531*	

3.3.3 Call-up estimates versus camera-trap estimates

The mean call-up estimate of 12.22 (±0.97) was lower than 16.72 (±2.22) generated from the camera trap surveys between 2013 and 2018. Over this period, the predator prediction model for hyaenas or expected density (Hayward, O'Brien et al., 2007) maintained a steady 14.37 (±0.31) (Figure 3.3-3).

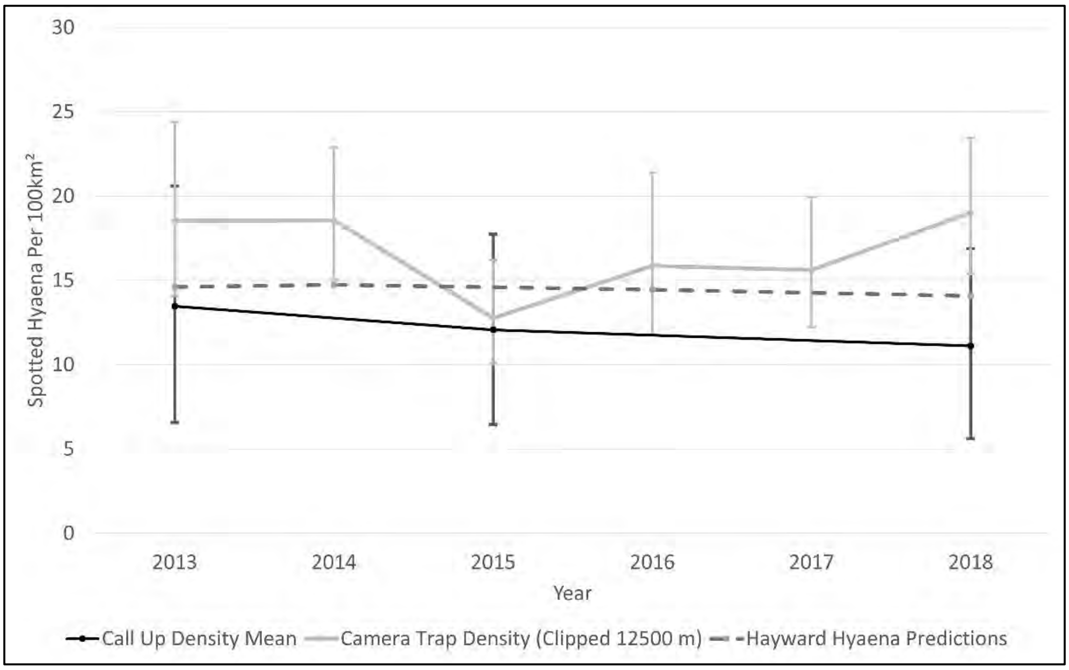


Figure 3.3-3: Hyaena density estimates from call ups and camera trapping (Clipped 12,500 m), compared with Hayward et al.'s Carrying Capacity prediction between 2013 and 2018. LCL = 95% Lower Confidence Limit. UCL = 95% Upper Confidence Limit.

3.3.4 Ecological determinants

Three models with ecological variables as ecological determinants had support as models fitting the data (Appendix 3.5). These three models were rainfall, lion density and prey abundance each fitted as single determinant variables (Table 3.3-6). While neither lion density (P = 0.387), average rainfall (P = 0.173), nor prey abundance (P = 0.496) were significant predictors of hyaena density, hyaena density tended to increase when prey availability and rainfall increased and decrease when lion density increased (Table 3.3-6).

Table 3.3-6: Results from the best-fitting GLMs, showing the parameter estimates for hyaena density.

Model	***Parameters***	***Estimate***	***Std Error***	***t value***	***P***
Rainfall Model					
	Intercept	13.680	2.340	5.848	0.004
	Rain	0.074	0.045	1.658	0.173
Lion Model					
	Intercept	21.618	4.323	5.001	0.007
	Lion Density	−0.365	0.376	−0.941	0.387
Prey Model					
	Intercept	10.381	9.494	1.093	0.336
	Prey Abundance	0.002	0.003	0.747	0.496

3.4 Discussion

Long-term datasets are powerful tools in biodiversity conservation (Magurran et al., 2010), as are reliable estimates of population sizes (Balme, Hunter et al., 2009; Balme, Slotow et al., 2009). More specifically, population estimates are vital for the management and conservation of cryptic and persecuted carnivores (Balme, Slotow et al., 2009). Finding techniques to achieve reliable estimates can be challenging, especially with limited resources. My study successfully estimated hyaena density through the SECR approach, using existing camera trap data (Efford et al., 2009; Mann et al., 2019). Furthermore, I was able to compare these estimates with the more traditional call-up technique (Mills et al., 2001; Graf et al., 2009) over the same period, and quantify the possible ecological determinants of hyaena density in HiP between 2013 and 2018.

3.4.1 Density estimates and methodology

SECR

Camera trap surveys, and subsequent SECR analysis of these data, are increasingly being used to estimate hyaena density throughout different parts of Africa (Table 3.4-1). My study is the first of its kind to look at trends in hyaena density over six years from camera trap data and compare these with estimates from call-ups over the same period. Furthermore, at 19.01 hyaenas per 100 km^2, the estimate from the SECR analysis used in my study is the highest reported for any hyaena population monitored in this way.

Table 3.4-1: Summary of studies in which hyaena density estimates have been made through the SECR approach using camera trapping data.

Location	Density Estimate Per 100 km^2	LCL	UCL	Model	Study
Hluhluwe–iMfolozi Park, South Africa	19.01	15.39	23.46	Likelihood	This Study (2018 results)
uMkhuze Game Reserve, South Africa	10.59	6.69	14.86	Bayes	De Blocq 2014
Hardap Region, Namibia	0.85	0.64	1.10	Bayes	Fouché et al. 2020
Ngamiland District, Botswana	10.10	8.69	11.63	Likelihood	Rich et al. 2019
Majete Wildlife Reserve, Malawi	2.62	2.06	3.34	Bayes	Briers-Louw 2017
Queen Elizabeth National Park, Uganda	13.43	9.07	18.81	Bayes	Braczkowski 2020
Mpala Ranch, Kenya	4.93	2.68	9.03	Likelihood	O'Brien and Kinnaird 2011

Using the most recent SECR estimates, my study confirms that comparing against historical estimates for the park, the hyaena population in HiP between 2013 and 2018 is currently close to half of what it was between 2003 and 2010 (Graf et al., 2009). Although not the 66% decline observed through most recent call-up estimates, the population has undergone a notable decline. Between 2013 and 2018, the population was 48% of its previous average abundance. Thus, my hypothesis in this regard is partially supported.

Hyaena estimates from the SECR approach decreased dramatically in 2015. This decreasing trend was supported by estimates in 2016, which were 15% lower than in 2014. However, a 33% drop in population from 2014 and then subsequent recovery of 28% between 2015 and

2016 does not seem biologically plausible and is more likely a statistical phenomenon resulting from the SECR methodology.

To understand this underestimation as a statistical phenomenon, it helps to look at the available data and ecological conditions at the time. It is evident that despite a similar number of captures and individuals recognised compared with previous years, hyaenas moved significantly further in 2015 (Table 3.3-4). This increased movement coincides with a drought period in which we would expect hyaenas to increase their foraging area (Trinkel et al., 2004). The SECR approach uses this spatial information to better inform density estimation (Efford et al., 2009) and we would expect the predicted AC for hyaenas to have been more spread out across the relative ETAs in this year. Depending on the ETA used for the analysis, the impact of this dispersion would have had different consequences on density. I observed this clearly when comparing the relative drop in density estimates between permeable (12,500 m ETA) and impermeable fence (Fenced) approaches, and the significant difference in respective mean density estimates for 2015 (Figure 3.3-2). The 12,500 m ETA estimates dropped by approximately 35% in 2015 and the Fenced ETA by only 23%. For the latter, when all AC for hyaenas were restricted to be within the fenced boundary, the relative impact of increased movement of hyaenas on density estimates was substantially less than for the 12,500 m ETA. This anomaly within the six-year dataset highlights the importance of ongoing long-term monitoring efforts (Mann, Theron et al., 2020).

Population estimates are often the preferred demographic parameter used by protected area managers to manage the ecology of these systems. The process of extrapolating population estimates from density needs to be done in a conservative manner (Efford & Fewster, 2013) and with relevance to the specific system being studied. The most recent density estimates from 2018, extrapolated across the park's 896 km^2 boundary, puts the hyaena population in HiP at 163 (95% CI: 131–202), 170 (95% CI: 138–210) and 199 (95% CI: 162–244) individuals for the 12,500 m, Clipped 12,500 m and Fenced ETA approaches, respectively. Although extrapolating across the fenced boundary is ad hoc, the fact that all models fitted were integrated across nearly the entire extent of the park (±93% overlap with park boundary), makes it an appropriate approach for providing relevant population estimates to protected area management (Efford & Fewster, 2013).

Extrapolating population size across the total ETAs for respective approaches taken in my study would likely overestimate the population (Appendix 3.3), as predator density should decrease outside of the park boundary (Balme et al., 2010). Because my trapping effort did not extend outside the park's boundary and thus density estimates were not influenced by this change in "habitat type", such extrapolation would not be appropriate. Nevertheless, the

Clipped 12,500 m should produce the most plausible estimate of the three from my study. Here extrapolated estimates for density across the greater HiP region was 258 (95% CI: 209–318) individuals in 2018 (Appendix 3.3).

Although considered a conservative and reliable approach to density estimation (Noss et al., 2012; Rich et al., 2014), the different approaches taken within the SECR framework can significantly impact estimates (Williams et al., 2021). More specifically, fence permeability and the inclusion of habitat outside of the park into the state space for SECR analysis, dramatically influences density estimates (Williams et al., 2021). However, in my study, the influence of fence permeability did not change density estimates to the same extent shown by Williams et al. (2021). HiP is one of the largest fenced protected areas in South Africa at ±900 km^2. As shown by Williams et al. (2021), density estimates in larger fenced protected areas are less influenced by fence permeability. In smaller protected areas the camera trapping grid is more likely to sit closer to the fence line, and as a consequence the state space in these studies were more sharply clipped than those with trapping grids further from the fence. Therefore, in these smaller reserves, there might be a number of activity centres outside of the fence when the fence is permeable, and these will be "forced" inside when state space is clipped by the fence. The camera trap array in my study only covered the central third of the park and hyaena movement was not excessively clipped in areas north and south of the trapping grid when the fence was regarded as impermeable.

Although hyaenas might traverse areas outside the park, they are less likely to be resident in areas of high human density and hostility (Hofer & Mills, 1998a). To overcome the challenge presented by fence permeability and the relative state space outside of fences of protected areas, a number of approaches might be taken. Firstly, as with my study, a nuanced approach to the habitat mask can include areas more suitable to hyaenas and exclude those that are not (Kristensen & Kovach, 2018; Balme et al., 2019; Mann, O'Riain et al., 2020). Unfortunately, this approach is subjective and limited by a binary "suitable" verses "unsuitable" habitat, which has the consequence of leaving poor quality habitat categorised as suitable (Mann, O'Riain et al., 2020). A second approach that addresses this to some degree is the addition of covariates, or a resource selection function (RSF) layer (Royle, Chandler, Sun et al., 2013; Proffitt et al., 2015), over the habitat mask to represent the expected heterogeneity in hyaena density between inside and outside of the protected area. To make this covariate approach of value, however, data would need to be gathered from outside the park by extending the camera trapping grid over the fenced boundary. This sampling was not feasible for my study because of the high risk of camera theft outside of HiP. A further drawback of using covariates in this way is that it has the consequence of generating estimates with large confidence intervals (Pers. Comm. Murray Efford, 2021).

Call-ups

Results from my 2018 call-ups confirm stability within the hyaena population between 2013 and 2018. There was a slight decreasing trend in the mean density over these years, but the means from the 2013 and 2015 surveys fell within the 95% confidence intervals of the 2018 results. Compared with the camera trapping data, call-up estimates substantially underestimated the population from 2013 onwards. This finding supports my second hypothesis that the decline observed through the call-up surveys has likely been exaggerated. One possible reason for this could be that the response probability to call-ups in HiP decreased since Graf et al.'s (2009) work in 2003–2004. Response probability can differ spatially (Creel & Creel, 1996; Ogutu et al., 2005) and temporally (Ogutu et al., 2005; Cozzi et al., 2013). Such an example of spatial differences in response probabilities is well represented by comparison between two study populations from Kenya (Ogutu et al., 2005) and Tanzania (Creel & Creel, 1996), where probability of response was 0.583 versus 1 respectively.

Behavioural response to avoid humans might also explain a decrease in response probability to call-ups within HiP, as has been hypothesised for lions in the Masai Mara (Ogutu et al., 2005). Between 2011 and 2012, it is believed that there has been an increase in persecution of hyaenas inside and outside the park. In addition, in HiP there has been an increase in bush encroachment and of woody vegetation <4m high between 2007 and 2017 (Mbongwa, 2020). This finding, along with my own observations at call-up sites, supports the notion that visibility is poor at many current call-up sites throughout the park, which could decrease the detection of responding hyaenas. If call-ups continue to be used as the method of choice for population estimates of hyaenas within HiP, I recommend that the response probability be recalibrated through performing experimental call-ups in which hyaena responses are tested at varying distances from call-up stations (Graf et al., 2009).

Call-ups versus camera trapping

There was a clear difference between the density estimates obtained from call-up and camera trapping surveys in HiP. Camera trap estimates for 2013 and 2018 were substantially higher at 18.53 and 19.01, respectively, versus the mean call-up densities of 13.47 and 11.41. The 2015 estimates of 12.77 from camera trapping are comparable to the 2015 call-up mean density of 12.07. However, the 2015 camera trap estimate falls outside of ecological logic and seem to be a statistical phenomenon. Furthermore, call-ups and camera trap surveys took place at different times of the year. To control for these issues, I compared the mean average estimates between 2013 and 2018 for the two methods. By doing this I confirmed that the mean density of 16.65 (±2.35) between 2013 and 2018 (excluding 2015: 17.51 (±1.47)) for camera trapping was higher than the call-up mean density of 12.32 (±0.86) hyaenas per 100 km^2.

I have taken a conservative approach to the SECR analysis by including fence permeability, and I would expect these estimates to underestimate the population (Williams et al., 2021). Furthermore, the SECR approach to camera trap data has been shown to produce lower density estimates than traditional methods (Sollmann et al., 2011; Noss et al., 2012; Rich et al., 2014). Despite these shortcomings, camera trap estimates were greater than those generated from call-ups in HiP between 2013 and 2018, which supports the hypothesis that the latter has probably underestimated hyaena density over this time. Unfortunately, a statistical comparison between the monitoring techniques used in my study, without the control of a known population size (Balme, Hunter et al., 2009), was not possible. This is an area of research that needs further investigation to help conservation practitioners make sound monitoring and management decisions for hyaenas (Balme, Slotow et al., 2009).

3.4.2 Ecological determinants and trends in hyaena density

It is evident that the decrease in hyaena density after 2014 coincided with a high number of reported mortalities for the species in that year (9 mortalities = 5% of estimated population at the time) (Annex 3.7). Unfortunately, the causes of these deaths were largely unknown. Nevertheless, it is plausible that with the onset of the drought in 2014, intraspecific competition between carnivores increased (Palomares & Caro, 1999; Périquet, Fritz et al., 2015). Water availability would have been locally concentrated around specific areas and prey species would have responded accordingly (Smit et al., 2007; Ogutu et al., 2014). Hyaenas are expected to change their spatial movements in response to the movement of prey (Trinkel et al., 2004; Höner et al., 2005) and relocating or abandoning of dens in dry seasons is known to occur (Tilson & Henschel, 1986). In addition, increased movements into neighbouring clan's territories could have lethal consequences (Tilson & Henschel, 1986; Mills, 1990). Furthermore, increased interspecific conflict at water sources may have occurred during 2014, resulting in more lion-induced hyaena mortalities (Trinkel & Kastberger, 2005). Subsequent to the drop in mean hyaena densities between 2015 and 2017, the density estimates recovered to 19.01 in 2018. This was a ±20% increase from preceding years, which could represent a recovering population. This is further supported by a tenfold increase in the number of juvenile captures observed after 2016. However, analysis of subsequent camera trap data in 2019 onwards is required to determine if this is a true biological effect.

None of the three ecological determinants of lion density, rainfall or prey abundance appeared to influence hyaena density over my study period. The lack of any statistical significance may be due to the low sample size. One would expect hyaenas to be in some way impacted by these ecological factors, and although this relationship was not observed over my study period, that is not to say it is not present in HiP. The spatial distribution of hyaena density supports this hypothesis. Hyaena density in the iMfolozi section is 50% greater than that of Hluhluwe (Appendix 3.6). This trend is matched by hyaena prey availability, where iMfolozi boasts close to 30% more prey items per km^2 than Hluhluwe.

My study has successfully shown the efficacy of camera trapping as a means of monitoring trends in hyaena density over time. Furthermore, using existing camera trap surveys to establish density estimates for non-target species is a cost-effective means of monitoring these populations. I have also displayed the shortfalls of the traditional call-up technique, without ongoing calibration of the response probability factor. Finally, my findings further support the literature that show water availability is an important factor for hyaena populations across the continent.

CHAPTER 4 – SPOTTED HYAENA SPACE USE

4.1 Introduction

4.1.1 Carnivore spatial use

The home range of an animal is an area used for normal daily activities (Burt, 1943). Ultimately, this area is the space used by an individual that is less costly to maintain than it is beneficial to occupy (Powell, 2000). Home range studies are a common topic in ecology (Péron, 2019), with many of these studies assessing variation in space use between individuals, species and across seasons (Richard et al., 2014). Factors influencing home range can broadly be categorised into food and shelter resources, cost and constraints of movement, and social factors including competition, sociality and reproduction (Péron, 2019). The home range sizes of mammals have, more specifically, been shown to be influenced by habitat, resource availability, body size, predation risk, sex and season (Harestad & Bunnel, 1979; Swihart et al., 1988; Jurczyszyn, 2006; Sprent & Nicol, 2012; Richard et al., 2014). Against this backdrop, a territory can be defined as an area that an animal has either exclusive or priority use of (Powell, 2000) and the boundary of which is often actively demarcated and defended (Kruuk, 1972; Powell, 2000). For social animals, the shape and extent of these territorial boundaries, along with respective group sizes, can often be linked to the dispersion and availability of food (Macdonald & Johnson, 2015).

Understanding space use of carnivores can be important for their conservation (Micheli & Peterson, 1999; Caro, 2007). Individual species with larger home ranges are more susceptible to conflict with humans (Woodroffe & Ginsberg, 1998) and space use size can be directly influenced by habitat quality (Riley et al., 2003). When space use is analysed in relation to habitat type, a better understanding of habitat selection can be achieved (Broomhall et al., 2003; Welch, 2014; Bowden et al., 2015; Quinton, 2016). Such information can inform carrying capacity predictions for a species within a system (Ryan & Jamieson, 1998). Understanding the home range sizes and habitat use of carnivores can, therefore, support conservation planning by identifying key habitat types to be protected across their existing ranges and identifying important corridors between isolated populations (Riley et al., 2003; Kaszta et al., 2020).

4.1.2 Space use methodologies

The minimum convex polygon (MCP) was one of the first approaches adopted by behavioural researchers to estimate home range in the 1940s (Mohr, 1947). This approach uses the outermost spatial data points from a dataset to draw the smallest possible area to form a convex polygon (Mohr, 1947; Worton, 1987). The MCP approach is still often used for home range estimation (Quinton, 2016), especially for capture-recapture trapping data (Lira & dos Santos Fernandez, 2009; Gil-Sánchez et al., 2011). The approach is comparable between studies (Swihart et al., 1988; Harris et al., 1990) and has been consistent between telemetry versus camera trap studies (Jones & Sherman, 1983). However, there are drawbacks to this simple approach. Critics have argued that peripheral data points disproportionately influence home range size and incorporate areas very seldom used by the animal (Franzreb, 2006; Scull et al., 2012).

The kernel utilisation distribution approach is a common alternative to the simpler MCP (Worton, 1989). This approach uses a probability function and a smoothing parameter to estimate the utilisation distribution of an individual from spatial data points (Worton, 1989; Quinton, 2016). Choosing the correct smoothing parameter is important and can substantially influence final home range estimates (Seaman & Powell, 1996; Powell, 2000). Despite the kernel approach being favoured in many studies, the MCP method is still favoured when data are limited (Jones & Sherman, 1983; Harris et al., 1990) and, as such, has been used successfully for several camera trapping studies (Gil-Sánchez et al., 2011; Welch, 2014; Srivathsa et al., 2017; Kumbhojkar et al., 2020).

Jurczyszyn (2006) showed that the MCP approach for home range size estimation can be useful for comparing space use between individuals of the same species. In addition, Quintin (2016) and Welch (2014) both used MCPs in habitat selection studies for Florida black bears (*Ursus americanus floridanus*) and brown hyaena respectively. Quintin (2016) found that the home range size estimates generated from the same dataset using the MCP approach were comparatively larger than the kernel estimates, and the more conservative polygon approach known as Characteristic Hull Polygon (CHP). In a study on spotted hyaenas' space use, over a 20-month period, Boydston et al. (2003) found that the MCP generated from telemetry data more closely resembled the territorial boundaries of the collared individuals than the smaller kernel utilisation distribution estimates.

Comparing MCPs generated from telemetry data versus camera trap spatial data for brown hyaenas, Welch (2014) found that camera traps underrepresented the home ranges of these individuals. It is worth noting, however, that this camera trap study only lasted 3 months, compared with the 9–12 month's telemetry data. This may have affected the comparability of the two methods (Péron, 2019). Péron (2019) advocates for the use of the term "space use", as opposed to "home range" when studies, such as Welch's (2014), investigate spatial data over a relatively short time frame and may only represent a periodic (or snap-shot) distribution that does not reach an asymptotic home range estimate (Haines et al., 2009; Péron, 2019).

4.1.3 Hyaena spatial behaviour

Hyaenas exist within complex social structures called clans (Kruuk, 1972; Smith et al., 2008). Subgroups exist within these clans, and their behaviour and composition changes under varying conditions (Smith et al., 2008). Hyaenas maintain an often-stable home range (Trinkel et al., 2006) which is shared with other individuals within their clan (Kruuk, 1972) and territorially defended against invaders (Kruuk, 1972; Mills, 1990; Boydston et al., 2001). Disputes over territorial boundaries can result in "clan wars" (Kruuk, 1972). Despite the risk of a hostile reception (Hofer & East, 1993b), movement into neighbouring clan territories does take place, and Kruuk (1972) categorises this movement into two types, permanent and short visits. The former occurs predominantly by males who disperse from their natal clan into new clans (Mills, 1990; Van Horn et al., 2003; Höner et al., 2007) or become nomadic (Mills, 1990). Short visits into neighbouring clan territories are often related to extra-territorial foraging expeditions (Hofer & East, 1993b; Höner et al., 2005).

The social and activity centre of a hyaena clan is the communal den (Kruuk, 1972), the location of which has great importance for the space use for the respective clan (Kolowski & Holekamp, 2009). The communal den is where clan members regroup and head out in hunting or territorial patrol parties of seldom more than five individuals (Hofer, 1998; Holekamp & Smale, 2000), where new cubs are introduced into the clan and where social ranking is further settled (Cooper, 1993; White, 2006). All cubs within the clan that have been moved from their natal dens are collectively reared at the communal den (Kruuk, 1972). However, it is noteworthy that females only suckle their own offspring (Kruuk, 1972; Mills, 1990).

Territorial behaviour has been shown in almost all hyaena populations across Africa (Holekamp & Dloniak, 2010). However, both the type of territorial behaviour and home range size can vary substantially between study sites (Kruuk, 1972; Holekamp & Dloniak, 2010). Important factors contributing to differences in territorialism and home ranges are prey dispersion (Mills, 1990), variation in prey type (migratory versus resident) (Kruuk, 1972), and the abundance of respective prey sources (Kruuk, 1972; Trinkel et al., 2006). An additional complexity for hyaena spatial studies is that, although clans occupy territories (Kruuk, 1972), variation in space use between individuals is evident. Both the sex and respective rank of an individual are important factors in influencing space use (Henschel & Skinner, 1991; Holekamp, Cooper et al., 1997; Boydston, Kapheim, Szykman et al., 2003; Van Horn et al., 2003). Although both sexes display territorial behaviour (Boydston et al., 2001), the benefits derived from this behaviour are different. Male territorial behaviour seems to be related to mating opportunities, whereas females cooperatively defend territories to ensure sufficient food supply for them and their offspring (Boydston et al., 2001).

With regards to social rank, it has been noted that lower-ranking females and all males are more likely to move greater distances than higher-ranking females (Boydston et al., 2005; Boydston, Kapheim, Szykman et al., 2003; Kolowski & Holekamp, 2009). This, in part, is due to both foraging effectiveness and life history traits (Van Horn et al., 2003; Holekamp & Dloniak, 2010). Lower-ranking individuals are less likely to obtain their necessary caloric intake at a carcass when competing with higher-ranking individuals and must, therefore, forage further and more frequently (Holekamp, Smale et al., 1997; Kolowski & Holekamp, 2009). Furthermore, males do not take part in parenting (Holekamp & Dloniak, 2010; Estes, 2012) and may thus not be restricted to the den site to the same degree as breeding females (Boydston, Kapheim, Szykman et al., 2003).

Den site selection is influenced by water availability in both mesic (Boydston et al., 2006) and arid (Tilson & Henschel, 1986) systems, with hyaenas largely selecting den sites near water. This selection has significance to the distribution of hyaena territories in any system, as the den is the activity centre for hyaena clans (Kruuk, 1972) and an important determinant for space use (Kolowski & Holekamp, 2009). It is worth noting that the selection of a den site and frequency of its use, is also influenced both by the presence of hyaenas' main competitor, lions (Périquet et al., 2016) and the aggregation of prey (Kruuk, 1972; Hofer & East, 1993a).

Furthermore, the dispersion of food resources can play an influential role in territorial behaviour, social composition and the space use of most social carnivores (Macdonald & Johnson, 2015). In the case of hyaenas, much evidence is available to support the notion that hyaena spatial behaviour is largely determined by the abundance and dispersion of prey across the landscape (Tilson & Henschel, 1986; Henschel & Skinner, 1991; Mills, 1990; Hofer & East, 1993b; Trinkel et al., 2004).

In systems with an abundant and stable prey source for hyaenas, territorial boundaries are largely stable over time (Höner et al., 2005; Trinkel et al., 2006). Trinkel et al. (2006) suggested that when prey availability is greater than 5.5 prey per km^2, hyaena clan territories remain stable. Kruuk (1972) found clan territories to be largely stable over time in the Ngorongoro Crater. Despite hyaena abundance decreasing by more than 70% between 1960s and 1990s, likely due to reductions in prey availability (Höner et al., 2005), the number of clans in the area remained constant, as did the average territory size (Kruuk, 1972; Höner et al., 2005). Additionally, in prey-rich ecosystems, clan territories exist in a largely "uninterrupted mosaic" across the landscape (Kruuk, 1972; Hofer & East, 1993a; Holekamp & Dloniak, 2010). This tightly packed territorial landscape contrasts against prey-poor systems, where vacant land between clan territories has been observed (Tilson & Henschel, 1986).

Prey abundance can also influence the movement of hyaenas into neighbouring clan territories. In areas of high hyaena abundance, there is increased territorialism as competition over valuable resources is greater (Henschel & Skinner, 1991; Kruuk, 1972; Trinkel et al., 2006). In these systems, a high frequency of intrusion into neighbouring clan territories takes place (Hofer & East, 1993b; Höner et al., 2005), and long-term stability in territorial borders is evident (Höner et al., 2005; Trinkel et al., 2006). The high incursion rate observed in the Ngorongoro Crater is believed to be a function of the high reward-to-risk ratio experienced in the Crater compared with larger areas like the Serengeti (Hofer & East, 1993b; Höner et al., 2005). In the Ngorongoro Crater, extraterritorial trips can be quick and beneficial, and Höner et al. (2005) found that hyaenas were less likely to make extraterritorial trips when prey was densely available within their own ±30 km^2 territories. However, incursion rates were greater when prey dispersed thinly and into neighbouring clan territories. Although competition between clans does take place in regions of low-prey abundance (Tilson & Henschel, 1986; Mills, 1990), it occurs at a lower intensity (Tilson & Henschel, 1986). The wide dispersion of prey, leading to very large territories, results in the costs of territorialism being disproportionate within these systems (Henschel & Skinner, 1991; Macdonald & Johnson, 2015). Incursion rates are also low in these systems because of the increased risk of interaction with the natal clan as a result of spending more time searching for thinly dispersed prey (Mills, 1990).

Home range size and territorialism has been shown to significantly vary between seasons (Hofer & East, 1993a, 1993b; Trinkel et al., 2004, 2006), as prey dispersion (Mills, 1990) and the migration of prey species (Kruuk, 1972; Hofer & East, 1993b; Trinkel et al., 2004) is often correlated with water availability. Mills (1990) found that when prey was concentrated around river lines in the arid Kalahari system, hyaenas responded to these spatial changes in "food patches" and increased their activity around these specific areas within their territories. In the similarly arid Etosha National Park, it was found that in response to the wide dispersion of prey between dry and wet seasons, hyaenas increased their occupied territories two-fold from 160 km^2 to 320 km^2 (Trinkel et al., 2004). By contrast, in the hyaena dense landscape of the Serengeti, hyaenas did not change the size of their 55.5 km^2 territories (Hofer & East, 1993a), but rather adopted a "commuting" strategy in response to migratory herds. In this system, hyaenas moved into neighbouring clans' territories to follow migratory herds (Hofer & East, 1993b), but always returned (Kruuk, 1972). It is worth noting that with increased levels of foraging movement by mothers away from den sites, as may occur with increased dispersion of prey, there may be an increased risk of reduced cub growth rate (g/day) and survival (Hofer and East 1993c).

Habitat selection

Hyaenas are highly adaptable and occur throughout Sub-Saharan Africa across a wide range of ecological conditions and habitats (Holekamp & Dloniak, 2010). Occurring from sea level (Tilson & Henschel, 1986) through to altitudes of >4,000 m (Young & Evans, 1993), this species experiences temperatures ranging from −10° to 40°C (Mills, 1990). Furthermore, being adapted for both deserts and forests, it is not surprising that hyaenas occupy areas with annual rainfall ranging from 18 mm in the Namib Desert (Tilson & Henschel, 1986) to 1,406 mm in the miombo woodlands of Selous Game Reserve in Tanzania (Creel & Creel, 2002, p. 249). In areas of extremely low rainfall, such as the Namib Desert, it is believed that much of the hyaena's water intake is through the body of their prey (Green et al., 1984; Holekamp & Dloniak, 2010). For a species that occupies such a vast array of habitats, it is difficult to describe their habitat preferences. However, within systems, spatial use has been researched extensively, as discussed above. Both the ecological (Tilson & Henschel, 1986; Mills, 1990; Trinkel et al., 2004) and anthropogenic (Kolowski & Holekamp, 2009; Yirga et al., 2012; Sogbohossou et al., 2018) settings of each system play important roles in influencing where in space hyaenas occur. Ecologically speaking, the distribution of prey (Mills, 1990; Trinkel et al., 2004), habitat type (Kolowski & Holekamp, 2009; Stratford & Stratford, 2011) and competitor presence (Périquet, Fritz et al., 2015; Périquet et al., 2016) all influence habitat use. The extent to which these variables contribute towards dictating space use is variable, and their contributions are not mutually exclusive (Mills & Biggs, 1993; Kolowski & Holekamp, 2009).

Kolowski and Holekamp (2009) showed that hyaenas favoured areas close to water, with high prey density and shrubland vegetation. It has been postulated that this is a risk avoidance strategy and that the selection for thicker habitat is to support concealment from anthropogenic pressures, such as retaliation killings for livestock predation (Frank & Woodroffe, 2001; Boydston, Kapheim, Watts et al., 2003). Thickets were also favoured in a population studied within the KNP (Mills & Biggs, 1993). Further, although Broekhuis et al. (2013) found that hyaenas favoured grasslands, they also selected for mixed woodland in the Okavango Delta of Botswana. In the Ongava Game Reserve, Namibia, hyaenas concentrated in areas close to thicker vegetation cover in the wet season. Interestingly, the authors believed this finding was linked to the dispersion of prey into these thicker vegetation patches, as opposed to a risk-avoidance strategy (Kolowski & Holekamp, 2009).

Space use in Hluhluwe–iMfolozi Park

Hyaena space use in HiP was first investigated in the 1970s by Whatelely and Brooks (Whateley & Brooks, 1978; Whateley, 1981). This study, which focused on the Hluhluwe section, estimated the average home range to be approximately 13 km^2 (Whateley & Brooks, 1978). However, only an area north-east of the Hluhluwe river was sampled in their study and this area was poorly sampled by the camera trapping grid in my study (see Chapter 3). The 13 km^2 estimate is the smallest clan home range on record for the species (Holekamp & Dloniak, 2010). By contrast, the home range estimate of a clan in the iMfolozi section over a similar period was 39 km^2 (Whateley, 1981). However, this second estimate was generated from only one clan, compared with the three used in the Hluhluwe study (Whateley & Brooks, 1978).

4.1.4 Aims and objectives

There have been several ways in which the space use and distribution of hyaenas have been studied. These include direct observation of individuals (Kruuk, 1972; Mills, 1990), analysis of call-up data (Graf et al., 2009; Cozzi et al., 2013), den monitoring (Boydston et al., 2006) and telemetry data (Kolowski & Holekamp, 2009). More recently, camera trapping data and occupancy models have been used to better understand spatial use in hyaenas (Mhlanga et al., 2018; Sogbohossou et al., 2018). Additionally, camera trap sampling has been used to better understand the association between individual hyaenas (Stratford et al., 2019).

By studying seasonal and annual variations in space use, conservation managers are better informed with regards to the habitat use requirements of species as conditions change. This information can improve management's effectiveness at supporting the long-term survival of a species (Schofield et al., 2010). For this reason, I explored the annual variation in space use of hyaenas in HiP between 2013 and 2018.

I used the annual 45-day camera trap study data (see Chapter 3) to describe the space use of hyaenas in HiP between 2013 and 2018. Using these data, I:

1) Estimated the average home range size of hyaenas and compared these against the average home range sizes of identified adult females. I tested the hypothesis that adult females use smaller areas compared with the rest of the population.

2) Using the home range estimates of adult females, I estimated the number of clans and their territorial size across HiP.
3) Described annual changes in space use between 2013 and 2018 and tested the hypothesis that space use in hyaenas would decrease with decreasing rainfall but increase with any decrease in prey abundance.
4) Determine any habitat preferences of hyaenas across HiP. I hypothesised that hyaenas would distribute themselves uniformly across vegetation types within HiP.

4.2 Methods

The methodology used to acquire and process the camera trapping data used in this chapter is described in detail in Section 3.2.1 of Chapter 3. More specifically, the dataset used for the spatial analyses was the Right-Hand Side (RHS) independent Capture Histories for all identified individuals. The RHS dataset was selected as it contained both the greatest number of independent captures (1,315 captures versus 1,292), and identifiable individuals (230 versus 212).

4.2.1 Home range estimates

Individuals home range

To estimate the home ranges of hyaenas across my sampled area between 2013 and 2018, I processed the capture histories for all individuals. All individuals that were captured at four or more different trapping localities over the six surveys were filtered out and kept for home range analysis (Welch, 2014). In total, 62 individuals satisfied this criterion. For each individual, a 100% MCP (referred to as “MCP” from here on, unless otherwise stated) or “Convex Hull” was created from the peripheral captures in QGIS (QGIS Development Team, 2020). Using the area for each of these MCPs, I estimated the home range sizes for each individual (Lira & dos Santos Fernandez, 2009; Gil-Sánchez et al., 2011). Capture probability decreases with distance from an individual’s activity centre (Hayne, 1949; Efford, 2004), therefore, there is a low probability that individuals would be captured during the occasional foray beyond their home range, and I thus regarded these home range estimates to be reasonable estimators of overall home range size.

From these 62 individuals, 19 females were successfully identified (Appendix. 4.4). Because of the morphological similarities between males and females (Hamilton et al., 1986), females were identified through the visibility of nipples (Frank, 1986b; Glickman et al., 1992) and other distinguishable features (Frank et al., 1990). The nipple diameter of adult females is significantly greater than males (Glickman et al., 1992) and these large black appendages can be diagnostic (Hofer, 1998). The ventral profile is also generally straighter in females compared with the upward curving profile in males (Frank et al., 1990). The angle, or posture, of individuals within certain images did not allow for a confident determination of sex. Therefore, I was not able to confidently identify all females.

Figure 4.2-1: An example of an individual confirmed as female through identification of large nipples and ventral profile.

The MCP area of these 19 females was averaged to calculate an estimate of average home range size for females. The average home range sizes of the 43 other individuals were also calculated.

Clan territories

For calculating clan territory ranges, I used only adult females, as recommended when combining and comparing space use for social animals (Harris et al., 1990). In the context of hyaenas, because of the matrilineal nature of clan structure and the concentration of females' movements closer to the centre of a clan's territory compared with males (Boydston et al., 2005), the use of female space use patterns to represent clan territorial distribution is further justified.

Using the MCP of the 19 females over the six-year study period, I regarded individuals who had predominantly overlapping MCP to be individuals of the same clan (Kruuk, 1972; Boydston, Kapheim, Szykman et al., 2003). Specifically, 66% of an individual's MCP needed to overlap with another individual for them to be considered part of the same clan (Henschel & Skinner, 1987; Boydston, Kapheim, Szykman et al., 2003). In QGIS, I stitched the convex polygons of these related individuals to create a new polygon that represented a clan's territory over my 2013–2018 study period (Welch, 2014). Given that clan boundaries are largely stable in prey-rich ecosystems (Höner et al., 2005; Trinkel et al., 2006) such as HiP, I expected the polygon created to be a reasonable representation of the spatial distribution of clans across my study area. Using these newly created clan territorial polygons, I estimated territorial size (km^2) and distribution across the trapping grid.

4.2.2 Ecological determinants for space use

Annual space use estimates

To calculate annual estimates of space use for hyaenas, I created a 100% MCP for all individuals captured at more than two camera trap sites per year. These individual MCPs were then averaged within each year to calculate the annual estimated space use of hyaenas over my study period. Outliers were removed if their space use was greater than the largest territorial area identified in 4.2.1.2. No individuals satisfied this criterion and thus space use data from all individuals were included in the GLM analysis below.

General linear model for determinants of space use

I compared the average annual MCPs for hyaenas against two ecological determinants of space use, namely prey abundance (kg prey biomass per km^2) and water availability (average monthly rainfall mm). The prey abundance estimates were the same estimates derived from bi-annual game counts in the park, described in Chapter 3. Rainfall was used as a proxy for water availability in the park, and the annual totals were calculated in the same way as described in Chapter 3.

Using these two variables, I ran a GLM in the R platform (R Core Team, 2020). I ran a global GLM model with both ecological variables included. I compared the AIC$_c$ scores from these respective models to establish which was the best predictor of hyaena space use (Burnham

& Anderson, 2002). Models were considered to have some support relative to the best model if the change in AIC_c score (ΔAIC_c) was less than 10 (Burnham & Anderson, 2002; Shipley, 2013)

4.2.3 Habitat preference

I used the *Design II* approach to analyse habitat selection (Manly et al., 2002) and processed all spatial data and conducted the analysis in QGIS (QGIS Development Team, 2020). This approach compares the actual habitat used versus the expected habitat type use. The expected habitat type use is simply the proportional abundance of each habitat type available to hyaenas. Available habitat for hyaenas was generated by creating a convex hull to incorporate all camera trap localities over the six surveys and cropped using the park's boundary. This area totalled 373 km^2. Using an existing vegetation cover map (EKZNW unpublished data), I broadly categorized habitat types according to vegetation type (Broomhall et al., 2003). This process resulted in five habitat types: forest, grassland, riverbed, thicket and woodland. Grassland and Riverbeds were, however, removed from the habitat preference analysis. These habitats were removed because they covered only a very small area of the study site, and small values can disproportionately influence habitat selection analyses (Zar 1999; Manly 2002). Hyaena habitat use was calculated as the proportion of habitat existing within each individual's home range MCP (Roy & Dorrance, 1985; Broomhall et al., 2003). The summed area (km^2) of each habitat used, and the total MCP area for all 62 individuals between 2013 and 2018, were calculated to determine proportional habitat use for each habitat type. I followed the same process with the subset of the 19 confirmed females.

To calculate whether hyaenas displayed habitat preferences, I ran a chi-square goodness-of-fit test in R (R Core Team, 2020) between the expected habitat use and the observed use (Broomhall et al., 2003; Welch, 2014).

4.3 Results

4.3.1 Home range estimates

Individuals' home ranges between 2013 and 2018

Based on 727 photographic captures, the mean home range size for all 62 individuals captured at a minimum of 4 localities between 2013 and 2018 was 21.65 km^2 (SD: ±18.37) (Appendix 4.1). By contrast, the 19 females had a mean home range size of 18.13 km^2 (SD: ±11.18), based on 256 captures. The females' home range distributions are presented in Figure 4.3-1.

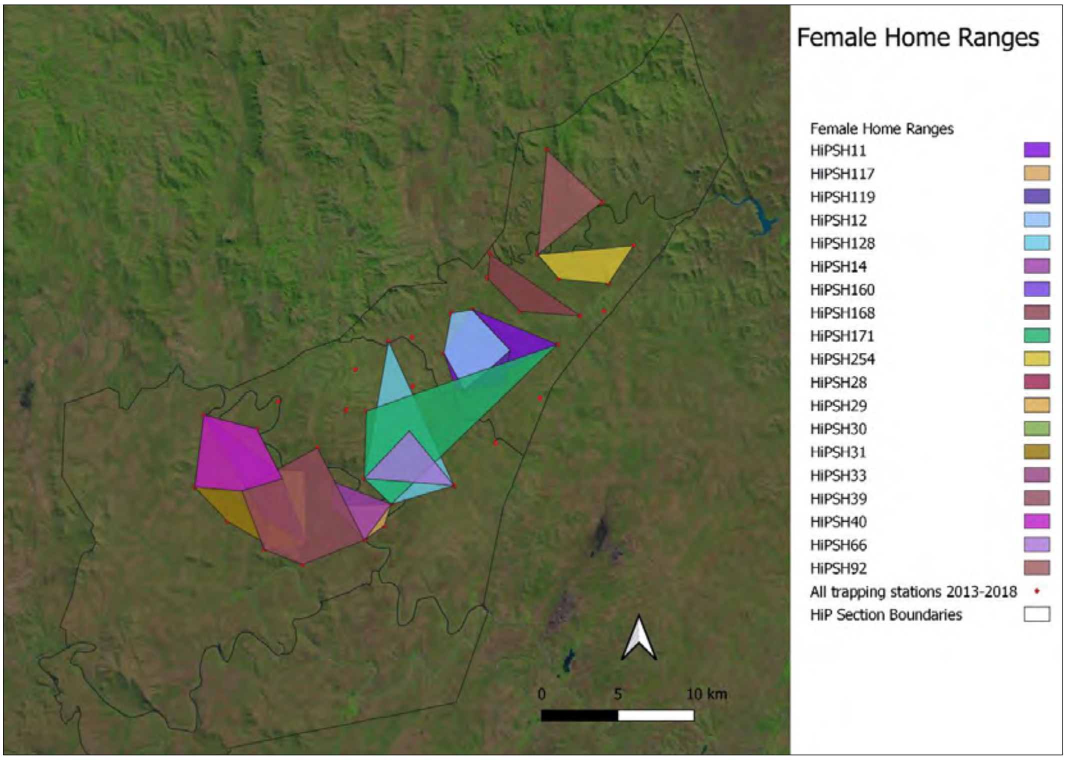


Figure 4.3-1: Females' 100% MCPs for individual captures at more than three localities between 2013 and 2018.

Clan territories

All 19 females appeared to be divided into seven distinct clans (Figure 4.3-2). Only the Nselweni and Upper Mbhuzane clans and the Central Masinda and Lower Nqumeni clans had overlapping boundaries (Figure 4.3-2). The Upper Mbhuzane clan overlapped by 25% with Nselweni's polygon; however, this is likely an overestimate due to the small size of the Nselweni territory, and its position at the periphery of the trapping array (Figure 4.3-2).

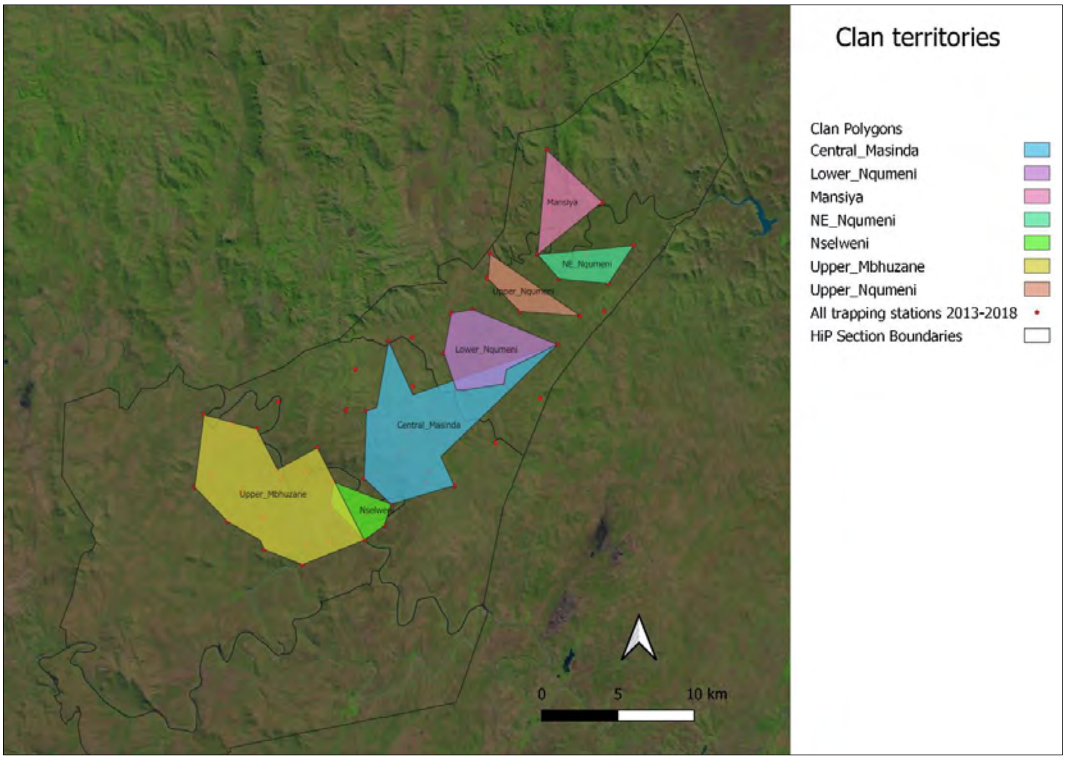


Figure 4.3-2: Clan territorial distributions based on overlapping female home ranges between 2013 and 2018.

Territory sizes ranged from 8.37 to 61.57 km^2 with an average territory size of 25.76 km^2 (SD: ±21.17) across the sampled area. The number of female home ranges that were used for each clan territory ranged from one to eight individuals. Hluhluwe clan territories seemed to be smaller than those in the iMfolozi section (Table 4.3-1), averaging 13.96 km^2 (SD: ±6.48) compared to 34.61 km^2 (SD: ±23.87) in iMfolozi. Nselweni had the smallest clan territory, but it lies on the periphery of camera trapping grid array, and likely extends beyond this area.

Table 4.3-1: A summary of clan territories, their location, size and the number of individuals used to establish the approximate territorial boundaries.

Sample size	***Clan***	***Area km^2***	***Section***	***Average***
1	NE Nqumeni	9.731	Hluhluwe	13.96 (SD: ±6.48)
3	Lower Nqumeni	23.106	Hluhluwe	
1	Upper Nqumeni	9.032	Hluhluwe	
1	Mansiya	13.485	iMfolozi	34.61 (SD: ±23.87)
3	Central Masinda	55.039	iMfolozi	
2	Nselweni	8.368	iMfolozi (Cropped)	
8	Upper Mbhuzane	61.565	iMfolozi	
19	Total			25.76 (SD: ±21.17)

4.3.2 Ecological determinants of space use

Annual space use estimates

From the annual 100% MCP space use analysis for individuals captured at three or more camera trap sites in one year (Table 4.3-2), the space used by individuals was greatest in 2015.

Table 4.3-2: Average space use (km2) and standard deviation of individuals captured on 3 or more camera traps in any given 45-day survey.

	2013	**2014**	**2015**	**2016**	**2017**	**2018**
Average 100% MCP Space Use (km^2)	7.54 (±2.61)	7.46 (±10.15)	10.84 (±7.16)	4.81 (±3.60)	7.65 (±10.58)	6.88 (±5.32)

Determinants of space use

Prey availability and rainfall contributed to model selection when independently incorporated as ecological determinants for space use (Appendix 4.3), but not when combined. Although both variables were positively correlated with space use, neither of these variables were significant determinants (P >0.05; Table 4.3-3).

Table 4.3-3: General linear model parameters for models including one determinant variable, namely, rainfall and prey abundance.

Model	***Parameters***	***Estimate***	***Std Error***	***t value***	***P***
Rainfall					
	Intercept	6.864	3.782	1.815	0.144
	Rainfall	0.014	0.076	0.181	0.865
Prey					
	Intercept	-0.924	12.660	-0.073	0.945
	Prey abundance	0.002	0.003	0.669	0.540

Although not significant, both variables showed positive correlation with space use in hyaenas (Table 4.3-3).

4.3.3 Habitat preference

The chi-square goodness-of-fit test for all 62 individuals, and the subset of 19 females, showed that hyaenas did not use the landscape uniformly, but rather selectively (P <0.05; Table 4.3-

4). Both groups showed a preference for woodland habitat. All other habitat types were used at less than the expected frequencies (Table 4.3-4).

Table 4.3-4: Chi-square goodness-of-fit analysis of habitat use versus availability for 62 hyaenas, and a subset of confirmed 19 females. Expected and observed habitat values are the accumulative km² across all MCP home ranges.

		Forest	***Thicket***	***Woodland***	X^2	***df***	***P***
19 Females							
	Expected	49.15	114.02	178.94	13.21	2	<0.01
	Observed	44.31	86.21	211.60			
62 Individuals							
	Expected	190.80	442.57	694.59	56.72	2	<0.01
	Observed	172.38	328.14	827.44			

4.4 Discussion

Understanding the space use of carnivores is integral for improving the conservation management of these species (Woodroffe & Ginsberg, 1998; Johansson et al., 2016). Using capture-recapture methodology to better understand the space use of mammals has been used for more than 70 years (Hayne, 1949). With the advent of improved camera trapping technology, this non-invasive means of gathering spatial data has become common (Karanth & Nichols, 1998; Royle, Nichols et al., 2009; Efford, 2011). However, home range estimates, habitat preference and space use studies have preferred to use GPS telemetry data for fine-scale analyses (Karanth et al., 2010; Périquet et al., 2010; Stratford & Stratford, 2011). Nevertheless, there are many instances where collaring individuals is not possible nor ideal for specific studies. Collars might not be used in some instances because it is prohibitively expensive to track only a few individuals (Jones & Sherman, 1983). A non-invasive, cost-effective, individual- and population-level approach to space use studies can, however, be achieved through camera trap surveys (Gil-Sánchez et al., 2011), specifically for individually recognisable cryptic carnivores (Gil-Sánchez et al., 2011; Srivathsa et al., 2017). Nevertheless, estimating home range and space use from camera trap recapture data has limitations, as it is restricted by the camera trap array (Lira & dos Santos Fernandez, 2009), and imperfect detection across the study site (Hayne, 1949; Efford, 2004). Therefore, results should be interpreted with caution.

4.4.1 Home ranges and clan territories

Home range size estimates for hyaenas in my study were similar to historical studies for the species in HiP (Whateley & Brooks, 1978; Whateley, 1981). However, a substantial variance was observed for these estimates, with a standard deviation of ±18.37 km^2 for a mean home range of 21.65 km^2. This was expected for two reasons. Firstly, the MCP approach capture-recapture data to estimate space use is known to have high variance (Lira & dos Santos Fernandez, 2009), and secondly, variation in spatial behaviour occurs between sex groups and differences in social ranks (Holekamp, Smale et al., 1997; Boydston, Kapheim, Szykman et al., 2003; Kolowski et al., 2007). Despite the separation of females from the rest of the population, a high variance was still observed.

Analysis of the home range sizes of identified females versus the rest of the population revealed that the mean home range size of identified females was approximately 22% smaller than the rest of the population. Interestingly, although high variance was observed for both groups, there was less variation in the home range estimates for identified females (11.18 km^2 standard deviation on a mean of 18.13 km^2) when compared with the rest of the population (20.58 km^2 standard deviation on a mean of 23.20 km^2). Since members of the same class within a population are likely to maintain similar space use patterns (Harris et al., 1990), and the group of 43 individuals included not only males, but those females I was unable to sex, this finding is unsurprising.

Females with cubs have smaller home ranges than those without (Boydston, Kapheim, Szykman et al., 2003). However, the identified females in my study were not all reproductively active and thus did not necessarily have smaller home ranges simply because of dependent cubs. The use of nipples to identify the sex of hyaenas does not exclusively represent reproductively active females, as female nipples are already twice the diameter of adult male nipples before they are reproductively active (Glickman et al., 1992). Therefore, it is plausible that both clan and site fidelity in females (Henschel & Skinner, 1987; Kruuk, 1972), along with den dependence, may have contributed towards lower space use in females in HiP.

Female hyaenas generally have a strong site fidelity in rich resident prey systems (Kruuk, 1972; Höner et al., 2005) and overlap in space use between individuals within a clan has been shown to be no less than 66% (Henschel & Skinner, 1987; Boydston, Kapheim, Szykman et al., 2003). I successfully used female home ranges and overlapped associated individuals to create a realistic distribution map of seven clan territories across my 378 km^2 study area in HiP. A similar methodology has been used previously for brown hyaenas (Welch, 2014), but this is the first-time long-term camera trapping data have been successfully used to outline hyaena clan territories. As a result of the temporal stability in clan territorial size and location that is expected for a hyaena population in a resident and prey rich system (Höner et al., 2005; Trinkel et al., 2006), information on the location and size of hyaena territories is important for both the long-term ecological management of HiP and the species itself (Ryan & Jamieson, 1998).

Clan territory size averaged 25.76 (±21.17) km^2 across my study site. These estimates are comparable with other studied populations such as the Ngorongoro Crater, where clans occupy 23.8 - 27.6 km^2 (Kruuk, 1972; Höner et al., 2005), and the Amboseli and Aberdare National Parks' clans who occupy territories of 27 and 32 km^2, respectively (Sillero-Zubiri & Gottelli, 1992; Watts & Holekamp, 2008). Both unpublished GPS collar data from EKZNW, and the historical work of Whateley and Brooks (Whateley & Brooks, 1978; Whateley, 1981) in the park agree with the findings of my study. More specifically, clan territories in the 1970s were estimated to be between 13 and 39 km^2 by Brooks and Whateley. In 2020, a 95% MCP generated from GPS telemetry data from 2 collared individuals produced home range estimates of 25.46 km^2 and 16.15 km^2 (EKZNW unpublished data) over 11 and 5-month periods, respectively.

Despite confidence that territory size estimates are reasonable, it is worth noting that every clan boundary has peripheral points on the outermost traps of the camera trap array. What this might indicate is that because of the shape and extent of the trapping array, the territorial estimates are not completely representative of true clan territories (Lira & dos Santos Fernandez, 2009). Lira and dos Santos Fernandez (2009) recommended only using recapture techniques for home range estimates over multiple years and over a large area. My study achieved both criteria by pooling the 6 camera trapping surveys, and including a trapping array that spanned 10 times the known home range size estimate for hyaenas within HiP (Whateley, 1981).

Dividing clans into those north of the corridor road (Hluhluwe) and those south (iMfolozi), I found that territory sizes were 13.96 (±6.48) km^2 and 34.61 (±23.87) km^2, respectively. The high variation found in iMfolozi is probably due to a heavily clipped clan boundary of the Nselweni Clan (Figure 4.3-2). Nevertheless, the historical estimates from the 1970s of 13 km^2 in Hluhluwe (Whateley & Brooks, 1978) and 39 km^2 in iMfolozi (Whateley, 1981) are remarkably similar to my study. Interestingly, the trends observed in territory size followed two ecological gradients across the survey area. Firstly, annual rainfall is greatest in the Hluhluwe section and decreases into the iMfolozi section, ranging from 920 to 490 mm, respectively (Davies et al., 2021). Secondly, gross primary productivity increases into Hluhluwe from iMfolozi (Davies et al., 2021). The trends in lion density across HiP also follow a similar gradient, with iMfolozi hosting the greatest density compared to Hluhluwe (Pers. Comm. Park Ecologist – Dave Druce, 2021).

Nevertheless, the spatial behaviour of prey and predators across a multi-prey/multi-predator landscape is complex and cannot easily be summarised or attributed to just one or two factors, but rather a combination of interacting dynamics (Davis et al., 2021). Factors such as vegetation cover, food availability and predator avoidance also all influence the dispersion of prey across HiP (Davies et al., 2021). Since prey dispersion is such an integral part in space use for hyaenas (Mills, 1990; Trinkel et al., 2004), this is an important variable that needs to be more closely investigated when attempting to better understand space use in the future. Future studies may investigate fine scale space use of hyaenas in relation to the distribution of their prey, and possible changes in feeding strategies to improve our understanding of the variations in territory size identified in this and previous studies on HiP (Whateley & Brooks, 1978; Whateley, 1981). In this regard, it is worth noting that since Whateley and Brooks work in the late 1970s, the prey structure has changed from being predominantly medium to small prey species, to now being dominated by larger herbivores such as buffalo, elephant and rhino (Le Roux et al., 2017).

4.4.2 Ecological determinants for space use

Seasonal variation in space use is not considered in my study as all data were captured annually over 45-day periods during the autumn months. This approach limits my ability to infer patterns in annual space use.

Neither of the two factors I tested against space use showed any significant influence. Nevertheless, the positive relationship observed between rainfall and space use aligns with my hypothesis that, because of the dispersion of prey across the landscape (Mills, 1990), hyaenas may increase their space use in response to increased water availability across HiP. Although this finding was not statistically supported, the observed trend may aid in future investigations with a larger dataset.

The annual 100% MCP's created during the 45-day period were indicative of space use rather than home range extent (Péron, 2019). The greatest average space use for any given year was 10.84 (±7.16) km^2 in 2015, which is half of the average home range size calculated over the six surveys (21.65 km^2). Welch (2014) showed that the 100% MCP's generated for brown hyaena individuals from 107 days of camera trap data was 37% (±17%) of the 95% MCP generated from their respective collar data over a greater than 9-month period (Welch, 2014).

The annual space use results in my study followed a similar trend of being approximately a third of the estimated territories. This large difference between the areas used in one survey versus over six surveys, highlights the importance of long-term datasets and understanding space use in context (Péron, 2019).

4.4.3 Habitat preference

Hyaenas within my study seemed to show a preference for woodland habitat. The distribution of prey across the landscape of HiP may play a significant role in this observed preference (Davies et al., 2021), and future studies should investigate to what extent this is true. Female space use is largely centred around den sites (Kruuk, 1972; Kolowski & Holekamp, 2009), and thus the trends observed for habitat use in my study may also be closely linked to den site selection. Additionally, with human persecution of hyaenas occurring around the periphery of HiP (Pers. Comm. Park Ecologist – Dave Druce, 2021), increased cover might be favoured by hyaenas within the park in response to this persecution (Boydston, Kapheim, Watts et al., 2003).

4.4.4 Conclusion

In conclusion, I have shown that long-term camera trapping datasets can be useful in better understanding space use behaviour of hyaenas. Although I did not find any definitive ecological determinant for space use in my study, hyaenas used woodlands preferentially over other habitats. Finally, I successfully used camera trapping data to establish estimates of both territory and home range of hyaenas within HiP. I found that the home ranges of identified females were smaller than for the rest of the population, and clan territories varied substantially across the landscape. However, since the late 1970s, clan territory size does not seem to have changed. I recommend further investigations into better understanding the spatial behaviour of this important hyaena population.

CHAPTER 5 – PROJECT SYNTHESIS AND MANAGEMENT IMPLICATIONS

5.1 Project synthesis

Advances in technology over the past 30 years have provided conservationists with monitoring and surveillance tools previously inaccessible to them, including camera traps. With progressive advancements in the approaches available for analysing camera trap data (Karanth & Nichols, 1998; Efford, 2004; Royle, Nichols et al., 2009), camera trap surveys are becoming a dominant feature of vertebrate population monitoring throughout the world (Burton et al., 2015). This remote surveillance technique is similarly being used for behaviour studies (Caravaggi et al., 2017). Although many camera trapping surveys are focused on specific species (Mann, Smyth et al., 2020), the use of by-catch data to gain insights into the ecology of non-target species is also increasingly being conducted (Linkie et al., 2013; Mazzamuto et al., 2019; Williams et al., 2020). My study has used these technological advances and the availability of by-catch data to produce reliable spotted hyaena density estimates for the HiP in South Africa. Furthermore, I effectively used photo-capture histories over a 6-year period to investigate the space use of hyaenas within the park for the first time in 40 years (Whateley, 1981). Although the use of capture-recapture records from camera traps to produce home range estimates for individually recognisable predators has been done before (Gil-Sánchez et al., 2011; Srivathsa et al., 2017), this is the first time the technique has been used for spotted hyaenas.

In Chapter 3 of my study, I outlined and presented the SECR analytic approach to establishing hyaena density estimates from camera trap data. The number of new individual hyaenas that were identified in most years plateaued by survey night 45, and the high number of hyaena capture events and individual hyaenas identified indicates that the trapping design was appropriate for maximising hyaena capture probability (Tobler & Powell, 2013). However, if home range size is less than 25 km^2 in parts of HiP, as suggested by previous work (Whateley & Brooks, 1978) and my study (Chapter 4), then I would recommend that future trapping arrays have individual cameras separated by no more than 2 km (based on a ±12.57 km^2 home range) as opposed to the 2.3 km average used in this study. In addition, the total area covered may be reduced to improve camera distance issues, but still retain coverage multiple times the size of the average home range. Moreover, further research should use GPS collars to investigate detailed home range behaviour of hyaenas to understand the prevalence of missed captures and whether small home ranges impact upon capture probability and resultant density estimates.

I also compared the SECR estimates of density with those determined through the more traditional call-up methodology. The call-up estimates were consistently lower than those calculated from the more conservative camera trapping. My study showcased the consequences of not regularly calibrating the response probability factor used in density calculations using call-up data (Mills et al., 2001; Graf, 2008; Cozzi et al., 2013). Future monitoring efforts should take heed of these observations and ensure that calibration is done regularly. Although the call-up method is well used, and seemingly cost-effective compared to initiating camera trap surveys, the additional periodic experimentation needed for calibrating response probability makes this approach less practical than using existing data from an appropriately designed camera trap survey. For this reason, reserve managers, ecologists and researchers need to strike a balance between being pragmatic with the resources available and ensuring long-term, comparable density estimates.

Chapter 4 effectively used recapture data of individuals to not only establish annual variation in space use of hyaenas, but to also represent the distribution of clan territories across the survey grid. Of particular interest was the observed trend in spatial use between hyaenas in the Hluhluwe and iMfolozi sections. This trend of very small clan territories in the Hluhluwe section and larger territories in iMfolozi matches previous work in the park (Whateley & Brooks, 1978; Whateley, 1981). Further research should look more closely at this apparent gradient of variation in space use across the park and investigate which factors might be influencing this trend (Tilson & Henschel, 1986; Mills, 1990; Macdonald & Johnson, 2015).

5.2 Conservation management implications and recommendations

Hyaenas are in global decline (Bohm & Höner, 2015), and regional population estimates are poor across South Africa (Hunnicutt et al., 2016). It is important for the long-term successful conservation management of the species that improved, scientific and cost-effective monitoring efforts are coordinated across the region. Additionally, hyaenas are increasingly becoming a target species for trophy hunters in KZN (Pers. Comm. EKZNW Animal Scientist – Brent Coverdale, 2021), and incidental snare poaching continues to persist (Hunnicutt et al., 2016). The impact of these threats to hyaenas in the province is unknown, but a concerted effort needs to be made to better understand population trends, genetic connectivity, and the behavioural and demographic consequences of current offtakes.

Through my study, I have provided a clear outline and example of how existing monitoring programmes for leopards across KZN (Mann, Smyth et al., 2020) can generate hyaena density estimates across surveyed sites. The method is cost-effective and allows for reliable comparisons of density trends over time. As progress is made with further development of automated pattern recognition software (Crall et al., 2013), the person hours required for processing and analysing this by-catch data will become markedly reduced. By using existing surveys effectively in collaboration with partners across South Africa (Williams et al., 2020; Weyde et al., 2021; Mann, Smyth et al., 2020), we can obtain improved national and provincial estimates for hyaenas.

In addition to density estimates, a concerted effort should be made to understand genetic integrity and connectivity of populations residing in fenced reserves of KZN (Naude et al., 2020) through genetic studies. As with leopards, inbreeding of these “free roaming” carnivores may be greater than anticipated (Naude et al., 2020). Advances in hyaena genetic sequencing over the years (Wilhelm et al., 2003; Yang et al., 2020) has improved our ability to better understand the genetic landscape of this species. Genetic studies into relatedness have been undertaken previously through cross sectional analysis between clans and longitudinal analysis within clans (Van Horn et al., 2004). Using the sampling and analysis methodologies outlined by Van Horn et al. (2004), hyaenas across multiple protected areas should be sampled in order to understand relatedness. Efforts should also be made to sample hyaenas from different regions across South Africa and map the genoscape of the species, which will better inform national and regional conservation decisions with regards to translocation (Mills, 1998a), which has been taking place since the early 2000s (Hayward, Adendorff et al., 2007).

Furthermore, should inbreeding be shown to be a feature of the KZN population of hyaenas, studies should look into improved understanding of natal dispersal of hyaena across this landscape (Fattebert et al., 2015). By expanding our knowledge of the connectivity of the KZN hyaena population and identifying possible barriers to dispersal, landscape-level planning can be made to improve linkages between subpopulations.

Although some management interventions have taken place to reintroduce the species into parts of South Africa (Hayward, Adendorff et al., 2007), the species has largely been left unmanaged, with only culling operations representing population-level interventions (Ferreira & Funston, 2016). As hyaena populations become more fragmented, their numbers decline, and pressures increase from human–wildlife conflict, poaching and hunting offtakes, it would be advisable to implement management zones as has been done for leopards (Pitman et al., 2015), and take a conservative approach (Mills, 1998a) whilst implementing well-informed offtake strategies for both damage causing animals, trophy hunting and relocations (Pitman et al., 2015).

The guidelines and implementation of different offtake strategies for large carnivores can significantly influence population demographics (Packer et al., 2009). In addition, for a socially complex species such as the hyaena, lethal clan disruption can cause clan fission and have ramifications for space use (Holekamp & Dloniak, 2010). It is, therefore, vital that all possible outcomes of different offtake guidelines be understood so that recommendations in this regard can produce the best possible outcome for the species, ecological functioning and human–wildlife conflict mitigation.

Ultimately, investment into improving population monitoring and offtake and reintroduction strategies will aid in the long-term conservation of the species and in a more prudent use of conservation resources (Lindsey et al., 2005). For a population in decline, and under increasing pressure outside of protected areas, conservationists need to rather ensure investment now rather than when the species finds itself completely isolated to protected areas, requiring expensive intervention and management.

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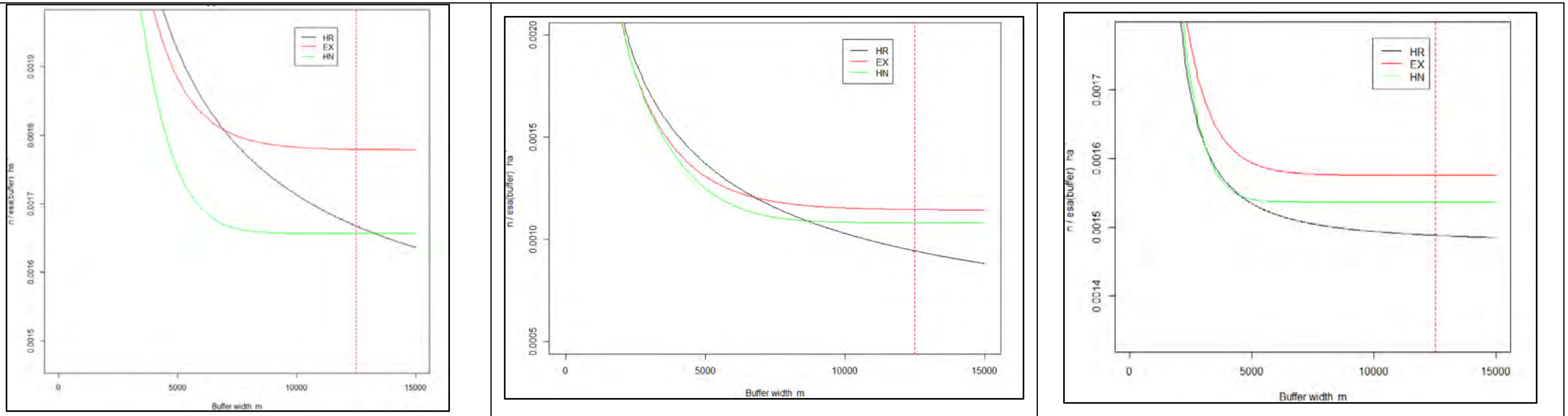
APPENDICES

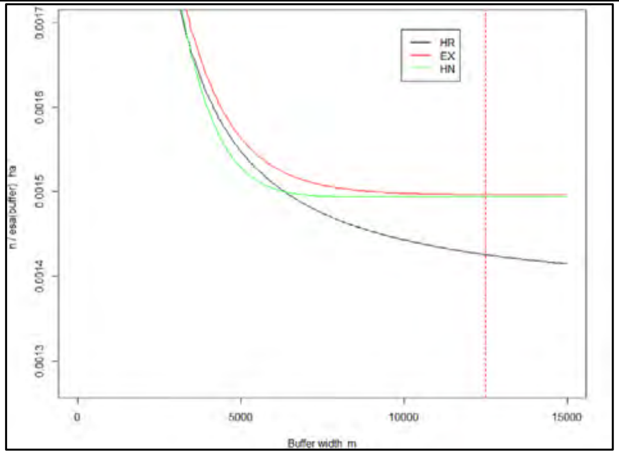
Appendix 3.1: The visual testing of the functions' respective sensitivity to change in density estimates beyond the 12,500m buffer width (red dotted line). The estimates derived from the Hazard Rate function were shown to be sensitive to change beyond the buffer in 2014, 2015, 2016, 2017 and 2018.



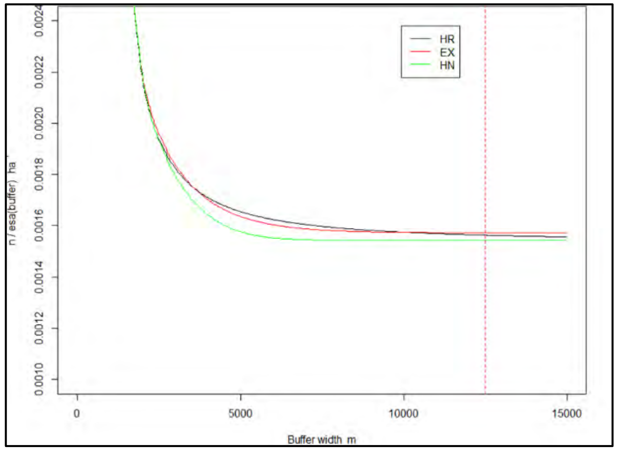
2014

2015

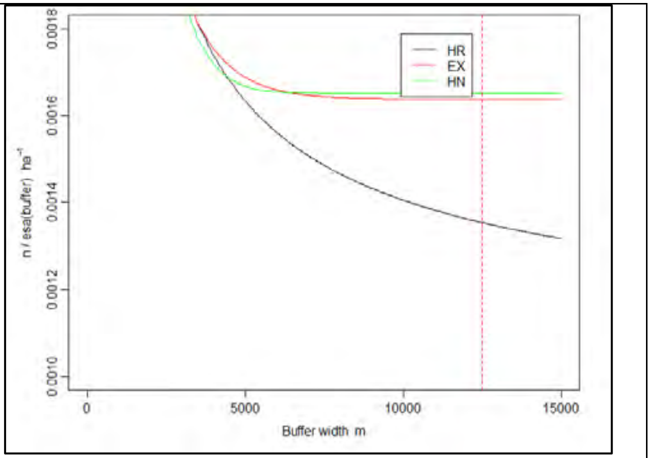
2016



2017 – 12,500m



2017 – Fenced



2018

Appendix 3.2: Prey availability for spotted hyaenas in HiP, 2012–2018.

Year	Species	Biomass (kg)	Density Hlu	Total Density Hlu	Proportionate Density Hlu	Density Imf	Total Density Imf	Proportionate Density Imf	Density HiP	Total Density HiP	Proportionate Density HiP
2012	Buffalo	432	7.21	22.10	32.62	5.59	31.70	17.63	6.08	28.80	21.11
2012	Duiker, Grey	16	0.71	22.10	3.23	0.54	31.70	1.71	0.59	28.80	2.06
2012	Impala	30	3.46	22.10	15.63	16.60	31.70	52.39	12.63	28.80	43.87
2012	Kudu	135	0.64	22.10	2.91	0.93	31.70	2.92	0.84	28.80	2.92
2012	Nyala	47	6.40	22.10	28.94	2.98	31.70	9.40	4.01	28.80	13.93
2012	Warthog	45	0.91	22.10	4.10	1.55	31.70	4.88	1.35	28.80	4.70
2012	Wildebeest	135	0.40	22.10	1.83	1.70	31.70	5.37	1.31	28.80	4.55
2012	Zebra	175	2.37	22.10	10.74	1.81	31.70	5.70	1.98	28.80	6.87

Year	Species	Biomass (kg)	Density Hlu	Total Density Hlu	Proportionate Density Hlu	Density Imf	Total Density Imf	Proportionate Density Imf	Density HiP	Total Density HiP	Proportionate Density HiP
2014	Buffalo	432	9.85	24.18	40.74	5.26	30.77	18.74	6.65	28.78	23.11
2014	Duiker, Grey	16	0.87	24.18	3.59	0.87	30.77	3.11	0.87	28.78	3.03
2014	Impala	30	2.79	24.18	11.54	17.20	30.77	61.21	12.84	28.78	44.63
2014	Kudu	135	0.46	24.18	1.90	0.67	30.77	2.39	0.61	28.78	2.11
2014	Nyala	47	6.78	24.18	28.03	2.57	30.77	9.16	3.84	28.78	13.35
2014	Warthog	45	0.90	24.18	3.71	1.51	30.77	5.39	1.33	28.78	4.61
2014	Wildebeest	135	0.40	24.18	1.66	1.23	30.77	4.37	0.98	28.78	3.40
2014	Zebra	175	2.13	24.18	8.83	1.45	30.77	5.15	1.66	28.78	5.75

Year	Species	Biomass (kg)	Density Hlu	Total Density Hlu	Proportionate Density Hlu	Density Imf	Total Density Imf	Proportionate Density Imf	Density HiP	Total Density HiP	Proportionate Density HiP
2016	Buffalo	432	8.43	25.76	32.73	4.71	30.75	15.32	5.83	29.24	19.95
2016	Duiker, Grey	16	1.04	25.76	4.04	0.69	30.75	2.25	0.80	29.24	2.73
2016	Impala	30	5.29	25.76	20.55	20.04	30.75	65.15	15.58	29.24	53.28
2016	Kudu	135	0.55	25.76	2.13	0.79	30.75	2.58	0.72	29.24	2.46
2016	Nyala	47	7.82	25.76	30.35	1.87	30.75	6.07	3.66	29.24	12.53
2016	Warthog	45	0.98	25.76	3.80	0.99	30.75	3.21	0.98	29.24	3.36
2016	Wildebeest	135	0.30	25.76	1.16	0.82	30.75	2.68	0.66	29.24	2.27
2016	Zebra	175	1.35	25.76	5.24	0.84	30.75	2.74	1.00	29.24	3.41

Year	Species	Biomass (kg)	Density Hlu	Total Density Hlu	Proportionate Density Hlu	Density Imf	Total Density Imf	Proportionate Density Imf	Density HiP	Total Density HiP	Proportionate Density HiP
2018	Buffalo	432	6.69	24.41	27.40	4.34	30.85	14.08	5.05	28.90	17.48
2018	Duiker, Grey	16	0.66	24.41	2.68	0.91	30.85	2.94	0.83	28.90	2.87
2018	Impala	30	4.28	24.41	17.55	18.57	30.85	60.21	14.26	28.90	49.33
2018	Kudu	135	0.36	24.41	1.46	0.43	30.85	1.41	0.41	28.90	1.42
2018	Nyala	47	9.07	24.41	37.17	2.13	30.85	6.91	4.23	28.90	14.63
2018	Warthog	45	1.32	24.41	5.43	1.93	30.85	6.27	1.75	28.90	6.06
2018	Wildebeest	135	0.20	24.41	0.80	0.77	30.85	2.49	0.59	28.90	2.06
2018	Zebra	175	1.83	24.41	7.51	1.76	30.85	5.70	1.78	28.90	6.16

Appendix 3.3: Population Estimates for hyaenas in HiP between 2013 and 2018 based on 12,500m, Clipped 12,500m and Fenced ETA approaches.

Approach	Year	ETA_km^2	Density Per 100km^2	Population	LCL_Density	UCL_Density	LCL_Population	UCL_Population
12,500m	2018	1,794.00	18.26	328	14.73	22.63	264	406
Clipped 12,500m	2018	1,356.00	19.01	258	15.39	23.46	209	318
Fenced	2018	863.00	22.24	192	18.13	27.28	156	235
12,500m	2017	1,793.00	14.96	268	11.62	19.26	208	345
Clipped 12,500m	2017	1,355.50	15.61	212	12.21	19.96	166	271
Fenced	2017	863.25	18.49	160	14.58	23.44	126	202
12,500m	2016	1,793.25	15.69	281	11.61	21.22	208	381
Clipped 12,500m	2016	1,355.25	15.85	215	11.75	21.39	159	290
Fenced	2016	863.25	17.28	149	12.94	23.07	112	199
12,500m	2015	1,792.50	11.47	206	8.87	14.85	159	266
Clipped 12,500m	2015	1,354.75	12.77	173	10.06	16.20	136	219
Fenced	2015	863.25	16.81	145	13.44	21.01	116	181
12,500m	2014	1,792.50	17.87	320	14.44	22.12	259	397
Clipped 12,500m	2014	1,354.75	18.56	251	15.04	22.90	204	310
Fenced	2014	863.25	21.88	189	17.85	26.82	154	232
12,500m	2013	1,869.50	18.43	345	13.93	24.39	260	456
Clipped 12,500m	2013	1,381.25	18.53	256	14.08	24.39	194	337
Fenced	2013	893.50	21.82	195	16.88	28.21	151	252

Appendix 3.4: Inputs used for determinants of hyaena density (per 100 km^2) through the GLM. Prey as a determinant for each year was the preceding year's estimate (kg per km^2). Rainfall was the monthly average (mm) for year ending in June of the year for which the estimate was entered. Lion density (per 100 km^2) was also estimated from the preceding year of respective entries. Hyaena density estimates were those pulled from 12,500m Clipped ETA SECR results, and 2015 estimate was an average of 2014 and 2016.

Year	Hyaena density	Prey	Rainfall	Lion density
2013	18.53	3,974.11	70.68	12.28
2014	18.56	4,032.21	52.05	12.17
2015	17.21	3,812.66	36.14	12.28
2016	15.85	3,593.10	39.49	11.94
2017	15.61	3,482.03	49.33	11.83
2018	19.01	3,370.97	58.77	7.81

Appendix 3.5: Model selection table for different combinations of determinant variables for hyaena density. Models were selected based on the Akaike Information Criteria for small samples (AIC$_c$). The ΔAIC$_c$ in relation to the best fitting model was used to attribute weight for each respective model. The models that had a ΔAIC$_c$ of less than 10 were considered to have some support towards representing the data.

	Intercept	Lion	Prey	Rain	AICc	dAICc	Weight
Intercept	17.46				28.6	0	0.948
Rain	13.68			0.07404	35.4	6.86	0.031
Lion	21.62	−0.3651			37.3	8.73	0.012
Prey	10.38		0.001908		37.8	9.22	0.009
Lion + Prey	4.888	−1.063	0.006649		44.4	15.81	0
Rain + Lion	16.87	−0.24		0.06517	64.6	36.03	0
Prey + Rain	9.04		0.001321	0.06895	64.8	36.26	0
Rain, Prey + Lion	6.559	−0.992	0.00622	0.01337	Inf	Inf	0

Appendix 3.6: Summary of hyaena density estimates for Hluhluwe and iMfolozi sections. The SECR analysis took place against a 12,500m ETA of respective sections. LCL = Lower Confidence Limit. UCL = Upper Confidence Limit. Estimates are measured in hyaena per 100 km^2.

Year	Hluhluwe Density	Hluluwe LCL	Hluhluwe UCL	iMfolozi Density	iMfolozi LCL	iMfolozi UCL
2013	24.06	14.14	40.94	22.34	16.56	30.15
2014	13.47	8.89	20.42	25.3	19.78	32.37
2015	10.63	6.39	17.7	8.67	6.19	12.13
2016	8.12	4.36	15.13	23.31	16.43	33.1
2017	10.64	6.1	18.55	17.98	13.21	24.46
2018	12.62	8.68	18.36	22.68	17.25	29.84
Mean	13.26	8.09	21.85	20.05	14.90	27.01
Stdev	5.12	3.12	8.68	5.54	4.34	7.21

Appendix 3.7: Hyaena mortalities reported annually in HiP between 2012 and 2018. These data were collected from field rangers, section rangers, researchers and monitoring teams.

Cause of hyaena deaths in HiP				
Year	Injury	Poaching	Roadkill	Unknown
2012	1		1	2
2013		1	2	1
2014		1		8
2015				1
2016		1		
2018		1		1
2019		1		1

Appendix 4.1: Table of 100% MCP Home Range areas for hyaenas in HiP between 2013 and 2018 that were captured at more than three different localities during the six surveys.

43 Others		Captures	19 Confirmed Females		Captures
Identity	Area (km^2)		Identity	Area (km^2)	
HiPSH116	12.95	15	HiPSH11	20.19	18
HiPSH124	39.19	67	HiPSH117	5.35	12
HiPSH125	45.28	8	HiPSH119	14.28	10
HiPSH130	6.94	7	HiPSH12	13.25	26
HiPSH131	39.24	41	HiPSH128	31.39	12
HiPSH136	23.09	10	HiPSH14	7.68	20
HiPSH139	43.48	13	HiPSH160	13.46	10
HiPSH143	18.45	8	HiPSH168	9.03	5
HiPSH153	10.84	6	HiPSH171	45.78	5
HiPSH156	7.74	4	HiPSH254	9.73	5
HiPSH157	89.17	10	HiPSH28	21.38	15
HiPSH16	20.72	12	HiPSH29	11.66	11
HiPSH17	12.95	7	HiPSH30	9.69	11
HiPSH184	12.30	5	HiPSH31	37.40	14
HiPSH195	51.89	7	HiPSH33	14.44	8
HiPSH199	5.27	16	HiPSH39	36.59	28
HiPSH20	8.63	6	HiPSH40	19.90	18
HiPSH204	14.60	9	HiPSH66	9.85	10
HiPSH205	7.99	5	HiPSH92	13.48	18

HiPSH206	14.14	6			
HiPSH21	2.31	5			
HiPSH222	8.86	15			
HiPSH23	20.73	7			
HiPSH234	8.62	7			
HiPSH236	27.27	9			
HiPSH237	12.01	6			
HiPSH24	28.41	20			
HiPSH25	12.86	7			
HiPSH26	17.09	10			
HiPSH262	22.76	5			
HiPSH292	5.58	8			
HiPSH315	11.00	6			
HiPSH38	35.12	12			
HiPSH381	10.08	4			
HiPSH42	34.02	14			
HiPSH67	13.92	13			
HiPSH68	51.11	12			
HiPSH71	8.63	9			
HiPSH73	24.50	5			
HiPSH8	34.05	11			
HiPSH85	5.59	6			
HiPSH87	17.00	13			
HiPSH94	101.19	5			
Group Mean	23.20 (SD: ±20.58)			18.13 (SD: ±11.18)	
Total Captures		471			256
Total Mean	21.65 (SD: ±18.37)				

Appendix 4.2: Table of inputs used in the GLM analysis of space use. Hyaena density was established in Chapter 3 and both rainfall and prey abundance records were described in Chapter 3.

Year	Hyaena Density (per 100 km^2)	Prey (per km^2)	Rainfall (Monthly average mm)	Mean Space Use (km^2)
2013	18.53	3,974.11	68.66	7.54
2014	18.56	4,032.21	54.25	7.46
2015	17.21	3,812.66	41.02	10.84
2016	15.85	3,593.10	34.21	4.81
2017	15.61	3,482.03	39.02	7.65
2018	19.01	3,370.97	51.19	6.88

Appendix 4.3: Model selection table for different combinations of determinant variables for hyaena space use. Models were selected based on the Akaike Information Criteria for small samples (AIC$_c$). The ΔAIC$_c$ in relation to the best fitting model was used to attribute weight for each respective model. The models that had a ΔAIC$_c$ of less than 10 were considered to have some support towards representing the data.

	Intercept	Prey	Rainfall	AIC$_c$	dAIC$_c$	Weight	df
Intercept	7.53			31.9	0	0.98	5
Prey	−0.9245	x		41.2	9.36	0.01	4
Rainfall	6.864		x	41.8	9.95	0.01	4
Prey + Rainfall	−1.787	x	x	71.2	39.30	0	3

Appendix 4.4: The 19 confirmed females from the 62 individuals captured at more than three different camera trap sites between 2013 and 2018. Females were identified based on ventral profile and nipple visibility, using their entire capture history over the study period (left-hand side and right-hand side).

HiPSH11	
	

HiPSH12	
	

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HiPSH30

HiPSH31

HiPSH33

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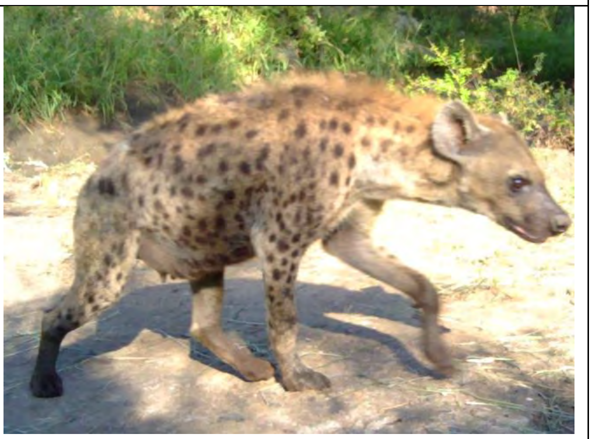
<tr><td></td><td></td></tr>
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HiPSH92

HiPSH117

HiPSH119

HiPSH128

HiPSH160

HiPSH168

HiPSH171	
	

HiPSH254