POPULATION ESTIMATES AND SPATIAL ECOLOGY OF BROWN HYAENAS IN KWANDWE PRIVATE GAME RESERVE

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by

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ABSTRACT

During the last 25 years, the Eastern Cape Province of South Africa has seen the establishment of many small to medium sized (≤ 440km^2) game reserves. These reserves have reintroduced many of the larger indigenous wildlife that had been extirpated by the early 20th century. As such, these reserves and wildlife introductions have created many research opportunities, including investigations on the ecology of reintroduced carnivores in the Thicket biome. Brown hyaenas (*Hyaena brunnea*) are one of the large carnivore species that have been reintroduced into the area. As these animals have predominantly been studied in more open, arid systems, their reintroduction has provided an excellent opportunity to study the species in an alternate natural habitat. Information gathered from such investigations adds to our knowledge of the species and also provides information for the management of brown hyaenas within small, enclosed reserves. Data were collected over the period of one calendar year, from February 2013 to February 2014 at Kwandwe Private Game Reserve in the Eastern Cape, South Africa. Brown hyaena population estimates were calculated using capture-recapture methods from individually identifiable images captured during a three month camera trapping survey. Images of brown hyaenas were separated into left- and right-side profiles. Twenty-eight individuals were positively identified from left-side images and 27 from right-side images. Non-spatial and spatially explicit capture-recapture analyses were both run in the program DENSITY 5.0. Density estimates ranged from 14 to 20 individuals/100km^2 (equivalent to a total abundance of 26-37 individuals) depending on the method used. Despite the range of estimates, all are considerably higher than in other areas where densities have been calculated. Satellite/GPS collars were fitted to three individual brown hyaenas (two males and one female) to measure their home range size and use of space. Home range size was calculated using two different methods, Kernel utilisation distributions and Brownian bridges. Home range estimates were similar using both methods; however Brownian bridge methods appeared to exaggerate the use of space by individuals. Kernel home range sizes for the three individuals ranged between 42.62km^2 and 79.88km^2. These estimates are considerably smaller than previous findings from other parts of Africa and suggest that sufficient resources may be available within this enclosed system. The results from this study suggest that brown hyaenas are successful generalists in this enclosed system and are able to persist at high densities and occupy relatively small home ranges. This information is important for the managers of small reserves who wish to reintroduce brown hyaenas. Should brown hyaenas be introduced into reserves in the Thicket biome with sufficient resources, the numbers are likely to increase rapidly. If high numbers are not desired then preventative measures (e.g. contraception) should be investigated before release.

CHAPTER 1.

GENERAL INTRODUCTION

“They are intelligent, powerful, and, yes, even beautiful” - Gus Mills.

Ecosystems consist of a complex web of interactions among numerous species, and a change at any level can ripple through the ecosystem, causing changes to higher or lower trophic levels (Miller *et al.* 2001). Under certain conditions, many ecosystems have been shown to be driven by top-down processes (Polis and Strong 1996; Terborgh *et al.* 1999; Estes *et al.* 2011). In these systems, predators have far-reaching implications for multiple trophic levels through what is known as trophic cascading (Polis and Strong 1996; Estes *et al.* 2011). Trophic cascading is defined as the downward transmission of effects on prey by consumers throughout food-webs (Paine 1980; Estes *et al.* 2011). In many terrestrial systems, large carnivores occur at the highest trophic level, filling the 'apex predator' role, providing the associated top-down driven control (Gittleman *et al*. 2001; Miller *et al*. 2001; Terborgh *et al.* 2001; Hebblewhite *et al*. 2005).

Predator-prey interactions form the basis of food-web studies (Paine 1980). Carnivores have been shown to affect their prey both directly through predation (Polis and Strong 1996; Estes *et al*. 1998; Crooks and Soulé 1999), and indirectly through non-consumptive processes associated with behavioural alterations (Lima and Dill 1990; Brown *et al*. 1994; Schmitz *et al*. 1997). Prey have been shown to adapt their behaviour in response to predation by altering diel activities, habitat utilisation, and food selection (Miller *et al.* 2001). Predators also mediate interactions among their prey, controlling the abundance of competitively dominant species, thus opening ecological niches for less dominant prey organisms (Estes *et al*. 2001). In addition, large carnivores regulate mesopredator abundance through competitive exclusion and direct predation (Doncaster 1992; Crooks and Soulé 1999; Elmhagen and Rushton 2007; Ritchie and Johnson 2009). In this context, mesopredators are defined as predators at lower trophic levels that are competitively inferior to the larger apex predators within their guild (Ritchie and Johnson 2009). In areas where apex predators are absent, mesopredator abundance is generally higher, which in turn leads to greater predation of smaller species (Crooks and Soulé 1999). Scavenging amongst large carnivores also plays an important role within ecosystems, whereby individuals feed on and remove carrion from the ecosystem (Kruuk 1998; DeVault *et* al. 2003; Wilson and Wolkovich 2011). Through feeding upon multiple species of prey, scavenging carnivores can add greater complexity to food-webs, which is believed to add stability to ecosystems (Wilson and Wolkovich 2011). Thus, given their important ecological contributions, conservation strategies recognise the importance of protecting all large carnivore populations irrespective of their trophic position (Ray *et al.* 2005).

Population estimates are critical in ecological investigations and are vital for the effective management and conservation of reserves and the animal communities within them (Gerber *et al.* 2012). The population size and demography of a species relates directly to its extinction risk (Mace *et al.* 2008). The smaller the population, the more vulnerable it is to stochastic events and perturbations in the environment (Shaffer 1981). In addition, population abundance estimates are vital for estimating carrying capacity and for minimum viable number studies (Shaffer 1981). For large carnivores to influence ecosystems through top down processes they must sustain a particular population density, and knowledge of carnivore population density is therefore fundamental for conservation management (Miller *et al.* 2001). However, collecting accurate species abundance figures can be problematic, especially for large carnivores because many species are solitary and elusive, as well as ranging over large areas and occurring at low densities (Karanth *et al.* 2004; Balme *et al.* 2009; Efford *et al.* 2009).

Complete counts of large carnivores are usually impractical due to time and cost constraints, and other methods have been developed for estimating abundance (Schwarz and Seber 1999; Williams *et al.* 2002). Most recently, camera-trapping, in conjunction with capture-recapture analysis, has become an effective way to estimate carnivore abundance (Karanth 1995; Wallace *et al.* 2003; Karanth *et al.* 2004; Thorn *et al.* 2009; Gerber *et al*. 2010; Gerber *et al*. 2012).

Carnivore population studies have shown that current extinction rates are approximately 100 times higher than those of background (natural) rates (Gittleman *et al.* 2001; Woodroffe 2001). Large carnivores are under considerable threat from anthropogenic pressure associated with persecution, habitat degradation and fragmentation (Crooks and Soulé 1999; Gittleman *et al*. 2001). In addition, the various life-history and behavioural traits of large carnivores intensify their risk and vulnerability to extinction. These animals are often relatively low in number, slow-growing and take a long time to reach sexual maturity (Western 1979). Furthermore, the encounter probability between carnivores and anthropogenic threats is high given that these animals cover large distances (Gros *et al*. 1996).

Conserving one species of large carnivore often means protecting the land they live in and therefore protecting other species living within the same area (Foreman 1993). For this reason, large carnivores are often referred to as ‘umbrella species’ and their protection can lead to the generation of protected areas (Foreman 1993; Caro 2003). In more heavily human populated areas, the best form of conservation is often the establishment of protected areas of land, where species can exist without the threat of persecution (Bangs and Fritts 1996). These areas of land are often bound by fences, which confine larger species to a designated area

(Hayward *et al*. 2007a). Such enclosed systems require careful management as certain natural processes such as emigration and immigration cannot normally take place.

Localised extinction has been observed for many species in numerous habitats, and the reintroduction of species into areas set aside for conservation is common (Hofmeyr *et al.* 2003; Hayward *et al.* 2007b; Ripple *et al.* 2014). However, monitoring the progress of these species post-release is far less common and therefore the success of reintroductions is frequently not studied (Hayward *et al*. 2007b). Post-release monitoring is critical to any reintroduction, especially those within enclosed reserves, as the monitoring should contribute to any consequential management decisions.

In the Western and Eastern Cape regions of South Africa, much of the indigenous wildlife (including the large carnivores) was driven to local extinction in the early 20th century (Skead 2007). As a consequence, much of the carnivore conservation in the region is as a result of relatively recent (i.e. in the last 25 years) reintroductions into small and medium-sized reserves (Hayward *et al.* 2007b). Many of these reserves have introduced predators such as leopards (*Panthera pardus*) and lions (*Panthera leo*), and scavengers such as brown hyaenas (*Hyaena brunnea*). However, given their positions higher up the food chain, the population sizes of these predators within enclosed reserves can have significant consequences for other species and it is therefore vital to know their population densities (Estes *et al*. 2001; Ray *et al*. 2005). The present study focuses on one such species in an enclosed reserve; the brown hyaena. This scavenging carnivore has been reintroduced into several national parks and private games reserves within the Eastern Cape, but it is among the least studied of all the charismatic predators of the region (Hayward *et al*. 2007b).

The hyaenidae represent the least diverse family group of extant carnivores, comprising four species; the striped hyaena (*Hyaena hyaena*), the brown hyaena, the spotted hyaena (*Crocuta crocuta*) and the aardwolf (*Proteles cristatus*) (Jenks and Werdelin 1998). The brown hyaena and striped hyaena form a separate genus (*Hyaena*) due to cytochrome b data that connects the two species more closely, relative to the spotted hyaena and aardwolf (Jenks and Werdelin 1998). In Eurasia, the presence of hyaenas in the fossil record is common, often occurring as dominant carnivores within an ecosystem. However, the fossil record also shows that previous forms of hyaena occupied a different ecological niche, being characterised by more generalised carnivores, compared to the specialised, bone crushing, hunter-scavenger forms of today (Jenks and Werdelin 1998).

Brown hyaenas are large carnivores (28kg-47kg), with long, well-developed front legs and less well-developed, weaker hind legs (Mills 1998a). The pelage is long and dark brown, except around the neck and shoulders where it is white. The under-parts are lighter and white stripes are present on the lower parts of the limbs. Average adult weight is approximately 40kg. Males and females measure approximately 0.79m at the shoulder and approximately 1.4m head to tail, with no obvious sexual dimorphism (Mills 1998a).

The social organisation of brown hyaenas, as with many other carnivores, is largely influenced by the availability and distribution of food (Mills 1982a). Brown hyaenas are solitary foragers and generally feed on the remains of vertebrates (Mills and Mills 1978). Their diet is supplemented by fruit, insects, birds' eggs and the occasional small mammal. Food availability has been shown to influence the home range and territory size of brown hyaenas, whereas group size is more heavily influenced by the quality of food within a territory (Mills 1981). Group size varies considerably, ranging between four and 14 individuals, comprising cubs, sub-adults and adults of both sexes with a high degree of genetic relatedness within a clan (Mills 1982b). Nomadic males represent approximately 33% of adult male brown hyaenas, and are solitary individuals not affiliated with any group and do not have fixed home ranges (Mills 1982b). In the southern Kalahari, nomadic males were responsible for mating and almost half of the interactions between group females and nomadic males were of a sexual nature, whereas group-living males exhibited very little sexual interest in females (Mills 1982b). However, in the central Kalahari, both nomadic and immigrant males were observed mating with females from other clans (Owens and Owens 1984). Nomadic males benefit from direct reproductive success as paternity is assured. Group-living males, however, benefit from indirect success, as individuals help with the survival of genetically related cubs (Mills 1982b; Owens and Owens 1984), or by direct reproductive success if individuals mate with females from other clans (Owens and Owens 1984). All cubs are raised at den sites, and generally stay within close proximity to their dens for approximately 15 months (Mills 1981). For the first three months, the cubs will feed solely on milk from their mother, after which their diet is supplemented by carcasses brought to the den by other members of the clan (Mills 1982b).

Brown hyaenas are typically scavengers and have an important role in the ecosystem by removing and feeding upon carrion (Kruuk 1998). In certain ecosystems (e.g. southern Namibian coastline) they may hunt actively (Kuhn *et al*. 2008), but have been found to have little impact on prey populations within protected areas (Mills 1990; Maddock 1993). However, less abundant prey or the establishment of prey into new areas could well be affected (Kruuk 1998). It has been suggested that in areas where the abundance of prey is great and/or prey are non-migratory, the relationship between predator and prey could adapt, whereby hyaenas can play an important role in balancing prey populations.

With the exception of a few areas in arid south-western Angola, brown hyaenas are endemic to southern Africa (Hofer and Mills 1998a; Wiesel *et al.* 2008). Historically, brown hyaenas were distributed across the drier areas of the southern Savannahs and the South West Arid Zone within the Sub region of southern Africa (Hofer and Mills 1998a). Currently, brown hyaenas are widespread across southern Africa, however their range has decreased significantly since the 18th century (Hofer and Mills 1998a; Wiesel *et al.* 2008), with total population size continuing to decrease. Estimates have placed minimum numbers between 5,000 and 8,000 individuals across the continent (Hofer and Mills 1998b). The largest population of brown hyaenas is found in Botswana, where the population is approximately 3,900 individuals (Hofer and Mills1998b).

Brown hyaenas are listed as near threatened by the World Conservation Union (IUCN), with their worldwide population size falling below 10,000 adult individuals (Wiesel *et al.* 2008). Due to deliberate persecution it is expected that this species may suffer a continued decline of 10% across the following three generations, which could potentially lead to the classification of threatened (Wiesel *et al.* 2008). Conflict is still prevalent between livestock farmers and brown hyaenas and a continual decline in brown hyaena numbers is expected (Wiesel *et al.* 2008). Poisoning, hunting and trapping all pose a threat to the species, whereby ignorance and lack of tolerance has often led to many individuals being killed (Hofer and Mills 1998b). In commercial farming areas, brown hyaenas have been heavily persecuted due to the perceived impact that the species has on livestock (Mills 1998b). Controlling predators in stock farming areas is inevitable; however focus should be placed upon reducing the damage by predators rather than increasing predator mortality (Mills 1998b).

The Eastern Cape Province of South Africa contains three of the World's 34 global hotspots, areas identified as containing 75% of the world's most endangered species, and contains all seven biomes found within South Africa (Berliner and Desmet 2007). Rural livelihoods depend significantly on the biodiversity of the area, whereby it is estimated to contribute between \$150 and \$240 to a household per annum (Berliner and Desmet 2007). In this area, most species of large carnivore no longer exist naturally; driven out by land-use change and persecution, leading to the development of a collection of small ($\leq$ 440km^2) national parks and private game reserves, where the reintroduction of species has occurred (Bissett and Bernard 2007; Hayward *et al.* 2007b). With over 300 game farms and game reserves within the Eastern Cape, the economic benefits of ecotourism have been significant (Berliner and Desmet 2007).

Brown hyaenas have been studied extensively in the Kalahari region of southern Africa (Mills and Mills 1978; Owens and Owens 1978; Owens and Owens 1979a; Owens and Owens 1979b; Mills 1982a; Mills 1982b; Mills 1982c; Mills and Mills 1982; Mills 1983; Mills 1984; Owens and Owens 1984). Research has also been conducted in the Namib Desert (Skinner and van Aarde 1981; Skinner *et al.* 1995; Wiesel 2006), the Makgadikgadi National Park in Botswana (Maude and Mills 2005), Pilanesberg National Park in South Africa (Thorn *et al.* 2009), the north-west province of South Africa (Thorn *et al.* 2011) and more recently in the Ghanzi district in Botswana (Kent and Hill 2013) These studies, however, have generally been conducted in relatively large systems. There is limited research within thicket habitat and on smaller fenced game reserves into which brown hyaenas have been introduced. In large, open systems, studies have shown that brown hyaenas have extensive home ranges and roam over very large distances (Mills 1981; Skinner and Van Aarde 1987; Skinner *et al.* 1995; Maude 2005). Additionally, these studies have shown that brown hyaenas scavenge over large territories and seldom hunt (Mills and Mills 1978; Owens and Owens 1979a; Maude and Mills 2005). However, in large, open and arid systems the abundance of prey is generally low and widespread compared to that of enclosed reserves (Mills 1982a; Sims-Castley *et al.* 2005; Wiesel 2006). Thus, when prey density is higher and animals are enclosed, it may be expected that territories will be smaller and animals will range over shorter distances (MacDonald 1983; Maude 2005).

The aims of this study are to estimate the population size of brown hyaenas in an enclosed reserve and to provide information on the individual spatial distributions and home ranges of selected individuals. This will be achieved by using a combination of intensive camera-trapping and satellite/GPS technology.

CHAPTER 2.

STUDY SITE

Galpin dam and surrounding vegetation

STUDY AREA

Field data were collected from Kwandwe Private Game Reserve (Kwandwe) in the Eastern Cape of South Africa from February 2013 to February 2014 (Figure 2.1). Kwandwe is approximately 35km north of Grahamstown, in the Great Fish River Valley. Kwandwe was established as a conservation area in 1999, after being purchased from small stock and ostrich farmers. Currently, Kwandwe operates as a privately owned area of conservation offering refuge for endangered wildlife and vegetation. At establishment, Kwandwe occupied an area of 160km^2; this was extended in December 2005 to 183km^2 when additional land was purchased. The land surrounding Kwandwe is either state owned or private farmland. Kwandwe and the surrounding areas are separated by electrified game fencing, which is required by all reserves in South Africa that introduce dangerous game. The Great Fish River is a perennial river and flows through the reserve for approximately 30km, and into which all surrounding watercourses drain. The other significant watercourse is the Botha's River, supplying water to three large man-made dams. These together with numerous dams and pans support the fauna of the reserve.

TOPOGRAPHY AND GEOLOGY

The elevation gradient of the Great Fish River Valley ranges from 170m above sea level at the Great Fish River to just over 600m above sea level on the high ridges (Figure 2.2). The underlying geology in the north of the reserve is derived from the Adelaide and Estcourt Formations and predominantly consists of shallow clay soils (Glenrosa and Mispah) (Hoare *et al.* 2006). The southern areas of the reserve are composed of sediments from the Ecca Group and bear skeletal shallow soils (Glenrosa and Mispah) (Hoare *et al.* 2006). The topography of Kwandwe is varied and complex, ranging from ground that rises steeply in the northern section of the reserve from the Great Fish River to the top of the Fish River Rand; to more gently sloping topography and vast open plains in the centre of the reserve; to the south where a succession of east to west orientated sandstone ridges are situated. The sandstone ridges are extremely resistant, whereas the nutrient-rich mudstones found in the river valleys are highly erodible.

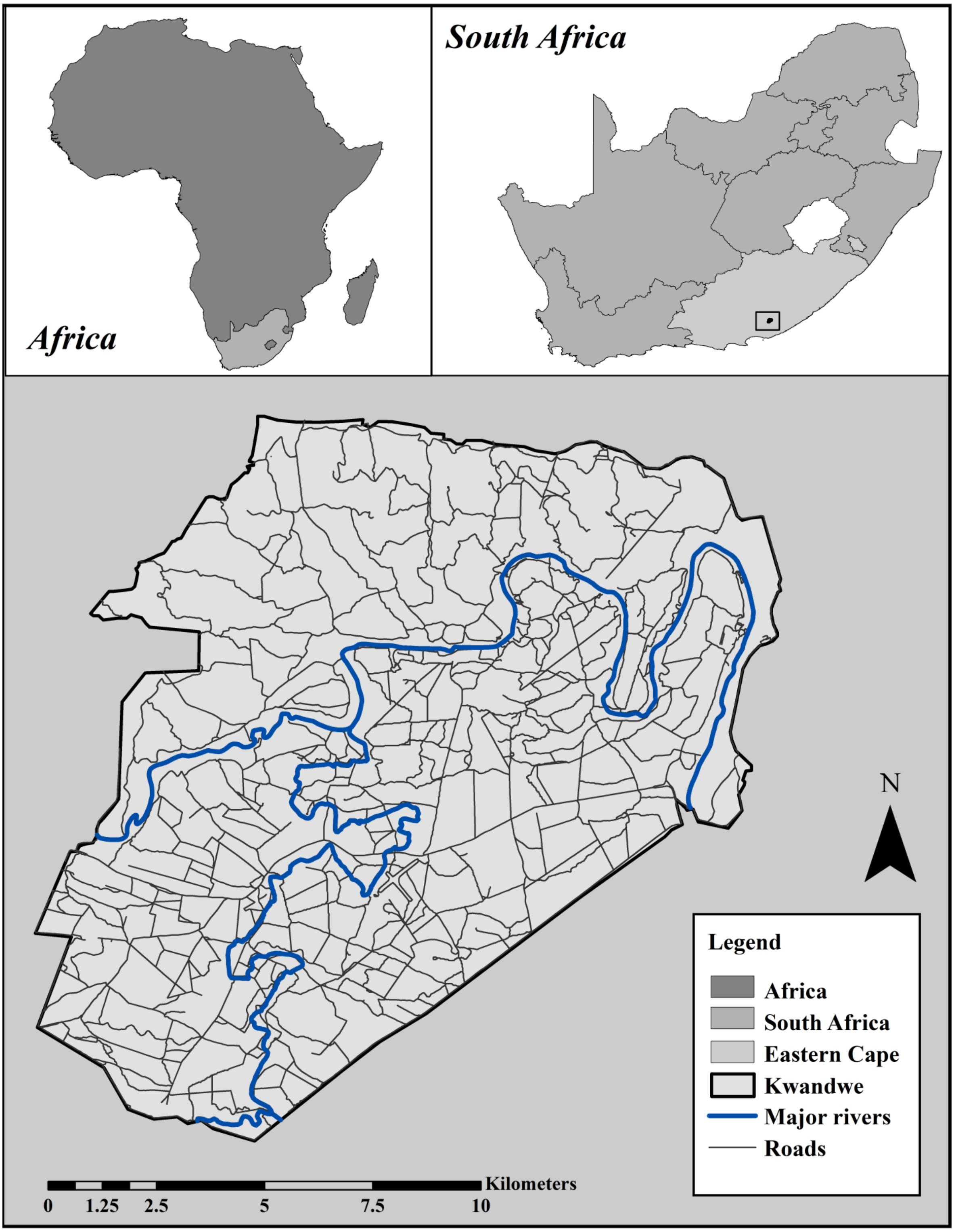


Figure 2.1: Kwandwe Private Game Reserve, Eastern Cape, South Africa. The map highlights the major rivers and road network within Kwandwe.

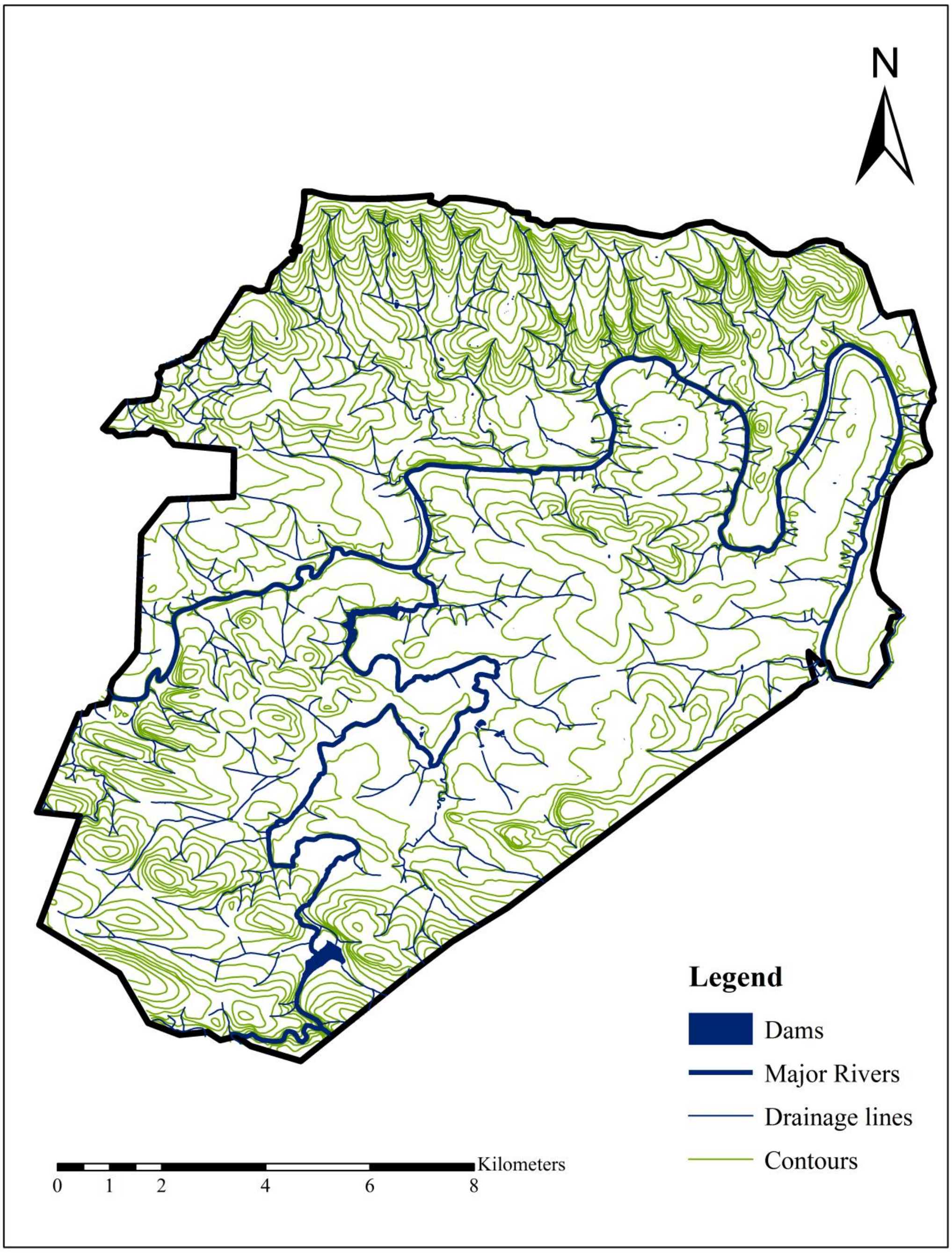


Figure 2.2: Topography and drainage pattern of Kwandwe Private Game Reserve, Eastern Cape, South Africa.

CLIMATE

The Eastern Cape is situated in a transitional zone and experiences various climates; this is further complicated by topological variations, which can have a marked effect on local climatic conditions (Stone *et al.* 1998). The topological variation within Kwandwe creates a complex climatic environment which has a distinct effect on rainfall and temperature conditions. The lower elevations experience higher mean annual temperatures and lower mean annual rainfall, producing a hot semi-arid environment (Bissett 2004). In contrast, the higher elevations experience lower mean annual temperatures and higher mean annual rainfall creating cooler, wetter conditions. Kwandwe is situated between the spring and autumn dominant rainfall region in the Eastern Cape and therefore rainfall is bimodal, with peaks in November and March for the study period (Stone *et al.* 1998). The mean annual rainfall for the area is 425mm. During the study period the total rainfall was 415.8mm (Figure 2.3).

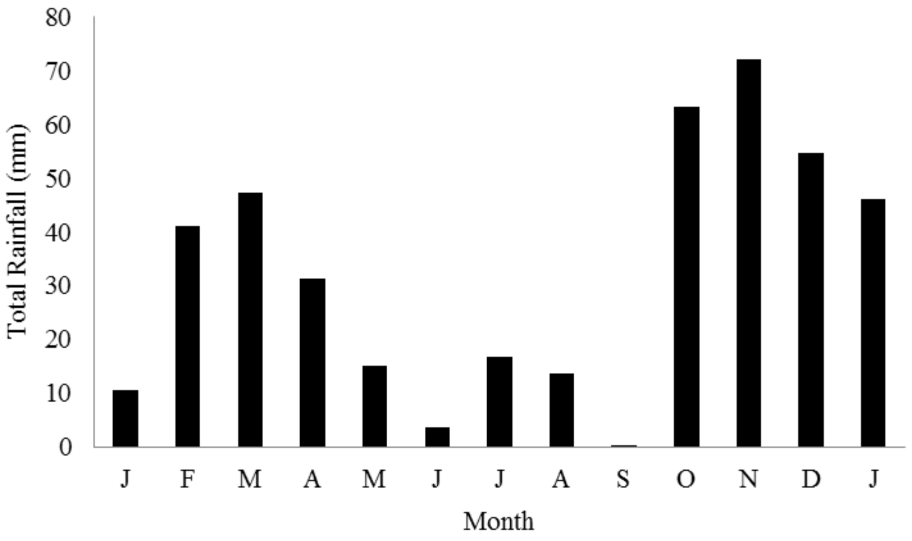


Figure 2.3: Total monthly rainfall for the period January 2013 to January 2014. Data recorded at Fort Beaufort weather station.

Kwandwe experiences a warm climate, with maximum daily temperatures reaching 41.6°C and minimum -0.5°C. During the study period, the temperatures were less extreme but fell within this range (Figure 2.4). Rainfall and temperature data were not recorded for Kwandwe during the study period, therefore climate data were collected from the weather station at Fort Beaufort. Despite Fort Beaufort being a greater distance from Kwandwe than Grahamstown, historical climate data from Kwandwe were more comparable to climate data from Fort Beaufort than that of Grahamstown (Bissett 2007).

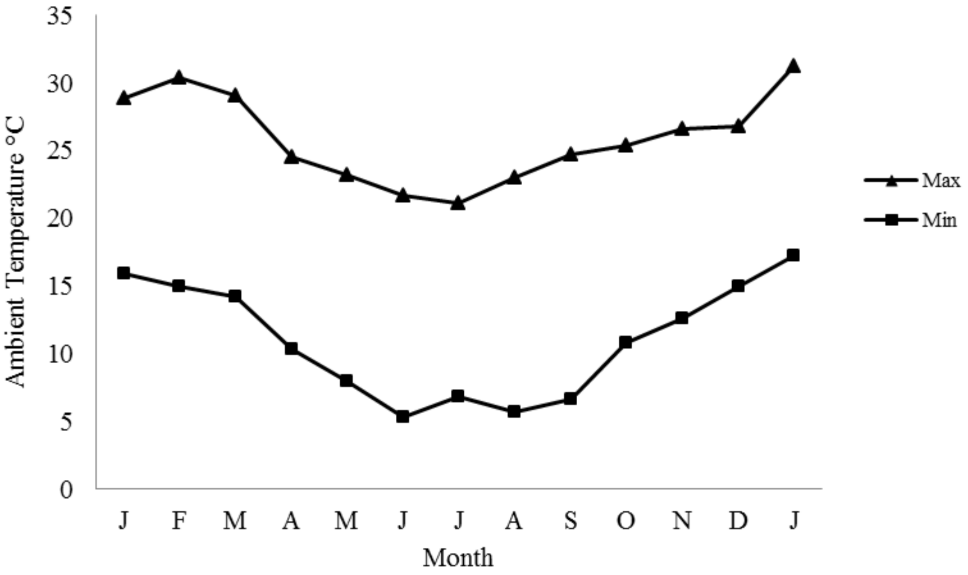


Figure 2.4: Mean daily maximum temperatures (triangles) and minimum temperatures (squares) from January 2013 to January 2014. Data recorded at Fort Beaufort weather station.

VEGETATION

Kwandwe is situated within the Albany Thicket Biome and the dominant vegetation types are the Great Fish Noorsveld and the Great Fish Thicket (Hoare *et al.* 2006). The Great Fish Thicket occurs in the northern-most part of the reserve and a small band in the south (Figure 2.5). The Great Fish Noorsveld is the predominant vegetation type and occurs across the centre and towards the south of the reserve. In the far south there are smaller areas of land that fall within the Kowie Thicket and Albany Broken Veld vegetation types. Woody trees, woody shrubs, succulents and spinescent shrubs are all well developed in the Great Fish

Thicket, with *Portulacaria afra* dominating (Hoare *et al.* 2006). The presence of *P. afra* varies with aridity, and in more arid areas it is replaced by *Euphorbia bothae.* However, with increasing moisture, and in riparian areas, *Euphorbia tetragona* and *E. triangularis* are more dominant (Hoare *et al.* 2006). High levels of heterogeneity are common in this vegetation type (Hoare *et al.* 2006). The Great Fish Noorsveld is more ubiquitous on gently sloping edges of ridges and on open plateaus (Hoare *et al.* 2006). This vegetation type supports low- and medium-height succulent thicket, 1-2.5m (Birch 2000), and is dominated by *E. bothae,* which is locally endemic. This is interspersed with *P. afra,* which dominates on rocky outcrops, sclerophyllous bush clumps, succulent shrubs and many species of grass flora (Hoare *et al.* 2006). Succulent euphorbias and aloes are dominant in the Kowie Thicket, which predominantly occurs on steep, arid, north-facing slopes and has a thick understory. On south-facing (moister) slopes, fewer succulent shrubs are present and the herbaceous layer is poorly developed (Hoare *et al.* 2006). The area is dominated by low evergreen trees and shrubs. The Albany Coastal Belt occurs on gentle and moderate slopes and short grasslands dominate (Hoare *et al.* 2006).

A more detailed vegetation map was developed in 2003, using 1:50000 aerial photographs (Bissett 2004). This map describes 11 vegetation types (Figure 2.6). A simplified vegetation map was developed from this work and vegetation categories were separated into either open or thicket (Figure 2.7), based on a visibility index and the density of vegetation, calculated using a modified point-centred-quarter method and checker board (Bissett 2007). Visibility indices greater than 69 formed open habitat. Open habitats represent 37% of the reserve, with 63% being represented by denser vegetation (Figure 2.7). The open habitat is represented by bushclump karroid thicket, bushclump savanna, karroid shrubland, old lands; and the thicket habitat is represented by drainage line thicket, dry forest, *Euphorbia Portulacaria* mosaic, *Portulacaria* thicket, riverine thicket, short *Euphorbia* thicket and tall *Euphorbia* thicket.

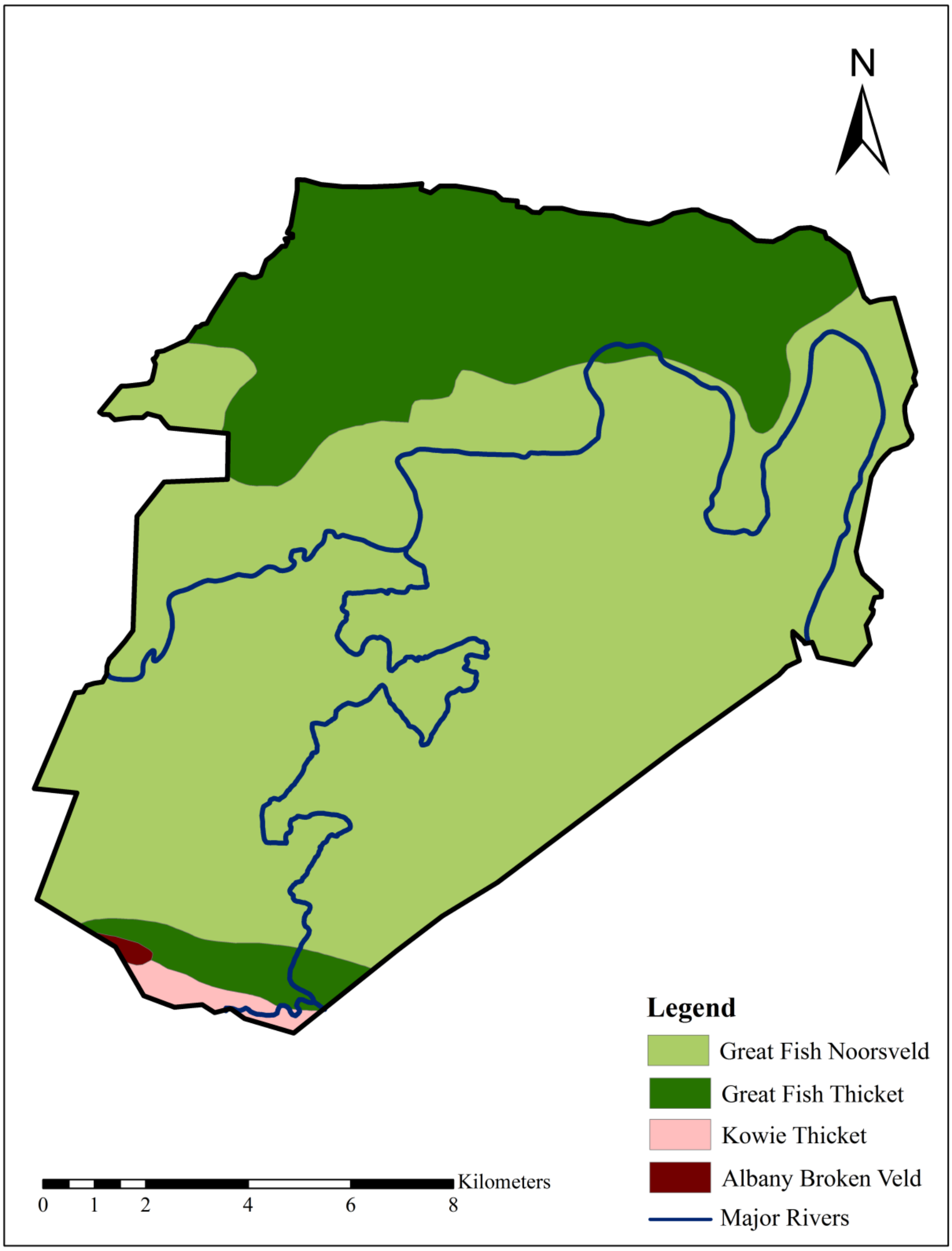


Figure 2.5: Dominant vegetation classification in Kwandwe Private Game Reserve according to Hoare *et al.* (2006).

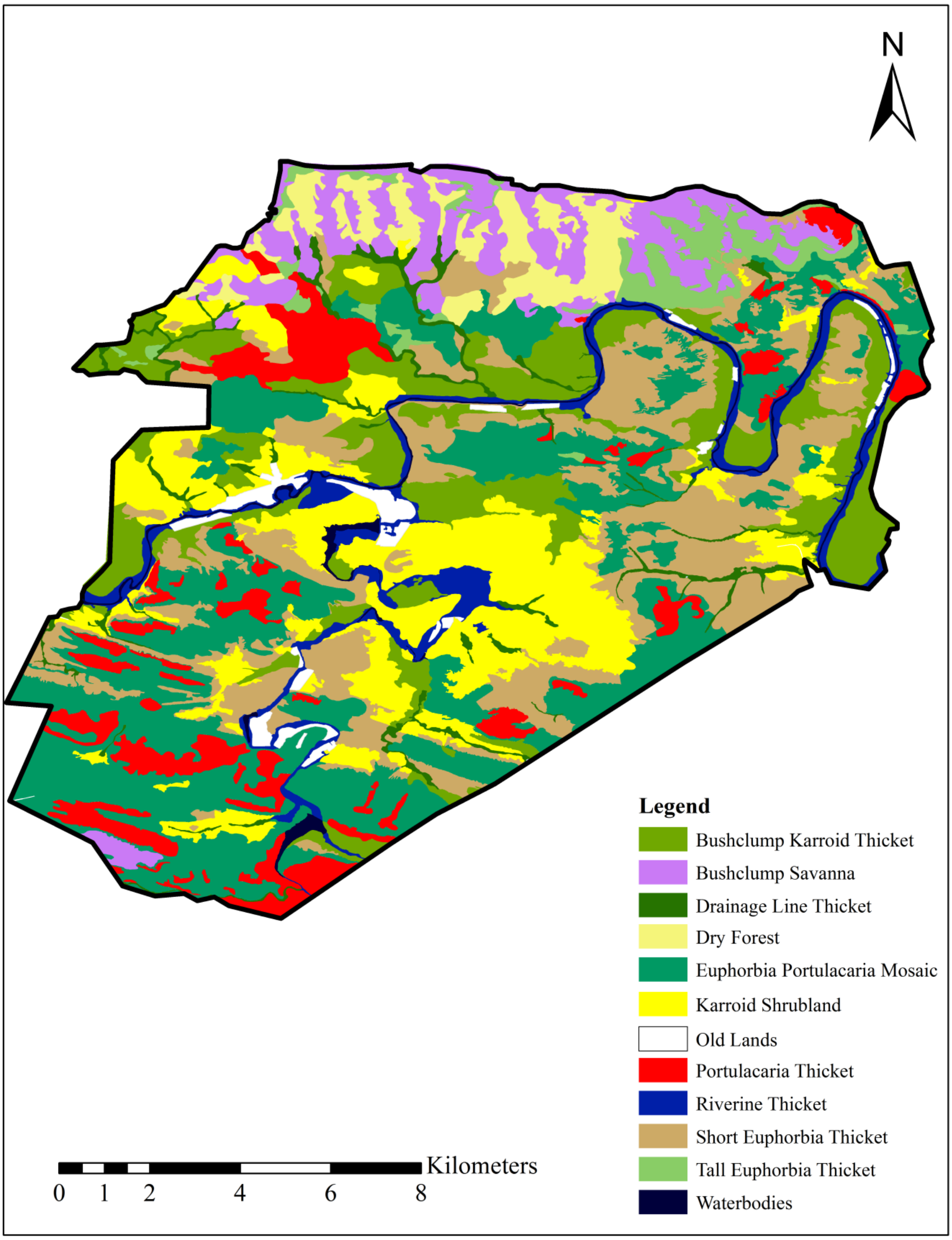


Figure 2.6: Distribution of 11 vegetation types in Kwandwe Private Game Reserve according to Bissett (2007).

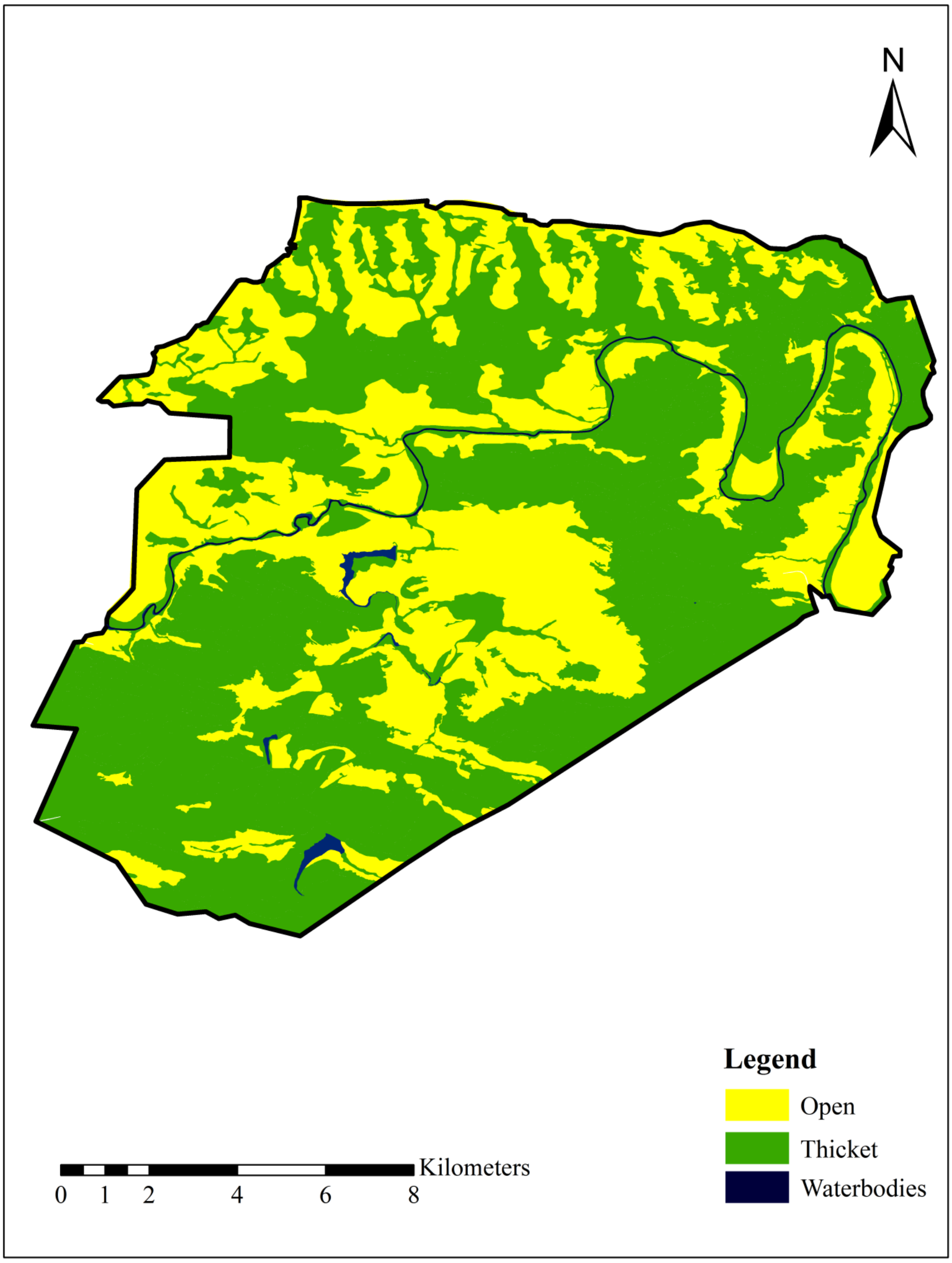


Figure 2.7: Distribution of open and thicket vegetation types in Kwandwe Private Game Reserve.

MAMMALIAN FAUNA

When Kwandwe was first established in 1999 only small and medium-sized ungulates were present; most other species had been eliminated from the area (Bissett 2007). These species included bushbuck (*Tragelaphus scriptus*), Cape grysbok (*Raphicerus melanotis*), common duiker (*Sylvicapra grimmia*), greater kudu (*Tragelaphus strepsiceros*), grey rhebuck (*Pelea capreolus*), mountain reedbuck (*Redunca fulvorufula*), steenbok (*Raphicerus campestris*), bushpig (*Potamochoerus larvatus*) and common warthog (*Phacochoerus africanus*). In the subsequent two years, additional ungulates, giraffes (*Giraffa camelopardalis*) and elephants (*Loxodonta africana*) were reintroduced. Historical records of carnivores in the Eastern Cape indicate that brown hyaenas, wild dogs (*Lycaon pictus*), serval (*Leptailurus serval*), cheetahs (*Acinonyx jubatus*) and lions all occurred in the area in the late 1800s (Skead 2007). As such, carnivore introductions began on Kwandwe in 2001 and included four lions, nine cheetahs and two leopards (C. Bissett pers. comm. 2013). In 2003, six brown hyaenas and an additional two cheetahs were introduced. In 2004, six wild dogs were introduced and ten serval were introduced in 2005. At the beginning of this study, carnivore numbers had changed considerably; there are currently 13 lions (two males, four females, three sub-adults and four small cubs); eight cheetahs (four males split between two coalitions, two females and two cubs approximately six months old); approximately two serval; approximately 12 leopards (the ratio of male to female is unknown) and no wild dogs. All mammals found in Kwandwe are listed in Appendix I. Aerial game counts are conducted biennially using a Jet Ranger III, ZS-HSV helicopter to obtain wild animal estimates (Bissett 2004). The helicopter flies at approximately 30-50m high in transects 250m apart. The biennial game count figures for 2011 and 2013 are represented in Table 2.1.

Table 2.1: Mammalian species recorded during the 2011 and 2013 census at Kwandwe Private Game Reserve.

Species	**2011**	**2013**
baboon	308	269*
black wildebeest	82	89
buffalo	110	133
bushbuck	54	38*
duiker	35	16*
eland	72	103
elephant	45	59
gemsbok	62	129
giraffe	40	36
hippo	17	9*
impala	362	429
jackal	26	9
greater kudu	980	426*
nyala	0	10
ostrich	22	33
red hartebeest	148	188
springbok	173	72*
steenbok	34	18
warthog	1042	405*
waterbuck	101	136
zebra	206	215

***Counts are believed to be underestimates for 2013. Temperatures on the ground were 30°C by 9am and this was believed to affect certain species.

STUDY ANIMALS

The reintroduced brown hyaenas consisted of three adult males, one adult female and two sub-adult females (Figure 2.8). Individuals were translocated from Mafunyane Game Reserve in the North-West Province. Firstly, two adult males arrived in April 2003 and were kept in a holding boma, one individual for two days and the other for four days. Both individuals were fitted with VHF transmitter implants (African Wildlife Tracking, Rietondale, Pretoria) by reserve management to allow regular relocation. The third male and the adult female arrived in May 2003 and were kept separately in holding bomas for three days before release. The adult female was fitted with a VHF collar (African Wildlife Tracking, Rietondale, Pretoria). The two sub-adult females arrived in May 2003 and were approximately seven months old.

Both sub-adults were the offspring of a problem female animal that had been shot. They remained in a boma for approximately six weeks. After the boma gates were opened, these two individuals were never seen again and it was unclear whether they survived. Initially no intense monitoring took place. However, animals were opportunistically relocated by reserve staff. The individual animals with implants were difficult to locate as no signal was received if they were in dense vegetation or in underground burrows. In 2003, six visual sightings were recorded and signals for individuals with collars or transmitters were recorded on 38 separate occasions. Three observations were made in January and February 2004; and no further observations were recorded until 2006. In 2006, 2007 and 2008, sightings were recorded opportunistically, with a total of 58 observations recorded across the three years. There was no subsequent monitoring until 2009, when a small study investigated brown hyaena abundance, which was estimated to be approximately 26 individuals (Marlton 2008).

Figure 2.8: Images of one of the introduced adult males in the initial holding boma; a. right-side profile; b. left-side profile; c. teeth and gums; d. damaged ear and facial scarring.

CHAPTER 3.

BROWN HYAENA DENSITY ESTIMATES

Brown hyaena individual caught on camera

INTRODUCTION

Reliable population estimates are crucial for effective wildlife management and conservation (Stander 1998; Gusset and Burgener 2005; Efford *et al.* 2009; Manning and Goldberg 2010; Núñez-Pérez 2011). This critical information should provide the basis for conservation initiatives and management decisions (Blake and Hedges 2004). Although the need for this information is recognised, it is not always obtained and management decisions in the past have often been based on deficient datasets (Karanth *et al.* 2003; Sutherland *et al.* 2004). The use of incomplete knowledge in conservation can be counterproductive, having undesirable consequences. One example of such an oversight is where key areas of land that should have been prioritised for the conservation of an endangered species were overlooked, due to insufficient knowledge on their abundance (Blake and Hedges 2004). Population estimates are particularly pertinent for large carnivores, as many are declining in number (Nowell and Jackson 1996). The need for reliable methods to determine population estimates and monitor population trends is therefore crucial (Stander 1998).

Collecting abundance data is, however, difficult for many species and acquiring perfect abundance data is impossible (Blake and Hedges 2004; Efford *et al.* 2009; Manning and Goldberg 2010). This problem is exacerbated when dealing with cryptic carnivores that are usually nocturnal, occur at low densities and are often secretive in their behaviour (Linkie *et al.* 2006; Kéry *et al.* 2011). As such, complete counts are unrealistic, expensive and time consuming (Blake and Hedges 2004; Balme *et al.* 2009). Alternative methods of abundance estimation are therefore necessary (Stander 1998). While numerous methods for estimating abundance have been developed, they fall into two categories: relative and absolute abundance (Gese 2001). Relative abundance provides an index of population size. It is assumed that the index has a constant ratio to the actual population size and therefore, for example, if the index is reduced to 50% it can be considered that the population size has also been reduced to 50% (Schwarz and Seber 1999). Methods of calculating relative abundance include the presence of animal signs, whereby the numbers of tracks or scats are recorded along a pre-determined path or transect (Hayward *et al.* 2002; Balme *et al.* 2009). These counts have been shown to vary in accuracy across environmental factors that affect animal sign recognition such as habitat or substrate and therefore differences in relative abundances are often linked to the level of detection (Henschel and Ray 2003). A measure of relative density that has been used for certain species is the number of breeding dens (Hewson 1986; Heydon *et al.* 2000). In species where the number of litters produced on an annual basis is known e.g. red foxes (*Vulpes vulpes*), the density of breeding den sites can indicate social group density. However, for species that exist in clans, e.g. brown hyaenas, the number of den sites can only indicate the number of social units within an area and as clan size is highly variable, would not signify population density (Mills 1982b; Gese 2001).

While relative abundance estimates may provide some use in terms of a localised monitoring tool for populations over time and space (Henschel and Ray 2003), absolute abundance estimates are preferred as they are comparable between habitat types and do not lose consistency when applied to larger areas (Hayward *et al.* 2002; Bart *et al.* 2004; Stephens *et al.* 2006; Balme *et al.* 2009). Absolute abundance estimates involve the direct counting of animals (Gese 2001). This can be achieved either by total counts or by sub-sampling an area and extrapolating to the remaining area of interest (Gese 2001; Foster and Harmsen 2012). However, in most population estimate surveys the probability of detecting an individual is less than one; often described as imperfect detection (Royle and Young 2008). There will always be uncertainty as to whether the individuals detected make up the entire population. If only a proportion of the population is captured, then what proportion does this represent?

(Ancrenaz *et al.* 2012). For species with individually recognisable markings, capture-recapture methods may be used to estimate abundance from a sample of the population, therefore accounting for individuals that may not have been detected. Capture-recapture is one of the most common methods for estimating absolute abundance within a population (Eberhardt 1990; Karanth 1995; Miller *et al.* 1997; Karanth and Nichols 1998; Sadlier *et al.* 2004; Soisalo and Cavalcanti 2006). Capture-recapture relies on the individual identification of animals, either through human-induced marking such as fur-clipping or PIT tags in small mammals (Gibbons and Andrews 2004; Kok *et al.* 2012) and ringing in birds (Besbeas *et al.* 2002), or through phenotypical variations (e.g. rosette patterns) in species that differentiate individuals (Royle and Young 2008).

More recently, capture-recapture techniques have been applied to camera trapping studies, which work on the same principles of individual recognition, but in a non-invasive manner (Karanth and Nichols 1998; Silver *et al.* 2004; Núñez-Pérez 2011). Estimating abundance via camera-trapping, using the individual capture-recapture principle was first developed to monitor tiger (*Panthera tigris*) abundance in India (Karanth and Nichols 1998). Due to the success of this method, it has since been used on other species such as leopards (Balme *et al.* 2009; Chapman and Balme 2010), jaguars (*Panthera onca*) (Trolle and Kéry 2003; Silver *et al.* 2004; Núñez-Pérez 2011), snow leopards (*Uncia uncia*) (Jackson *et al.* 2006; Janečka *et al.* 2011), ocelots (*Leopardus pardalis*) (Di Bitetti *et al.* 2006), cheetahs (Marnewick *et al.* 2008), brown hyaenas (Thorn *et al.* 2009; Kent and Hill 2013) and striped hyaenas (Harihar *et al.* 2009) where individuals can be unambiguously identified by stripe, rosette or spot patterns.

Capture-recapture methods require that several assumptions are met. The first assumption is population closure, both geographically and demographically. No births, deaths, emigration or immigration to the population are permitted for the duration of the survey (Otis *et al.* 1978; Wilson and Anderson 1985). However, for biological populations this is extremely difficult to control and the assumption is generalised to the definition that there are no unknown changes to the original population (White *et al.* 1982). To meet this assumption, survey duration is normally restricted to a short period to ensure population closure. For large carnivores this is usually between two and three months (Henschel and Ray 2003; Silver *et al.* 2004; Tobler and Powell 2013). The second assumption is that every individual in the population must have a capture probability of greater than zero (Karanth and Nichols 1998; Tobler and Powell 2013). To satisfy this assumption there must be no gaps within the study area where an individual can pass by a camera undetected (Tobler and Powell 2013). Therefore, there must be at least one camera situated in the home range of each individual. This requires prior knowledge of home range size of the study species, and many studies have based camera spacing on minimum home range estimates from the literature (Kelly 2003; Silver *et al.* 2004; Silveira *et al.* 2010). However, spatial data from the actual study site is preferable to maximise the effective trapping area (ETA) based on the number of cameras available (Tobler and Powell 2013). The final assumption is that every individual is identifiable and animals do not lose these individual features over the course of the survey (Otis *et al.* 1978; Royle and Young 2008).

Traditional capture-recapture analyses employ abundance estimates to calculate a measure of animal density. But in order to convert abundance into density one needs to know the ETA (Efford 2004; Foster and Harmsen 2012; Tobler and Powell 2013). This is often fraught with error and can result in exaggerated density estimates (Efford 2004). If the survey area is an open system, cameras may capture individuals whose home range falls largely outside the trapping grid and the failure to incorporate this area will lead to inaccurate and inflated estimates (Foster and Harmsen 2012; Tobler and Powell 2013). It is therefore accepted that a buffer strip should be added to the camera polygon and that this should equate to some measure of home range for the species (Balme *et al.* 2009). In the absence of telemetry data several *ad hoc* approaches are used to calculate this distance (Foster and Harmsen 2012). The mean maximum distance moved (MMDM) between cameras across all individuals is often calculated; this value or half this value, (HMMDM), appears to be the most widely used calculations (Wilson and Anderson 1985; Karanth and Nichols 1998; Trolle and Kéry 2003; Kawanishi and Sunquist 2004; Silver *et al.* 2004; Tobler and Powell 2013). These calculations act as a proxy for home range diameter and radius (Balme *et al.* 2009; Tobler and Powell 2013). This width can, however, be heavily influenced by the spacing between individual traps and is truncated at the edge of the sampled area resulting in an underestimated ETA and consequently an overestimated population estimate (Efford 2004; Efford *et al.* 2005). More recently, the buffer width has been calculated using GPS collar data when these are available, as these data represent actual distance travelled rather than a biased representation of movement offered with camera trapping (Soisalo and Cavalcanti 2006). The choice of buffer width is therefore crucial (Foster and Harmsen 2012).

However, spatially explicit capture-recapture (SECR) methods are a more recent advance in this technique and incorporate additional spatial information in density estimates, thus avoiding the need to estimate the ETA (Royle and Young 2008; Sollmann *et al.* 2011). This technique determines an individual's home range centre using its capture history (Royle and Young 2008; Royle *et al.* 2009). Individual detection history is then combined with capture probability at specific trap locations using the distribution of home range centres, thereby estimating the density of home range centres across a predefined trapping array (Royle and Young 2008; Royle *et al.* 2009; Sollmann *et al.* 2011; Foster and Harmsen 2012).

A few studies have estimated brown hyaena density; Mills (1984; 1990) calculated the mean density of brown hyaenas in the Kalahari to be 1.8 individuals/100km^2 (ranging from 0.4-4.4 individuals/100km^2) using indirect methods and extrapolating data from average group and territory sizes. Thorn *et al.* (2009) used data collected by Maude (2005), on the territory sizes of five collared brown hyaenas in Botswana. Data were extrapolated to density estimates of up to 2 individuals/100km^2. The authors also described how brown hyaenas were unambiguously identifiable at an individual level, and were the first to estimate density based on camera trapping alone. They calculated brown hyaena density as 2.8 individuals/100km^2 in Pilanesberg National Park, South Africa. Most recently, Kent and Hill (2013) estimated brown hyaena density using spatially explicit capture-recapture methods in west-central Botswana to be 2.3 individuals/100km^2.

The population density of brown hyaenas in Kwandwe will provide insight into how this species operates within a closed system and provide further information on their success in this type of system, based on the growth of the population since introduction. As the study area is truly geographically closed, the ETA is known with certainty and therefore both traditional capture-recapture and spatially explicit capture-recapture methods should provide reliable density estimates.

Aims

The aim of work reported in this chapter was to estimate brown hyaena density within Kwandwe Private Game Reserve, to aid in future management decisions. This aim was achieved via an intensive camera trapping survey and the use of capture-recapture techniques to estimate population size.

METHODS

A camera trapping survey was conducted from 30 April 2013 and ran for 107 nights. The investigation was based on previous studies that used camera trapping surveys to individually identify cryptic carnivores in order to estimate abundance and density using capture-recapture principles (Karanth and Nichols 1998).

Equipment and survey design

Three different models of infra-red cameras were used for this study: Cuddeback Expert (Non Typical Inc., Green Bay, Wisconsin), Cuddeback Attack (Non Typical Inc., Green Bay, Wisconsin) and Wildview Extreme 5 (Wildview, Grand Prairie, Texas) (Figure 3.1). Remote infra-red cameras work on the basis of emitting an infra-red beam that crosses the potential path of an animal (Ancrenaz *et al.* 2012). When an animal passes, the beam is broken and a photograph is triggered. Different models were deployed to maximise the number of units available and therefore to maximise the number of camera positions throughout the study area. Each model of camera boasts slightly different features, ranging from a flash range of 10m (Wildview Extreme 5) to a flash range of 30.28m (Cuddeback Attack), and different trigger speeds, the quickest being ¼ second (Cuddeback Attack), the slowest 5 seconds (Wildview Extreme 5). Each model produces an image with a date and time stamp. All cameras were placed in protective cases, as elephants and lions are present on the property and are known to damage cameras (Karanth and Nichols 1998). In total, 60 camera-trap locations were selected across the reserve. The availability of each different type of camera varied throughout the camera survey and therefore different numbers of each model were used for each camera rotation (Table 3.1). Cuddeback Attack and Wildview Extreme 5 cameras used SD cards (2GB), whereas Cuddeback Expert cameras used CF cards (4GB). Neither SD nor CF cards reached full capacity throughout the survey and therefore the different cards were not perceived to affect the results from cameras.

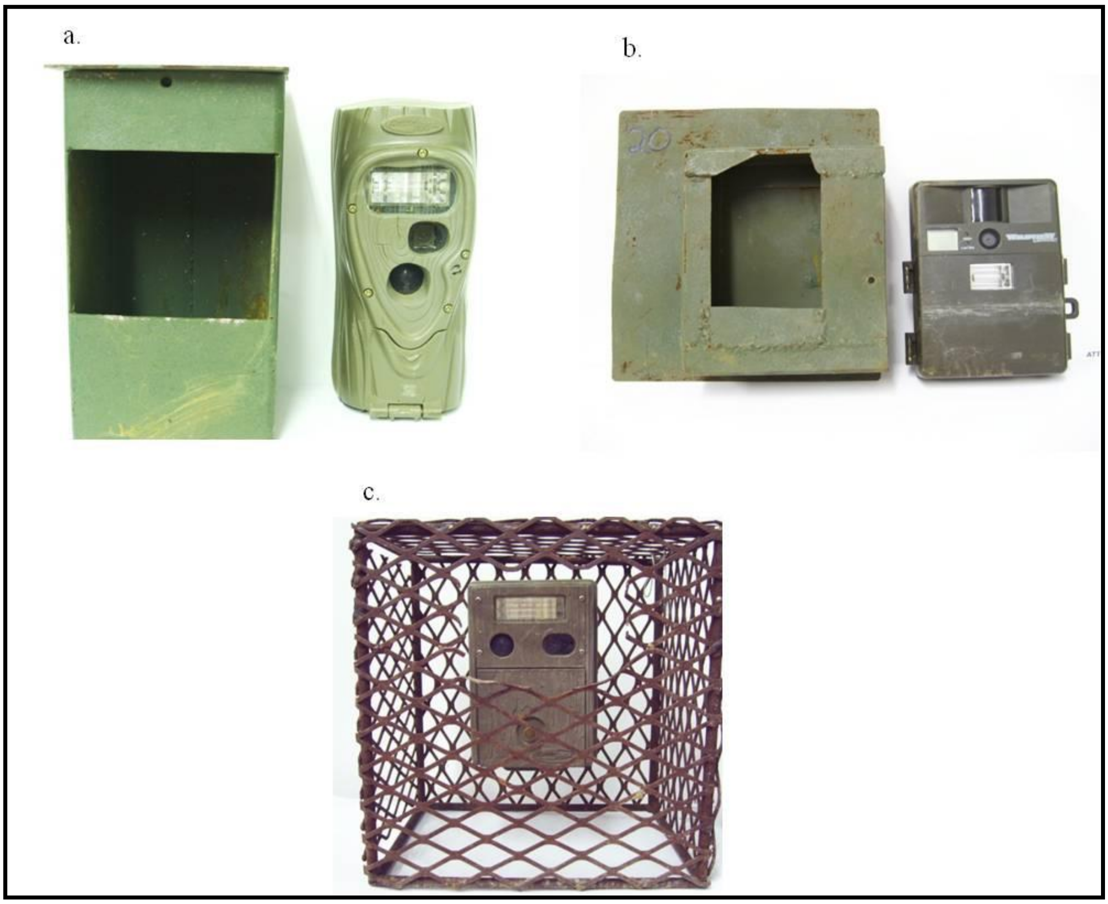


Figure 3.1: The three models of camera used in this study: a. Cuddeback Attack and protective casing, b. Wildview Extreme 5 and protective casing, c. Cuddeback Expert in protective casing.

Table 3.1: A breakdown of the number of different camera models and the total number of cameras used for each camera rotation.

		Cameras in operation			
Rotation	Dates	Cuddeback Attack	Cuddeback Expert	Wildview Extreme 5	Total
1	30/04-27/05/13	6	8	1	15
2	28/05-20/06/13	5	0	10	15
3	21/06-18/07/13	5	6	10	21
4	19/07-15/08/13	5	0	4	9

A pilot camera trapping study was conducted during March 2013 using seven Cuddeback ‘Expert’ cameras at seven locations to determine camera battery life, camera functionality and whether positions were suitable for capturing images of brown hyaenas. Battery life varied between individual cameras and lasted between 13 and 23 days.

The full camera survey consisted of four camera rotations over the 60 camera sites (Figure 3.2). The duration of the survey was limited to approximately 100 nights to comply with population closure assumptions and to minimise the probability of demographic changes within the brown hyaena population (Karanth and Nichols 1998; Silver *et al.* 2004; Thorn *et al.* 2009; Ancrenaz *et al.* 2012; Tobler and Powell 2013). Each rotation lasted between 23 and 28 trap nights and batteries were replaced approximately every 13 days to avoid camera failure. One sampling occasion was defined as 24 hours starting at 1500h. This time was selected to avoid the “midnight problem” (Jordan *et al.* 2011), whereby an individual animal is photographed either side of the cut off time creating two distinct sampling events, whereas at any other time this would be considered a single sampling event. For a nocturnal species, with potentially high activity patterns around midnight this could lead to results with a positively biased capture probability (Foster and Harmsen 2012).

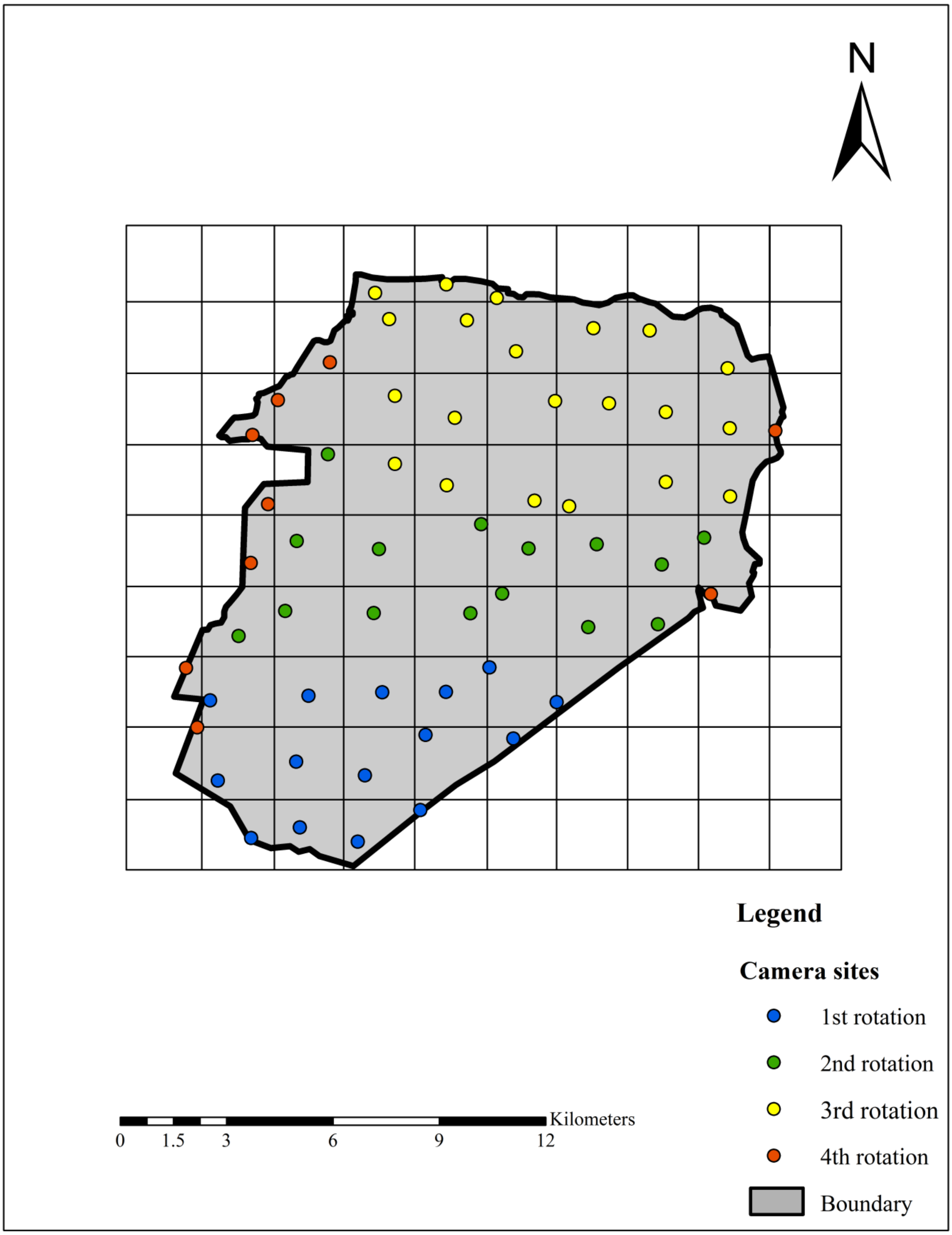


Figure 3.2: Camera placements in Kwandwe Private Game Reserve for each of the four camera rotations.

Site selection

Camera sites were selected using a grid system across the survey area to ensure that every individual brown hyaena had a capture probability of greater than zero (Karanth and Nichols 1998; Tobler and Powell 2013). Individual grid cells covered an area of 4km^2 and one camera was positioned in each of the 60 grid cells (Figure 3.2). Ideally, two cameras should have been used in each cell to capture both flanks of a passing brown hyaena, but this was not possible due to the limited number of cameras available for the study. To maximise the probability of photographing brown hyaenas, a scent lure was used in order to hold the animal in position to capture a clear image of at least one side. A mixture of rotten pilchards (*Sardinops ocellatus*) and oil was used at each site; 200ml of the mixture was buried just under the surface (approximately 8cm deep) in front of each camera (Figure 3.3). It was also intended that the scent lure would reduce the influence of the Wildview camera's slow trigger speed. Furthermore, use of the scent lure would also potentially allow for the capture of both sides of an individual as they investigated the lure. If both sides of an individual were captured in less than one minute they were considered the same individual. Brown hyaenas are solitary foragers (Mills and Mills 1978) and hence images captured in quick succession would most probably be the same individual.

Figure 3.3: Images showing the effectiveness of the scent lure: a and b are successive images of the same individual investigating the scent lure enabling a full profile to be captured; c and d show different individuals sniffing and licking the scent lure, immobilising the individuals for long enough to capture clear images of leg patterns, ears and a side body profile.

A review of camera trapping studies found that to obtain accurate jaguar population estimates the maximum distance between camera sites should be no more than the radius of the smallest home range within a population (Tobler and Powell 2013). This method is also applicable for brown hyaenas and therefore the spacing of cameras was determined using home range data collected from GPS satellite collars (see Chapter 4). The spacing was based on the smallest home range size from the first month's data (26.32km^2). The radius was subsequently calculated and this measurement was used as the maximum distance between cameras (2.89km). This approach ensured that (as far as possible) all home ranges would overlap with at least one camera station.

The first rotation covered the most southerly part of the reserve, with each subsequent rotation moving further north (Figure 3.2). The fourth rotation covered the northwest of the reserve and two final locations on the eastern boundary of the reserve (these two sites were inaccessible due to poor weather conditions on previous rotations).

Camera placement

Within every grid cell, camera sites were selected in areas where brown hyaenas were most likely to be photographed. Sites were pre-selected using 1 in 10000 aerial photographs in ArcView 9.3 (ESRI, Redlands, California, USA) following published recommendations (Ancrenaz *et al.* 2012). Site selection criteria were based on the three GPS satellite collars which indicated that the collared individuals made extensive use of the road network. Crossroads or T-junctions were selected to maximise the chances of capturing brown hyaenas. The GPS co-ordinates of these sites were recorded. On arrival at each pre-selected site, signs of brown hyaena activity were identified, such as latrines, pastings or tracks. If active sites were discovered, cameras faced the direction of activity in order to maximise capture probability (Tobler and Powell 2013). If no sign of hyaena activity was found, cameras were placed facing game paths or roads. Cameras were attached to trees using straps and cable ties (Figure 3.4). In open areas, iron standards were hammered into the ground and cameras were attached using cable ties (Figure 3.4). Previous studies placed cameras at a height of about 45cm, based on the shoulder height of brown hyaenas (Karanth and Nichols 2002, Thorn *et al.* 2009). However, the height of cameras varied in this study, dependent on the location and surrounding vegetation and ranged from 31cm to 126cm (Figure 3.4). When cameras were higher than 45cm they were angled down to capture leg markings. Once cameras were set, the angle and height were tested to select the best position for the scent lure and detection of an individual brown hyaena. Distances from the cameras to the scent lure ranged from 160cm to 570cm. Typically, when Wildview Extreme 5 cameras were used, the distance to the scent lure was increased due to the slow trigger speed of these cameras.

Figure 3.4: The use of different attachment points for camera placement, dependent on the surrounding area and vegetation.

Data analysis

Brown hyaena images were analysed and individuals were identified based on individually identifiable markings such as leg stripes, pelage pattern, facial scarring and ear notches (Silver *et al.* 2004; Efford *et al.* 2009; Thorn *et al.* 2009; Foster and Harmsen 2012). Images were separated into left and right side, as brown hyaena markings are bilaterally asymmetrical (Thorn *et al.* 2009). Images for both left and right sides were analysed and detection histories for each individual were compiled (Karanth and Nichols 1998; 2002). All analyses were separately applied to both sides. An independent capture event was defined as a record of an individual at a camera station separated by 30-minute intervals (Kelly *et al.* 2008). Trapping success was calculated as the number of brown hyaena events per 100 trap nights (Kelly *et al.* 2008).

Identities were assigned based on the adapted methodology of Heilbrun *et al.* (2003) and Jackson *et al.* (2006), whereby if an image of an individual could not be matched with a previous image it was regarded as an initial capture. A poor quality image, where individual markings were not clear, was considered a non-capture (Figure 3.5). Two or three clear features were selected per individual and these markings were required to class an image as a recapture (Figure 3.6). Where possible, numerous features indicated different individuals (Figure 3.7), but it was considered adequate to class images as two separate individuals when only one different feature was observed (Figure 3.8).

Figure 3.5: Two examples of unclear images of brown hyaenas which were discarded from population estimate analyses.

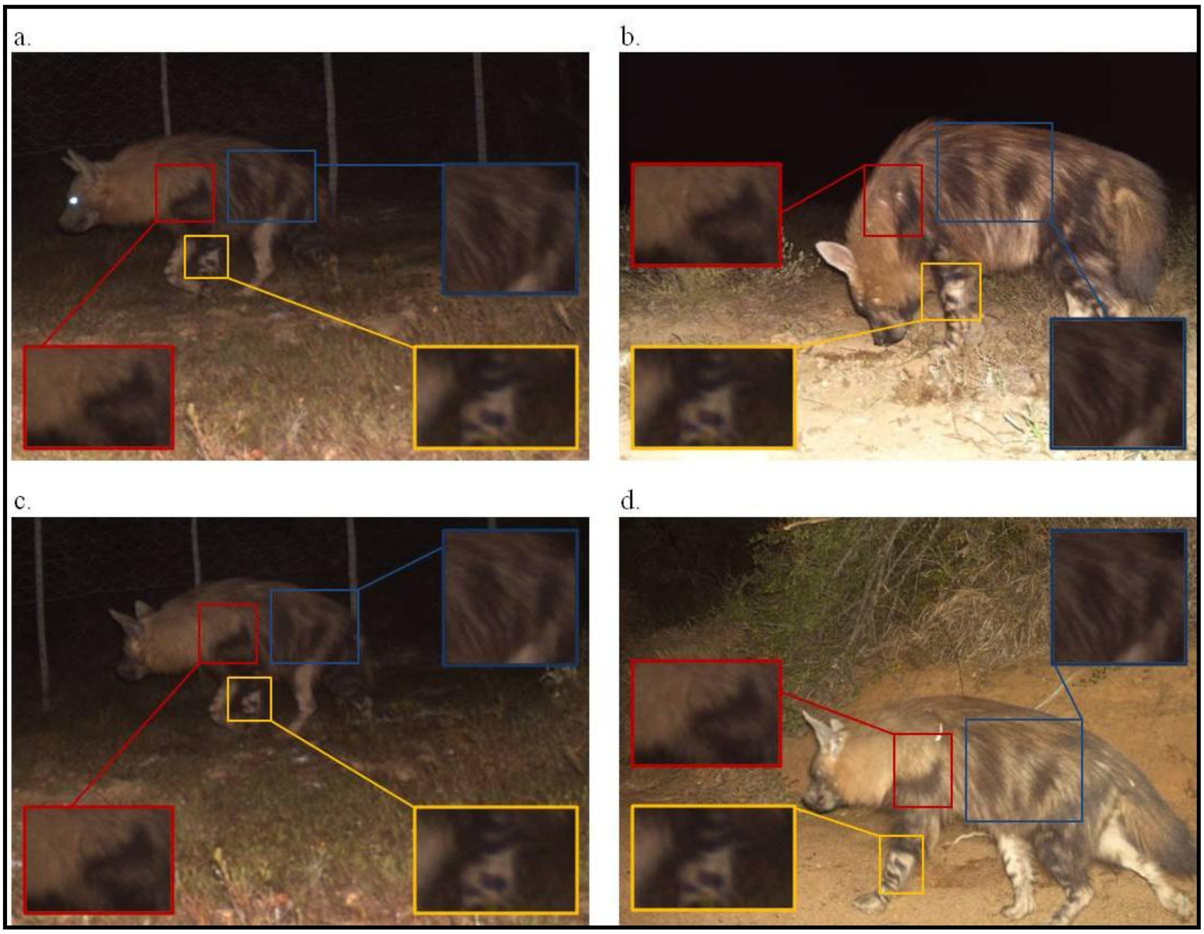


Figure 3.6: Four separate photos (a,b,c and d) showing the left side of the same animal and the key features used in the identification of this particular individual.

Figure 3.7: Two images indicating two individuals and the numerous unique features used in confirming their separate identities.

Figure 3.8: Two images indicating different individuals. The images reveal that the classification of two separate individuals only required one distinct feature; in this example using the leg striping patterns was sufficient to confirm the different individuals.

During the camera survey, two brown hyaenas (one adult male and one adult female) were translocated from the reserve. Detailed photographs were taken so that they could be recognised if they had previously been captured on camera. Analyses were run on datasets including and excluding the images of the two individuals (images captured of translocated individuals before relocation: female left side, n = 3, female right side, n = 1; male left side, n = 1, male right side, n = 2).

The program CAPTURE was used to test for population closure and to select an appropriate model for individual capture probability (Rexstad and Burnham 1992). Sampling occasions from each rotation were pooled, so that sampling occasion one consisted of captures for the first 24 hours for rotation one through four (Karanth and Nichols 1998, Trolle and Kéry 2003, Soisalo and Cavalcanti 2006). A binary matrix was created for individual captures across 28 sampling occasions, whereby a capture was represented by ‘1’ and non-capture by ‘0’ (Appendix II). The matrix was analysed by CAPTURE which calculates a ‘closed test’ statistic and selects the most appropriate model from seven (Rexstad and Burnham 1992; Karanth and Nichols 1998). Each model assumes different sources of variation in capture probability. The different sources of variation for capture probability incorporate Model M_t which permits capture probability to vary with time; e.g. variations in capture probability due to weather conditions. Model M_b allows capture probability to vary with behavioural response to the camera trap; e.g. variations in capture probability due to trap avoidance or encouragement. M_h (jack-knife) models for heterogeneity between individuals and assumes that capture probability will differ between individuals. M_o is the null model and assumes that variation in capture probability is constant and does not differ between individuals. CAPTURE then calculates a goodness-of-fit model and between-model test statistics and reveals the most appropriate model selected by the model selection algorithm (Otis *et al.* 1978; Rexstad and Burnham 1992; Karanth and Nichols 1998).

SECR analyses are based on two distinct approaches: Maximum Likelihood and Bayesian methods (Efford 2004; Royle *et al.* 2009). Bayesian methods were not used for this study, as despite calculating similar estimates to Maximum Likelihood methods (Kalle *et al.* 2011; Noss *et al.* 2012), they are more sensitive to buffer size and analyses run more slowly and require greater computation time than the Maximum Likelihood equivalent (Kalle *et al.* 2011).

Traditional capture-recapture analyses and SECR analyses were both run in the program DENSITY 5.0 (Efford *et al.* 2004). Both analyses required carefully formatted input files. The non-spatial capture-recapture analysis required one file with each brown hyaena assigned with an identification number and the number of sampling occasions on which it was photographed. Sampling occasions were once again pooled across each rotation, as though all sites ran simultaneously (Karanth and Nichols 1998, Trolle and Kéry 2003, Soisalo and Cavalcanti 2006). The different models were then applied to the data based on the model selection in CAPTURE, and the most suitable models were run in DENSITY 5.0. This process was repeated for both left- and right-sided images. For most non-spatial capture-recapture analyses, calculating the effective trapping area is fraught with bias and contentious *ad hoc* methods, such as adding buffer strips to the camera trapping grid. For this survey the reserve was geographically closed as a permanent fence is present along the perimeter. To further test that the population did not move outside the confines of the reserve, two adjoining properties were also sampled. These properties formed part of the fourth rotation and the camera design was an extension of that used for the reserve; grid squares were extended into these areas to ensure an identical spacing protocol and methodology. Geographical closure was also confirmed from additional data collected from collared individuals and fences were checked daily. Abundance estimates were calculated and converted to density estimates by using the area of the reserve as the effective trapping area. This is an acceptable method if individuals do not move outside the park boundaries (Foster and Harmsen 2012).

The SECR analysis in DENSITY 5.0 required two input files (Efford *et al.* 2004). The first consisted of trap layout and deployment information (Appendix III). This file was a matrix of binary information, which indicated the location of the camera stations and when they were operational. Trap site numbers and corresponding UTM coordinates (projected in ArcMap 9.3) formed the first two columns and the sampling occasions formed the header for each subsequent column. Each cell below consisted of information for a particular camera trap on a particular sampling occasion; displaying a ‘1’ if cameras were operational, and a ‘0’ if not (due to other camera rotations, battery failure or damage), allowing the analysis to take individual camera activity history into consideration. The second file consisted of individual brown hyaena capture information (Appendix IV). To test the effect of pooling sampling occasions, analyses were run with both pooled and un-pooled sampling occasions. Camera trap surveys have shown roads to be a potential source of bias (Sollmann *et al.* 2011; Tobler and Powell 2013), and a binary covariate was therefore included to differentiate between those cameras on roads and those set elsewhere. Buffer strips were required to run the analyses, but areas within the reserve were recorded as habitat and those outside as non-habitat. The two larger dams in the reserve were excluded and classified as non-habitat. Smaller pans were not excluded as these are often dry and make up less than 0.3% of the total reserve area. Four different buffer strips were added to each model for both left and right sides to evaluate the effect of the buffer size on density estimates. Firstly, the mean distance from outer camera sites to the reserve boundary (MDB). Secondly, the mean maximum distance moved for brown hyaenas that were photographed on more than one occasion during the camera survey (MMDM), and also half this distance (HMMDM) (Karanth and Nichols 1998; Silver *et al.* 2004). Lastly, the mean maximum distance moved from collar data (MaxDM) (Soisalo and Cavalcanti 2006). Both full maximum likelihood and conditional maximum likelihood SECR population density estimates were calculated in DENSITY 5.0. It was assumed that detection function was half normal and that home range centres followed a Poisson distribution (Gray and Prum 2012).

Various models were run: with and without a road covariate, with and without the inclusion of translocated individuals and with and without the pooling of sampling occasions. The models were then evaluated using Akaike’s Information Criterion (AIC; Akaike 1974), which allows the comparison of competing models (Symonds and Moussalli 2011). This method is becoming increasingly common in the ecological field and compares multiple contending models, which essentially compare different mathematical hypotheses (Burnham *et al.* 2011; Symonds and Moussalli 2011). The resulting models can only be an approximation of what is occurring ecologically, but AIC methods allow for the selection of the most appropriate model, allowing for model selection uncertainty to be evaluated (Symonds and Moussalli 2011). AIC values become meaningful only when compared with AIC values from other models, with the lowest AIC value representing the most appropriate model (Burnham *et al.* 2011; Symonds and Moussalli 2011). For small sample sizes (when n/k < 40; n=sample size, k = number of parameters), corrected AIC values (AIC_C) should be used to compare models (Symonds and Moussalli 2011). In this study n/k < 40 and therefore AIC_C values were examined. Models were weighted, with each model being given a value between 0 and 1; the highest weight being associated with the best performing model. Models were weighted using the formula:

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_\mathrm{i})}{\sum_{\mathrm{r=1}}^{\mathrm{R}} \exp\,(-\frac{1}{2}\Delta_r)}$$

where Δ_i represents the ΔAIC_c value of the model under investigation and $\Sigma_{r=1}^{R}$ exp (- $\frac{1}{2}$ Δ_r) represents the sum of exp (- $\frac{1}{2}$ Δ_i) values. The sum of Akaike weights for all models is equal to one (Symonds and Moussalli 2011).

RESULTS

In total, 60 camera sites ran over 107 nights for a total of 1375 trapping nights (Table 3.2). Altogether, 3965 images were recorded with a total of 2640 separate events. These included 41 mammalian species, 14 of which were carnivores, and 10 bird species. In total, 203 images of brown hyaenas were captured, 187 of which were considered independent events (i.e. images separated by 30-minute intervals). Overall, brown hyaena capture probability was 0.15 captures per trap night, which translates to a trapping success rate of 15%. Of the 203 images, many were partial images (an ambiguous feature) or were of poor quality, and were removed from the density estimation analysis (Figure 3.5). The results therefore represent the minimum number of individuals on the reserve (Silver *et al.* 2004). The remaining images were split into left and right sides; 75 images were included for left-side and 85 for right-side analyses. Seventy-one independent capture events were used for left-side analysis. The average number of captures per individual was 2.54 ± 1.37 and ranged from one to five. Eighty-two independent capture events were used for right-side analysis. The average number of captures per individual was 2.85 ± 1.90 and ranged from one to eight. Twenty-eight left-sided individuals and 27 right-sided individuals were positively identified, including the translocated individuals (Appendix V).

Table 3.2: Summary of the camera survey conducted on Kwandwe Private Game Reserve between 30 April and 15 August 2013.

	n	**%**
No. of trapping nights	1375	100
Total no. of image captures	3965	100
Total brown hyaena images	203	5.12
Total brown hyaena events	187	4.72
No. of individual brown hyaenas identified	-	-
Left side	28	-
Right side	27	-
Total mammal species	41	-
Total mammal events	2207	55.66
Total carnivore species	14	-
Total carnivore events	626	15.79
Total bird species	10	-
Total bird events	50	1.26
Vehicle events	383	9.66

Of the 60 camera sites, 36 were situated on roads and 24 on game paths. Cameras on roads were 94.44% successful in capturing brown hyaena images compared to 45.83% of those on game paths, indicating that capture probabilities were higher on roads.

Capture

Left-side images

The most appropriate model was the M_h, which scored a criterion of 1.0, followed closely by M_o, which scored a criterion of 0.97 (Table 3.3). Population closure was confirmed ($z = 0.91$, $p = 0.82$). All results were identical when translocated individuals were removed, with the exception of the M_o criterion score which changed to 0.95, but was still the second most appropriate model (Table 3.3).

Table 3.3: Brown hyaena left and right side model selection criterion score in CAPTURE when translocated individuals were included, (results in brackets reveal the differences when translocated individuals were excluded).

Model	**Left side** **Model selection criterion score**	**Right side** **Model selection criterion score**
M_h	1.00	1.00
M_o	0.97 (0.95)	0.95 (0.96)
M_b	0.58	0.63
M_t	0.00	0.00
M_t Chao	0.20	0.26
M_h Chao	0.73	0.56

Right-side images

The most appropriate model for ride-side images was also M_h, which scored a criterion of 1.0 (Table 3.3). This was followed closely by M_o, which scored a criterion of 0.95 (Table 3.3). Population closure was again confirmed ($z = -0.63$, $p = 0.27$) and all results were identical when translocated individuals were removed, with the exception of the M_o criterion score which changed to 0.96, but was still the second most appropriate model (Table 3.3).

Density

Non spatial C-R

When sampling occasions were pooled for non-spatial analysis the number of independent capture events dropped to 68 for left side and 78 for right side. The appropriate models were then selected for in DENSITY 5.0 to estimate abundance for both left and right sides (Table 3.4). For left-sided images, the estimated brown hyaena population size using the Jackknife estimator (M_h) was 36 individuals ± 5.6, with a capture probability of 0.07, and 31 individuals ± 2.2 for the null model (M_o), with a capture probability of 0.08. For right-sided images, population size was estimated at 29 individuals ± 3.4 using M_h and 28 individuals ± 1.4 using M_o.

The two translocated individuals were removed from the dataset and the analyses repeated (Table 3.4). Left-side analyses estimated an abundance of 33 individuals ± 4.6, with a capture probability of 0.07 under the M_h model, and an abundance of 28 individuals ± 1.9 with a capture probability of 0.08 under the M_o model (Table 3.4). Right-side abundance estimates were 26 ± 3.2, with a capture probability of 0.10 under the M_h model, and 26 ± 1.2, with a capture probability of 0.10 under the M_o model (Table 3.4). Density estimates were calculated from abundance figures using the area of the 183km^2 reserve (Table 3.5).

Table 3.4: Abundance estimates for left- and right-side brown hyaena images including and excluding translocated individuals, under the most appropriate model selections in DENSITY 5.0.

	M_h		M_o	
	Abundance estimate	**95% CI range**	**Abundance estimate**	**95% CI range**
Left side	36 ± 5.6	30.4-55.5	31 ± 2.2	28-36.4
Left side**	33 ± 4.6	27.9-48.9	28 ± 1.9	26-33.6
Right side	29 ± 3.4	27.2-46.8	28 ± 1.4	27-31.8
Right side**	26 ± 3.2	25-46.4	26 ± 1.2	25-29.1

**translocated individuals excluded

Table 3.5: Density estimates for left- and right-side brown hyaena images including and excluding translocated individuals, under the most appropriate model selections in DENSITY 5.0.

	M_h	M_o
	Density estimate	**Density estimate**
Left side	20	17
Left side**	18	15
Right side	16	15
Right side**	14	14

**translocated individuals excluded

For left-side calculations, density estimates differed slightly across the M_h and M_o models, ranging from 20 and 17 brown hyaenas/100km^2 respectively when translocated individuals were included, and 18 and 15 brown hyaenas/100km^2 when they were excluded (Table 3.5). Right-side density estimates were similar between the two models, ranging from 16 and 15 brown hyaenas/100km^2 when translocated individuals were included, and estimates were both 14 brown hyaenas/100km^2 when translocated individuals were excluded (Table 3.5).

Spatially explicit capture-recapture (SECR)

Four buffer widths were calculated and used for analyses. The mean distance from outer camera sites to the reserve boundary was 482m (Figure 3.9). The HMMDM measured 1734m for left side and 1808m for right side. The MMDM measured 3469m for left side and 3615m for right side. The MaxDM from collar data was 15760m.

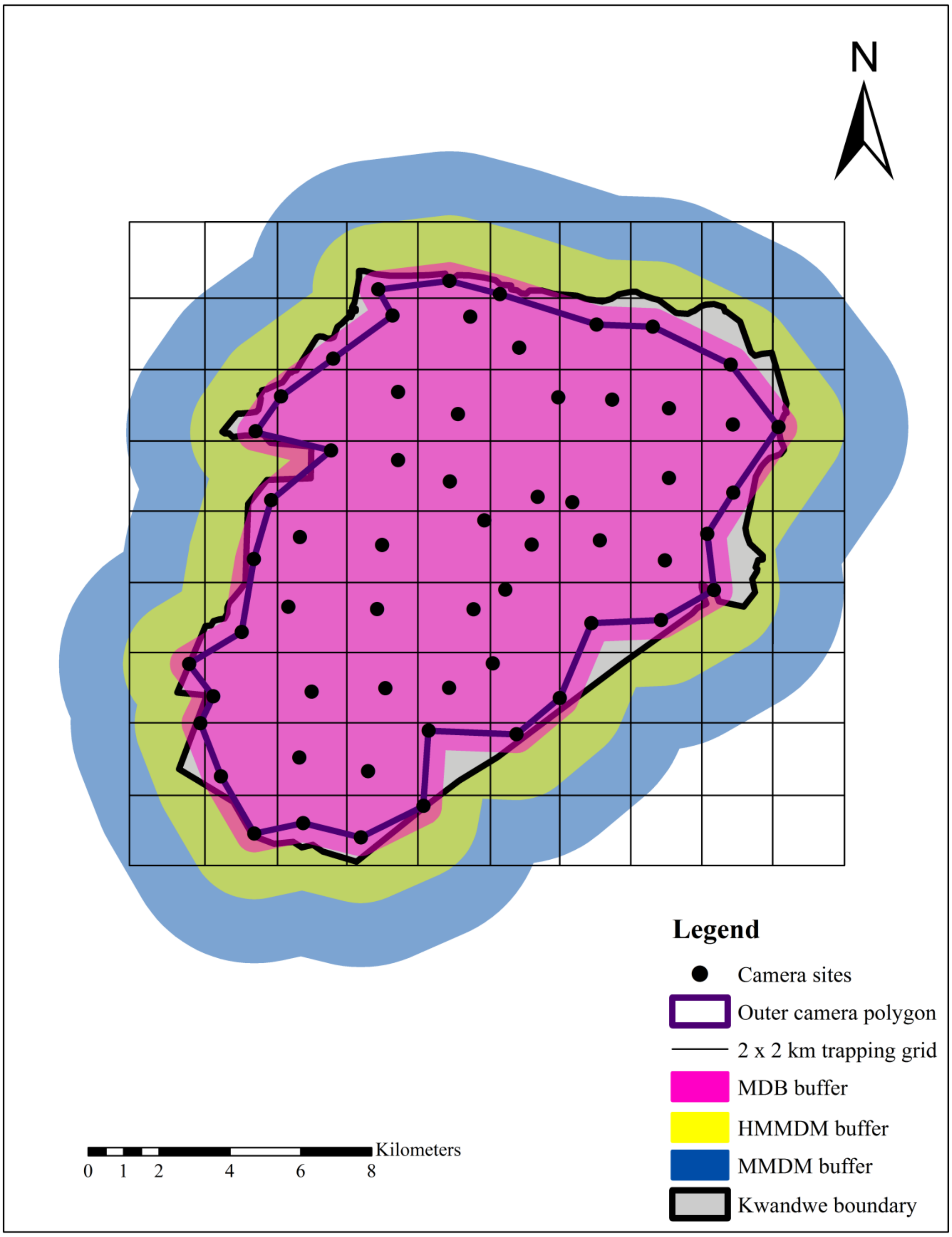


Figure 3.9: An example of the effectively sampled area, highlighting the camera positions with MDB (482m), HMMDM (left side: 1734m) and MMDM (left side: 3469m) buffer widths used for the density calculations in DENSITY 5.0.

Both left- and right-side SECR density analyses were robust to both differences in buffer width and the inclusion of different covariates (Tables 3.6 and 3.7). Conditional likelihood models that included a road covariate and excluded translocated individuals performed the best; for this model, left-side density estimates were 16 individuals/100km^2 ± 3.27-3.29 and right-side density estimates were 14 individuals/100km^2 ± 2.89-2.91; standard error values varied slightly according to different buffer size. The different buffer widths did not influence the density estimates and made little difference to AIC_C scores, suggesting that all models fit the data comparably (Symonds and Moussalli 2011). Pooling the sampling occasions for both left and right sides had little effect on the density estimates; however AIC_C values indicated that the unpooled data provided the most parsimonious fit (Tables 3.6 and 3.7). For left-side analyses the best model had a weighting of 0.28, indicating a 28% chance that model is the best approximating model and therefore highlighting some uncertainty in the model selection (Table 3.6). However, the top four models (the four different buffer widths combined with unpooled sampling occasions, translocated individuals excluded and a road covariate included) have a combined weighting of 0.99 and density estimates do not differ among them, indicating that these models and the resulting estimate of 16 individuals/100km^2 represent the most appropriate models with 99% certainty. In addition, ΔAIC_c values are < 2; $\Delta AIC_c < 2$ represent the best models (Symonds and Moussalli 2011). A similar pattern is seen for right-side analyses with the top four models (the four different buffer widths combined with unpooled sampling occasions, translocated individuals excluded and a road covariate included) all indicating density estimates of 14 individuals/100km^2 and representing the most appropriate models with 100% certainty. (Weighted values are rounded to two decimal places; Table 3.7). ΔAIC_c are also < 2, indicating near-equivalence of the four best-performing models.

Table 3.6: Results of the left-side Maximum and Conditional likelihood SECR analyses, together with the inclusion and exclusion of a road covariate and the translocated individuals; also highlighting the difference between pooled and unpooled sampling occasions. Four buffer widths were examined, MDB (482m), HMMDM (1734m), MMDM (3469m) and MaxDM (15760m).

Likelihood	**Pooled sampling occasions**	**Buffer**	**Translocated BH**	**Road covariate**	**Density/ 100km^2**	**S.E**	**95% CI**	**AIC**	**AIC$_C$**	**ΔAIC$_C$**	**AIC$_C$ weight**
Conditional	No	HMMDM	Exc.	Inc.	16	3.27	9.15-21.99	780.24	782.15	0	0.28
Conditional	No	MDB	Exc.	Inc.	16	3.28	9.17-22.04	780.45	782.36	0.21	0.25
Conditional	No	MMDM	Exc.	Inc.	16	3.28	9.17-22.03	780.46	782.37	0.22	0.25
Conditional	No	MaxDM	Exc.	Inc.	16	3.29	9.19-22.10	780.8	782.71	0.56	0.21
Conditional	Yes	MDB	Exc.	Inc.	16	3.26	9.16-21.93	792.52	794.43	12.28	6.05×10^{-4}
Conditional	Yes	HMMDM	Exc.	Inc.	16	3.25	9.14-21.88	792.29	794.20	12.05	6.8×10^{-4}
Conditional	Yes	MMDM	Exc.	Inc.	16	3.26	9.16-21.93	792.53	794.43	12.28	6.05×10^{-4}
Conditional	Yes	MaxDM	Exc.	Inc.	16	3.27	9.18-21.98	792.9	794.80	12.65	5.03×10^{-4}
Conditional	No	HMMDM	Inc.	Inc.	17	3.44	14.16-19.86	820.89	822.63	40.48	4.55×10^{-10}
Conditional	No	MDB	Inc.	Inc.	17	3.45	14.15-19.86	821.11	822.85	40.7	4.08×10^{-10}
Conditional	No	MMDM	Inc.	Inc.	17	3.45	14.14-19.85	821.12	822.86	40.71	4.06×10^{-10}
Conditional	No	MaxDM	Inc.	Inc.	17	3.46	14.06-19.73	821.54	823.28	41.13	3.29×10^{-10}
Maximum	No	HMMDM	Inc.	Exc.	17	3.27	11.56-24.57	824.07	825.07	42.92	1.34×10^{-10}
Maximum	No	MMDM	Inc.	Exc.	17	3.28	11.60-24.65	824.29	825.29	43.14	1.20×10^{-10}
Maximum	No	MDB	Inc.	Exc.	17	3.28	11.61-24.67	824.29	825.29	43.14	1.20×10^{-10}
Maximum	No	MaxDM	Inc.	Exc.	17	3.29	11.62-24.70	824.72	825.72	43.57	9.71×10^{-10}

Table 3.7: Results of the right-side Maximum and Conditional likelihood SECR analyses, together with the inclusion and exclusion of a road covariate and the translocated individuals, also highlighting the difference between pooled and unpooled sampling occasions. Four buffer widths were examined, MDB (482m), HMMDM (1808m), MMDM (3615m) and MaxDM (15760m).

Likelihood	**Pooled sampling occasions**	**Buffer**	**Translocated BH**	**Road covariate**	**Density/ 100km^2**	**S.E**	**95% CI**	**AIC**	**AIC$_C$**	**ΔAIC$_C$**	**AIC$_C$ weight**
Conditional	No	MDB	Exc.	Inc.	14	2.89	8.53-19.85	879.92	881.92	0	0.28
Conditional	No	MMDM	Exc.	Inc.	14	2.91	8.58-19.98	880.08	882.08	0.16	0.26
Conditional	No	HMMDM	Exc.	Inc.	14	2.89	8.54-19.88	880.17	882.17	0.25	0.24
Conditional	No	MaxDM	Exc.	Inc.	14	2.89	8.54-19.88	880.36	882.36	0.44	0.22
Conditional	Yes	MDB	Exc.	Inc.	14	2.89	8.52-19.83	899.4	901.40	19.48	1.63 x10^{-5}
Conditional	Yes	MMDM	Exc.	Inc.	14	2.91	8.58-19.97	899.53	901.53	19.61	1.53 x 10^{-5}
Conditional	Yes	HMMDM	Exc.	Inc.	14	2.89	8.53-19.87	899.65	901.65	19.73	1.44 x 10^{-5}
Conditional	Yes	MaxDM	Exc.	Inc.	14	2.89	8.53-19.87	899.85	901.85	19.93	1.30 x 10^{-5}
Conditional	No	MDB	Inc.	Inc.	15	3.04	9.48-21.40	912.59	914.41	32.49	2.44 x 10^{-8}
Conditional	No	MMDM	Inc.	Inc.	16	3.06	9.54-21.54	912.71	914.53	32.61	2.30 x 10^{-8}
Conditional	No	HMMDM	Inc.	Inc.	15	3.05	9.49-21.43	912.82	914.63	32.71	2.19 x 10^{-8}
Conditional	No	MaxDM	Inc.	Inc.	15	3.05	9.49-21.44	913.14	914.96	33.04	1.86 x 10^{-8}
Maximum	No	MDB	Inc.	Exc.	15	3.02	10.57-22.56	915.73	916.77	34.85	7.50 x 10^{-9}
Maximum	No	MMDM	Inc.	Exc.	16	3.03	10.63-22.70	915.85	916.89	34.97	7.06 x 10^{-9}
Maximum	No	HMMDM	Inc.	Exc.	15	3.02	10.60-22.62	915.96	917.00	35.08	6.69 x 10^{-9}
Maximum	No	MaxDM	Inc.	Exc.	15	3.02	10.60-22.61	916.27	917.32	35.40	5.70 x 10^{-9}

DISCUSSION

Population estimates

Reliable population estimates are essential in being able to conserve populations effectively (Stander 1998; Gusset and Burgener 2005; Efford *et al.* 2009; Manning and Goldberg 2010; Núñez-Pérez 2011). The diversity of methods available for population density estimation is considerable and collecting perfect data is often unrealistic, especially when estimating the population density of cryptic carnivores (Blake and Hedges 2004; Linkie *et al.* 2006; Efford *et al.* 2009*;* Manning and Goldberg 2010; Kéry *et al.* 2011). This study used a method to estimate absolute abundance as opposed to relative abundance, as the former are generally more comparable in different environments and are more consistent on a larger scale (Hayward *et al.* 2002; Bart *et al.* 2004; Stephens *et al.* 2006; Balme *et al.* 2009). It is critical that this type of research is consistent and results are comparable over time, in order to monitor animal populations successfully (Gese 2001; Balme *et al.* 2009).

The density estimates obtained in the present chapter were considerably higher than estimates for brown hyaenas elsewhere. Indeed, the estimated 14-20 individuals/100km^2 is among the highest of brown hyaena estimates on record. Although there has been little work conducted in this regard, the range of brown hyaena densities across all other published studies is estimated at between 1.8 and 4.4 individuals/100km^2 (Mills and Mills 1982; Mills 1984; Mills 1990; Maude 2005; Thorn *et al.* 2009; Kent and Hill 2013). The variation in results across different studies is probably related to a number of factors, including vegetation type, predator and prey density, land-use and the presence or absence of spotted hyaenas (Owens and Owens 1978; Skinner and Van Aarde 1981; Balme *et al.* 2007; Mills 1990). As brown hyaenas have never been studied in the Thicket biome, it is unclear whether these density estimates reflect natural densities for this type of habitat, or whether they are un-naturally high due to the site being an enclosed and actively managed reserve.

The number of individual brown hyaenas within a clan has previously been associated with the availability of food resources within that territory (Mills 1984; Mills 1990). As the abundance of potential food resources is relatively high in Kwandwe (see Chapter 2), individual clans could potentially support a large number of individuals, and this could possibly explain the high population estimate in Kwandwe. In addition, Kwandwe has a particularly high predator density in comparison to other areas, e.g. Kwandwe lion density of 5 individuals/100km^2 *cf.* Kalahari lion density of 2 individuals/100km^2 (Mills *et al.* 1978); Kwandwe leopard density of at least 7 individuals/100km^2 *cf.* Namibia and Kalahari leopard density of 1.5 individuals/100km^2 (Stander *et al.* 1997); Kwandwe cheetah density of 4.37 individuals/100km^2 *cf.* Kalahari cheetah density of 0.57 individuals/100km^2 (Kleine 2007). These high predator numbers, and the associated high abundances of prey to support the predators, may provide increased scavenging opportunities for the brown hyaena population in the reserve and further add to their success in this environment. This theory is supported by a recent study in Limpopo which described that apex predators facilitate brown hyaena scavenging, leading to higher brown hyaena densities, when compared to areas with no apex predators (Yarnell *et al.* 2013). Predator density is often associated with prey density, and if prey are supplemented annually, the predator densities may be artificially high (Fuller and Sievert 2001). In addition, the Kwandwe brown hyaena population may have more scavenging opportunities as spotted hyaenas have not been reintroduced to Kwandwe. While other predators such as lions are known to scavenge, the dominant scavenging competitors for brown hyaenas in the Kalahari are spotted hyaenas (Mills 1990). Brown hyaena distribution and numbers can be influenced by spotted hyaenas, with the latter dominating brown hyaenas, and in areas where spotted hyaenas are present, brown hyaenas are often rare or absent (Skinner and Van Aarde 1981; Mills and Mills 1982; Mills 1990). In the present study, there were no reports of lion-induced brown hyaena mortality, and the high brown hyaena population estimates suggest that lions have little influence on these scavengers. Indeed, in other regions it has been suggested that lions are more beneficial than detrimental to brown hyaenas, despite occasional antagonistic encounters (Mills 1990). These factors are likely to increase scavenging success through increased carcass availability and this may be associated with the population number, potentially explaining the considerably higher density estimates made in the present study.

Finally, it is uncertain whether brown hyaenas are merely scavenging, or whether this dense vegetation type could allow for more successful hunting. Brown hyaena individuals have been observed carrying a whole carcass on camera within Kwandwe and on other similar sized reserves in the area (C. Bissett and K. Muller pers. comm. 2013). Brown hyaenas are predominantly scavengers and their hunting technique is described as primitive, involving zig-zag chases or short dashes (Owens and Owens 1978; Mills 1990). The prevalence of extensive cover in the thicket environment could facilitate ambush scavenging (and possibly hunting) tactics compared to the more arid areas where they have previously been studied, further adding to their success. Indeed, one of the main threats to brown hyaenas outside protected areas is associated with human-carnivore conflict (Mills 1998b). They are often perceived as a threat to livestock and therefore are persecuted by farmers. Knowledge of their hunting abilities, or lack thereof, in thicket habitat could be used as a conservation tool through the education of farmers and others persecuting brown hyaenas outside protected areas.

Methodology

The density estimates from this study varied slightly depending on the different methods used to analyse the data, which is common with these analyses (Tobler and Powell 2013). Studies that have evaluated the various methods for estimating densities have found that SECR methods produce the best results due to the option to add covariates, and the addition of spatial information used in the sampling process (Tobler and Powell 2013). In many capture-recapture analyses these additional factors have been shown to influence capture probability (Borchers and Efford 2008). To avoid bias in estimates, capture probabilities of the least catchable individuals must be modeled and when location can influence capture probability, it is important to incorporate this (Borchers and Efford 2008). Additionally, the incorporation of spatial information allows abundance estimates to be reliably converted into density estimates (Borchers and Efford 2008).

Firstly, the data were analysed with DENSITY 5.0 (non-spatial analysis) to acquire abundance estimates. Models M_h (Jack-knife estimator) and M_o were selected as the most appropriate models for the analysis, using CAPTURE. M_o assumes all members within the population have a constant and equal probability of capture over the duration of the study, which is convenient mathematically; however this assumption is usually violated in wild populations and is considered too simplistic (Burnham and Overton 1978). M_o has therefore been found to consistently underestimate true abundance figures (Burnham and Overton 1978; Chao and Huggins 2005; Tobler and Powell 2013). Model M_h, which assumes heterogeneous capture probability, is more realistic in wild populations as individual capture probability will vary with age, sex and social status (Harmsen *et al.* 2011; Foster and Harmsen 2012), justifying this model as the default choice for most camera trapping studies (Karanth and Nichols 1998; Soisalo and Cavalcanti 2006; Tobler and Powell 2013). M_h

assumes that there is no behavioural response to capture by individuals and use of a scent lure could, in theory, promote a behavioural response and induce ‘trap addicted’ behaviour (Otis *et al.* 1978). However, many individuals were captured only once at particular camera sites and the use of the lure does not appear to have attracted the same individuals to the same spot repeatedly. For both left- and right-side analyses the criterion score for the model that assumes individual behavioural responses (M_b) was much lower than that for M_o and M_h. The M_h model is considered more robust than the M_o model, however when capture probabilities are small (< 0.1), this model has been found to be a poor estimator and can often be imprecise (Harmsen *et al.* 2011; Tobler and Powell 2013). Abundances can also be overestimated with the M_h model if there are high levels of heterogeneity in the detection probabilities between animals (Link 2003; Harmsen *et al.* 2011). Additionally, if almost all animals in the population are captured the M_h model can sometimes overestimate the true population size (Chao and Huggins 2005), as this method does not provide a technique to quantify the level of heterogeneity between the animals. Thus caution is needed when estimating the abundance of populations that have low and heterogeneous capture probabilities, and findings have suggested that when these conditions are met the M_h estimator may be unreliable (Harmsen *et al.* 2011). Pooling the sampling occasions has been suggested as a way of increasing overall capture probability (Harmsen *et al.* 2011). However, collapsing the data can reduce the number of individuals captured several times and this can result in poorer, more biased results (Tobler and Powell 2013). Furthermore, many species display a difference in ranging behaviour between the sexes (Sunquist and Sunquist 2002), with males having larger home ranges and therefore higher capture probabilities. Brown hyaenas exist in clans and clans will defend their territories (Owens and Owens 1979a; Owens and Owens 1979b; Mills 1982a), while nomadic males also exist outside of clans and have a very large and non-fixed home range (Mills 1982b). If nomadic males cover larger areas they may have higher capture probabilities. Unfortunately, it was not possible to sex brown hyaenas from profile photos in this study as there is no obvious sexual dimorphism and no identifiable differentiation between clan-living and nomadic males (Owens and Owens 1996).

The assumption of closure, required by capture-recapture methods, is often violated when studying natural populations (White *et al.* 1982; Karanth 1995; Soisalo and Cavalcanti 2006). Indeed, closure was violated in this study as two individuals were translocated from the reserve in the middle of the camera survey. However, closure was tested for in the program and the violation was not detected, highlighting potential inaccuracy of this statistical test.

Non-spatial analyses are beneficial as the inclusion of buffer widths is not required in a closed system where the size of reserve is known. The ETA was defined as the reserve area; results from collar data and sampling bordering properties revealed it unlikely that individuals regularly leave the fenced reserve. In open systems the inclusion of buffer widths to non-spatial density estimates has been found to alter density estimates dramatically (Sollmann *et al.* 2011).

SECR models have been found more accurate than the non-spatial models, as site information and covariates can be included in the analysis, producing unbiased results (Tobler and Powell 2013). This study ran various SECR models, including differing buffer widths with a combination of a road covariate and inclusion and exclusion of the translocated individuals. Results were compared statistically using AIC_C values; left- and right-side data were compared separately. Results for left-side SECR analyses varied by 1 individual/100km^2, whereas for right-side analyses results varied by 2 individuals/100km^2. For both left- and right-side analyses, results revealed that the most appropriate model was achieved when a road covariate was included, translocated individuals were excluded and when sampling occasions were not pooled. Adding a road covariate has also been found to improve estimates in other studies (Sollmann *et al.* 2011). Density estimates were not affected when sampling occasions were pooled, but this method was found to be less appropriate according to AIC_C values. Pooling data can lead to biased results and can reduce the number of individuals captured several times (Tobler and Powell 2013). In each scenario the buffer width did not affect the density estimate and made little difference to AIC_C values. SECR analyses require buffer widths to be added to the models, but these have been found to have less of an effect on density estimates than when they are included for non-spatial population estimates (Sollmann *et al.* 2011). Although different buffer widths were used, the area inside the reserve was always defined as habitable and the area outside the reserve as uninhabitable for each model.

Roads were extremely successful in capturing brown hyaenas on camera and this study recommends the use of roads in future studies of this nature. It has been suggested that preferential placement of cameras in certain places may select for a subset of the population, for example, placing cameras solely on game trails for jaguar studies, may exclude many females from the survey as these pathways are dominated by males (Foster *et al.* 2010). Recommendations are that camera placement is selected based on background information and that placement should maximise capture probability to increase accuracy and precision of results (Tobler and Powell 2013). As the sex of individuals was unknown in this study it is suggested that this is investigated further before prioritising road use for such camera studies. However, collared animals of both sexes were found to use roads extensively, although the sample sizes were very low (see Chapter 4).

Using one camera per site produced enough data for analysis, however only half the data could be used, as building full profiles of individual brown hyaenas was not possible. A scent lure was used to try to hold the individuals at the camera for longer in the hope that both sides would be recorded. Although the scent lure did hold individuals in position for longer, both sides were usually not recorded. If repeated, two cameras per site would be more beneficial (Negrões *et al* 2010). If both cameras are positioned on a road and a scent lure is used it is more likely that a clear image of both sides of the animal would be captured and a full profile created. However, when camera numbers are restricted, using one camera per site has been found to produce adequate data for analysis. A scent lure was used rather than bait, as the function was to keep the animal stationary in front of the camera; not draw individuals in from outside their home ranges (Ancrenaz *et al.* 2012). The scent lure was successful in this function as collared individuals were observed to use roads parallel to game paths with scent lure and did not deviate from their route. If use of a scent lure is standardised and effort is constant across all sites it poses no statistical concerns for capture-recapture studies (Henschel and Ray 2003).

This study concludes with a population density estimate based on left-side results, as more individuals were identified using this set of images. From these images, the SECR analysis with the lowest AIC score (including a road covariate, excluding translocated individuals and sampling occasions not pooled) of 16 individuals/100km^2, equivalent to an abundance of 29 individuals in the reserve, is presented as the most appropriate estimate. This estimate is to be considered a minimum estimate for the reserve, as some photos were discarded due to poor quality and the estimate is very close to the number of individuals positively identified. It is likely that the density estimate will fall within the 95% confidence intervals for this analysis (9-22 individuals/100km^2). However, since 26 individuals were positively identified (excluding the translocated hyaenas), it is more reasonable to say that the density will fall within 14 to 22 individuals/100km^2, equivalent to an abundance of between 26 and 40 individuals.

This study has successfully produced the first brown hyaena density estimate in the Eastern Cape, South Africa, using camera trapping. The work suggests that Kwandwe Private Game Reserve has among the highest density of brown hyaenas recorded in their range. Furthermore, this study has highlighted camera trapping as a successful method of estimating brown hyaena population density in an enclosed reserve/thicket vegetation, and that when the number of cameras is limiting, the use of one camera per site is sufficient when used in conjunction with a lure. In addition, SECR methods have proven successful, and when the ETA is fixed these methods are robust to differences in buffer width in the program DENSITY 5.0.

CHAPTER 4.

CHARACTERISTICS OF HOME RANGE AND SPACE USE BY BROWN HYAENAS

The collaring of BHM2

INTRODUCTION

Wild carnivore habitats are often isolated and inaccessible due to physical barriers such as mountains, deserts, rivers or dense forests (Karanth *et al.* 2010). Previously, the predominant method of attaining information on carnivore behaviour, use of space, and social interactions was through a more classic natural history approach, involving physical observations (Karanth *et al.* 2010). Within the past 50 years, however, technologies have developed rapidly, revolutionising the field, and ecologists are now presented with a wide range of exciting new tools to study carnivore biology, ecology and behaviour (Karanth *et al.* 2010). Because of the problems in observing wild, elusive carnivores, radio telemetry and GPS collars present one of the most important tools currently available to ecologists in carnivore ecology and behaviour (Amlaner and Macdonald 1980; Kenward 1987; Wilson *et al.* 1996). Telemetry data can provide answers to questions on space use, intra-specific relationships and behaviour that would be difficult to obtain otherwise (Karanth *et al.* 2010).

In an animal's use of space, 'home range' is a fundamental concept that was first described by Burt (1943) as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range." This definition has been adapted with time as it contains recognised problems, such as the term "occasional sallies", which is vague and can only be truly defined within the context of a known home range (Kie *et al.* 2010). The more recent statistical definition was described by Van Winkle (1975) as a utilisation distribution, defining it as "the two-dimensional relative frequency distribution for the points of location of an animal over a period of time." Utilisation distributions reveal the relative amount of time spent in any one place (Seaman and Powell 1996). Territories differ from home range by being described as an area within a home range that an animal has exclusive use of (Powell 2000). Territories can be the same size as home ranges, but have also been found to be both larger and smaller in different study areas (Ewer 1973; Powell 2000; Boydston *et al.* 2003a). Several factors determine the use of space and habitat selection. For carnivores this is typically the distribution of resources, in particular food, with wider resource distribution leading to larger home ranges (Macdonald 1983; Spong 2002).

Brown hyaenas occupy territories that are actively defended against members of neighbouring clans and the distribution of food has been found to affect both territory size and movement patterns (Mills 1982a). Territory size is correlated with the average distance travelled to find food and where food is widely available, territory sizes are smaller (Mills 1982a). Consequently, it was suggested that the territory size of brown hyaenas was directly related to food distribution. This was also observed on livestock farms in Botswana, where livestock carcasses provided a closely distributed, abundant food source throughout the year. As predicted, home range sizes were smaller than in a neighbouring national park that provided fewer scavenging opportunities (Maude 2005). Skinner *et al.* (1995) observed that home range size was not so much affected by the availability of food, but rather the dispersion of food items across the environment.

Another key resource that may affect home range and use of space in brown hyaenas is the availability of secluded den sites (Mills and Mills 1982; Mills 1990). The locations of den sites are usually found centrally, far from territory boundaries and can indicate the quantity and quality of resources within a home range (Doncaster and Woodroffe 1993). Brown hyaena den sites are commonly scattered with carcasses because adults bring food back for cubs (Mills and Mills 1982). The strong smells are often an attractant for other larger carnivores and therefore secluded den sites are important within a home range and this will certainly affect space use (Mills and Mills 1982; Mills 1990). Mills (1990) found that the locations of den sites were not random and that they were located in areas that attracted few competitors. The availability of fresh water also influences space use in brown hyaenas, with increases in home range size observed under low fresh-water availability (Owens and Owens 1978; Skinner and van Aarde 1981; Mills 1987; Wiesel 2006). In Namibia, individuals were found to travel outside their home ranges in search of water during the dry season (Wiesel 2006). While the influences of food and water availability and den site location on brown hyaena space use are relatively well understood, the link between home range size and vegetation type is less clear. This is presumably due to the paucity of research on the species, as most space use studies have been conducted in arid regions where dense vegetation is not a major feature. Indeed, vegetation type has been identified as a feature in determining space use in the closely related spotted hyaena (Boydston *et al.* 2003b) and other carnivores such as cheetahs (Bissett and Bernard 2007; Pettorelli *et al.* 2009).

The understanding of how a species interacts with its environment is fundamental in ecology (Worton 1987; Mills 1991). Knowledge of factors influencing space use and habitat selection by a species is essential in developing appropriate management strategies (Mills 1991; Marker *et al.* 2008; Pettorelli *et al.* 2009; Wiesel *et al.* 2008), especially in enclosed systems where the use of space is restricted.

Aims

The aims of this chapter were to investigate the home range and space use of individual brown hyaenas in Kwandwe Private Game Reserve, South Africa. It was predicted that because of the large numbers of potential prey items in the reserve (see Chapter 2), home ranges would be smaller than those observed in the more arid regions of southern Africa where prey is relatively scarce. In addition, this chapter also provides baseline information on habitat use, specifically information on the use of elevation, slope, distance to drainage lines and habitat type.

METHODS

Three adult brown hyaenas (two males and one female) were caught and collared in February 2013 and were subsequently monitored over one calendar year. The collars did not have remote drop offs, but management agreed to recapture animals and remove collars after the research was conducted.

Capture and immobilisation

Iridium satellite GPS/VHF collars (African Wildlife Tracking, Rietondale, Pretoria) were attached to the three brown hyaenas to obtain global positioning data on which to base home range estimates. Various methods are used for trapping large carnivores, including free-darting, cage trapping and foot-loop trapping (Mills 1990; Logan *et al.* 1999; Reagan *et al.* 2002; Frank *et al.* 2003; Maude 2005; Wiesel 2006; Grant 2012). Foot-loop trapping has been shown to cause minimal injury to captured animals (Frank *et al.* 2003) and was therefore used to capture the intended study animals (Figure 4.1). Five locations were chosen as potential trapping sites based on the presence of brown hyaena latrines and were close enough to each other (~ 5.5km apart) to be checked quickly and efficiently, but far enough apart to capture individuals from different clans. Trap sites were built up with vegetation creating a cubby set (Figure 4.2), the foot-loop device was initially left unarmed at each site and the sites were baited with pieces of warthog to entice brown hyaenas into the trap sets. Infra-red cameras (Bushnell Trophy Cam 119636c, Bushnell Outdoor Products, Kansas City, Missouri) were placed at each site to monitor potential brown hyaena activity. This “pre-baiting” practice was conducted for approximately three weeks to allow brown hyaenas to become familiar with the sites and the equipment before being captured.

Figure 4.1: Equipment used in the foot-loop trapping method, a. The throw arm or spring b. Using measuring tapes allows enough pressure to be placed upon them so the animal commits to foot placement c. Once the animal has committed to foot placement the measuring tape collapses d. The throw arm is buried into the ground and the treadle rests on the measuring tape e. The hole in the ground is covered with cloth f. Finally the cloth is covered with substrate and the loop is placed above.

When trapping commenced, traps were covered with vegetation to disguise their presence. Rocks and thorny vegetation (*Acacia karroo* and *Azima tetracantha*) were used to create a pre-defined path of entry into the cubby-set and guide the animal's foot placement onto the trigger (Frank *et al*. 2003) (Figure 4.2). An additional, older VHF collar was hung above each trap. A magnet was carefully attached to the collar on top of a piece of string with masking tape and to the throw arm of the trap. If the trap was triggered, the magnet detached from the collar and a signal could be detected using telemetry equipment (Communications Specialists Inc. Model R1000, California, USA) from a safe distance (~ 200m). Once traps were prepared, blood was dripped over the equipment and intestinal contents were scattered in the area to attract the hyaenas and to cover the smell of human activity. The traps were set at 1700h and were first checked at 2200h and then every two hours until 0600h. If nothing was caught by 0600h, the traps were disarmed. The capture effort was calculated by multiplying the total number of nights to catch the three hyaenas by the number of traps set.

Figure 4.2: Setting the foot-loop traps a. Natural cubby set with bait placed at the far end b. Man-made cubby set built up with acacia vegetation c. Foot placement set for a front left foot capture d. Foot placement set for a front right foot capture.

Captured hyaenas were darted by a qualified veterinarian from the back of a vehicle using a Dan-Inject CO_2 pressured dart gun (Dan-Inject, Skukuza, South Africa) set at a pressure of 5 bars with a 1.5ml dart and a 30mm collared needle. Large muscle groups of the hindquarters or shoulders were targeted for a dart entry point (Kreeger and Arnemo 2007). Zoletil 100 in combination with Medetomidine was administered. Zoletil was diluted within the range of 20-40mg/ml and Medetomidine was diluted between 2 and 4mg/ml (Appendix VI). Once the animal was recumbent, the collar was attached around its neck, ensuring that there was sufficient space for the collar to move without friction (Sikes *et al.* 2011). Morphological measurements, weight, hair samples, blood samples and ectoparasite samples were also collected (Figure 4.3 and Appendix VI). Temperature, pulse rate, respiration rate and blood pressure were monitored throughout the procedure. Necrospray was administered to any cuts or injuries and all hyaenas were given long-acting penicillin injections, multi-vitamins and anti-inflammatory injections (meloxicam). The Medetomidine was reversed with atipamezole and recovery times varied amongst the individuals (Appendix VI). Individuals were left to recover in open areas to prevent injury and were observed until mobile. Capture and handling was in accordance with the Rhodes University ethical standards protocol under the ethical clearance number ZOOL-11-2012.

Figure 4.3: The capture and collaring of BHM1, a. Attaching the collar b. Right-side profile c. Teeth were in reasonably good condition, indicating this individual to be a young adult d. Natural ear notches that can be used in the identification of individuals.

Collars had both GPS and VHF components included and weighed 740g, which is less than 2% of the average overall body weight of brown hyaenas and within acceptable ethical limits (Sikes *et al.* 2011) (Figure 4.4). The GPS allowed for the regular collection of data. The collars recorded the longitudinal and latitudinal locations every time the collars were set to record a fix. GPS fixes were set to record at 1700h, 2100h, 0100h and 0500h. Brown hyaenas are nocturnal and these times would capture positional data on active animals. Additional times were not set, so as to preserve battery life. However, for approximately two weeks after all data were collected, collars were set to record every hour to observe whether any data would be missed during the day. Individual animals were seldom active during the day and therefore collecting only nocturnal data was justified. Additionally, brown hyaenas typically rest in burrows or under bushes during the day (Owens and Owens 1979a; Mills 1990) where the satellite signal is weaker, and therefore setting fixes to record during the night increased the chances of location data being recorded. Positional data were viewed on a daily basis by accessing AWT's website (www.awetelemetry.com) and downloaded on a monthly basis in the form of excel spreadsheets (.xls).

Figure 4.4: GPS/VHF collar; VHF is the larger unit on the underside of the collar and the GPS unit is smaller and points upwards towards satellites.

Home range estimation

Home ranges were calculated since the active territory sizes of the clans were not known with certainty.

Kernel utilisation distributions

Kernel home range methods are commonly used and are well documented in the literature (Worton 1989; Worton 1995; Seaman and Powell 1996; Hemson *et al.* 2005; Laver and Kelly 2008). This method was first introduced as a home range estimator in 1989 (Worton 1989), and has since been incorporated in many computer and statistical packages (Seaman and Powell 1996). The resulting kernel density estimate represents an estimate of the amount of time spent in any one place. The technique operates by placing a density estimate (a kernel) over each GPS observation in a sample. A grid is subsequently superimposed over the kernels and density estimates are calculated at intersection points of the grid. This value is the average density of kernels overlapping that point. Observations in close proximity to the GPS point of consideration will contribute more to the density estimation than points further away. Consequently, areas with many observations will have high density estimates, and areas with few observations will have low density estimates (Seaman and Powell 1996). Home range estimates are then deduced in the form of isopleths that represent the 95% and 50% utilisation distribution of an animal across their home range (De Solla *et al.* 1999). The 95% (home range) and 50% (core area) utilisation distributions were calculated using home range tools (HRT) in ArcMap 9.3 (ESRI, Redlands, California) (Rodgers and Kie 2011).

Bandwidth

A crucial parameter in the estimation of utilisation distributions using kernels is the smoothing parameter, also commonly known as the h-value, window width or bandwidth

(Seaman and Powell 1996). The width of the kernel ultimately determines the kernel utilisation distribution output. When narrow kernels are applied to data, density estimates are more influenced by nearby fixes and therefore narrow kernels indicate the fine scale detail of distribution data (Worton 1995; Seaman and Powell 1996). Wider kernels are more influenced by outlying fixes and therefore reveal a more general distribution (Worton 1995; Seaman and Powell 1996). Choice of the smoothing factor should be objective and automated measures are available for the selection of this parameter. The H_{ref} value is described as the reference choice method (Worton 1995). It is automatically generated and is specific to each dataset. However, if the GPS data are not normally distributed, using the H_{ref} value can often lead to over-smoothed utilisation distributions (Kie *et al.* 2010). Solutions to this problem have been suggested in the literature and include fixing the H_{ref} values to a set proportion of 0.70 or 0.80 to reduce the over-smoothed results (Bertrand *et al.*1996; Kie and Boroski 1996; Kie *et al.* 2002). Alternatively, the H_{ref} value can be reduced until the point that the outermost polygon forms a continuous, non-fragmented line (Berger and Gese 2007; Jacques *et al.* 2009). Both methods are objective and repeatable. This study used a 0.70 proportion of the calculated H_{ref} value to reduce the over-smoothed isopleths.

Autocorrelation

Autocorrelation occurs when the assumption of independence between two successive observations is violated (Swihart and Slade 1985; Legendre 1993). One point in time and space is therefore a direct result of a previous point in time and space. Ecologists are often faced with this problem as animal movements are frequently non-random and therefore large GPS datasets are normally autocorrelated (De Solla *et al.* 1999). The regular monitoring of animal movements is not discouraged and autocorrelated data are often removed before analysis (De Solla *et al.* 1999). However, this topic has long been debated in the literature and the loss of information through the removal of autocorrelated data is fraught with contention, as critical biological information can be lost and fine-scale details of movement are removed (De Solla *et al.* 1999; Cushman *et al.* 2005; Kie *et al.* 2010). It is also argued that the original work describing negatively biased estimates caused by autocorrelated data is based on a flawed approach (Otis and White 1999). If the time between consecutive locations remains fairly constant, autocorrelation should not decrease the strength of home range estimates. However, due to the unequal observations of this study (De Solla *et al.* 1999), autocorrelated data were removed. Brown hyaena movements were monitored and individuals were observed traversing their entire home-range within a period of at least eight hours and certainly within 24 hours. Therefore, one fix per day (2100h) was analysed to ensure statistical independence between successive locations (Newdick 1983; Tew 1989; Mizutani and Jewell 1998; Maude 2005).

Brownian bridge

Brownian bridges are considered an improvement over existing utilisation distribution methods and base the estimation of an animal's utilisation distribution on movement patterns (Byrne *et al.* 2014). A Brownian bridge creates the probability of a movement trajectory based on a constant, random walk pattern between two points, and is dependent on the Brownian motion variance parameter (Horne *et al.* 2007). The Brownian motion variance is a critical parameter created for each individual animal based on its positional data and is associated with the activity of that animal. Brownian bridge home range estimations directly incorporate autocorrelation and location error values into analyses, therefore all spatial data can be included and the independence of successive points is not a concern (Huck *et al.* 2008). A grid is superimposed onto the study area and cumulative probabilities are generated across it, based on movement data between successive locations. Utilisation distributions can then be calculated from these probabilities. Two assumptions are associated with this method: the distribution of telemetry errors must follow a bivariate normal distribution, - an assumption which is suitable with GPS data - and that movement is random between successive locations. This latter assumption becomes less probable with an increase in time between successive locations (Horne *et al.* 2007).

All data were analysed in Animal Space Use 1.3 (Horne and Garton 2009). Input files consisted of the co-ordinates of observations, a cumulative time column, which indicated the cumulative time difference between each set of observations and a horizontal dilution of precision (HDOP) column, representing the precision of each observation based on the positions of overhead satellites (Van Sickle 1996). Probabilities were generated for each point of the grid, and from this cumulative probabilities were produced for grid points across the study area. These probabilities were analysed in ArcMap 9.3 to create 95% and 50% UD isopleths.

Home range overlap

The percentage overlap between animals was calculated for both methods of home range estimation. This was calculated by dividing each area of overlap by the relevant home range or core area for each individual and multiplying by 100. The results indicate the area of overlap as a proportion of the total home range for each individual.

Habitat and space use

The following analyses were conducted on Kernel home range data, as Kernel estimates appeared to represent actual space use more appropriately based on GPS data (see results).

Habitat selectivity was investigated at a broad scale, looking particularly at whether there was selection between open and thicket habitats. Water bodies were also included, as these occupied areas of land within each brown hyaena's home range. Simplification of habitat categories is an accepted method and has been used in other carnivore studies (Mills *et al.* 2004; Hayward 2006). At the individual level a chi-squared goodness-of–fit test was used to determine whether each brown hyaena was using the habitats as expected. Observed habitat use was calculated as the proportion of fixes that fell into each habitat type within an individual's home range. Expected figures were calculated by multiplying the total number of observations by the percentage of each habitat occurring within the 95% UD.

Further space use characteristics were calculated, including distance to drainage lines (m) and distance to roads (m) for each individual brown hyaena at the home range level, using ArcMap 9.3. Additionally, a digital elevation model (DEM) layer and a slope layer were created for Kwandwe and associated values were extracted for each brown hyaena observation within its home range.

Habitat selection was analysed at the home range level using a use vs. availability design (Johnson 1980). Resource selection functions (RSFs) were used to examine 3rd order habitat selection, investigating whether brown hyaenas select specific habitats within their home range (Johnson 1980). These analyses reveal selection patterns by comparing observed locations (GPS data) to random available locations (pseudo-absences) (Keating and Cherry 2004) using logistic regression models (Manly *et al.* 2002). Used locations were all points recorded within individual home range isopleths and available habitat was considered as the area within each home range. The number of random points generated was equal to the number of observed locations for each analysis (Klar *et al.* 2008). The variables investigated were elevation (m), slope (°), distance to roads (m), distance to drainage lines (m) and vegetation type (thicket vs. open). All variables were tested for co-linearity with no combination of predictor variables found to be co-linear (Dellinger *et al.* 2013).

Initially, use and availability data were combined across the three individual hyaenas to create a global RSF model. Subsequently, a sampling with replacement method was applied to ensure that each individual did not bias the global RSF model (Dellinger *et al.* 2013). This was achieved by excluding each individual from the analysis of a RSF model and remaining individuals were included, thereby creating preliminary RSF models (Dellinger *et al.* 2013). Coefficient signs and values were compared between global and preliminary analyses. If the coefficient sign changed between analyses and fell outside the confidence interval, the excluded animal was deemed to bias the global RSF model (Gillingham and Parker 2008). Logistic regression models began with key variables ($P < 0.05$) discovered using univariate logistic regression (Hosmer and Lemeshow 2000). Models were then built using a forward selection method, where variables were added to the model one at a time. Variables were selected using the method Alpha-to-Enter, using a value of 0.05 (Ghani and Ahmad 2010). Predictions were obtained by varying the variable in question over the range of observed values whilst keeping other variables at their mean. All analyses were conducted in R version 3.0.2 (R Development Core Team 2014).

Individual and clan home range estimations using camera data

Minimum convex polygons (MCPs) represent one of the simplest methods for calculating home range estimates (Worton 1987). Peripheral observations are joined and the resulting polygon represents the animal’s home range. MCPs are a form of polygon where each internal angle never exceeds 180 degrees, and the resulting polygon represents the smallest area to contain all observations (Worton 1987). MCPs are often criticised for incorporating outliers and therefore often include large areas of space that are infrequently used by animals (Harris *et al.* 1990). MCPs reveal the area of an animal's home range, but do not identify the intensity of use within a range (Worton 1987).

Nevertheless, rudimentary home range MCPs were calculated for the three collared individuals and an additional 10 brown hyaenas that were identified and photographed at four or more sites during the camera trapping survey (see Chapter 3). Right-side images were used, as this set of images contained a higher number of individuals photographed at four or more sites. MCPs from camera data were then compared with MCPs calculated from collar data to establish the accuracy of using camera data for the generation of MCPs. Putative clan (n = 3 based on camera trap and collar data) home range estimates were generated using the camera data MCPs.

RESULTS

Capture and immobilisation

Over a total of 13 trapping occasions (total number of traps set), all three brown hyaenas were caught, translating to a successful capture rate of one animal per 4.3 trapping occasions. Three collars were placed upon study animals on 13th February 2013 (BHM1, collar 603), 18th February (BHM2, collar 604) and 19th February (BHF1, collar 605). All three collars ran until 15th November 2013. After this date BHF1's collar (605) stopped recording her locations due to battery failure. BHM1 and BHM2's collars ran until February 2014.

Home range estimation

Home range sizes calculated using the Kernel method were 42.62km^2 for BHM1, 79.88km^2 for BHM2 and 72.40km^2 for BHF1 (Table 4.1, Figure 4.5). Core areas calculated using the same method were 17.53km^2 for BHM1, 30.09km^2 for BHM2 and 19.98km^2 for BHF1 (Table 4.1, Figure 4.5).

Table 4.1: 50% (core area) and 95% (home range) Kernel UD home range estimates, with the corresponding H values used, together with 50% and 95% Brownian bridge home range estimates for the three collared brown hyaenas. Number of fixes also indicated (N).

	Kernel UD (km^2)			**Kernel UD**	**Brownian bridge (km^2)**		
Brown Hyaena I.D.	**N**	**50%**	**95%**	**H value**	**N**	**50%**	**95%**
BHM1	361	17.53	42.62	519	1140	22.50	59.15
BHM2	366	30.09	79.88	653	1092	30.76	104.14
BHF1	259	19.98	72.40	638	1068	18.65	66.15

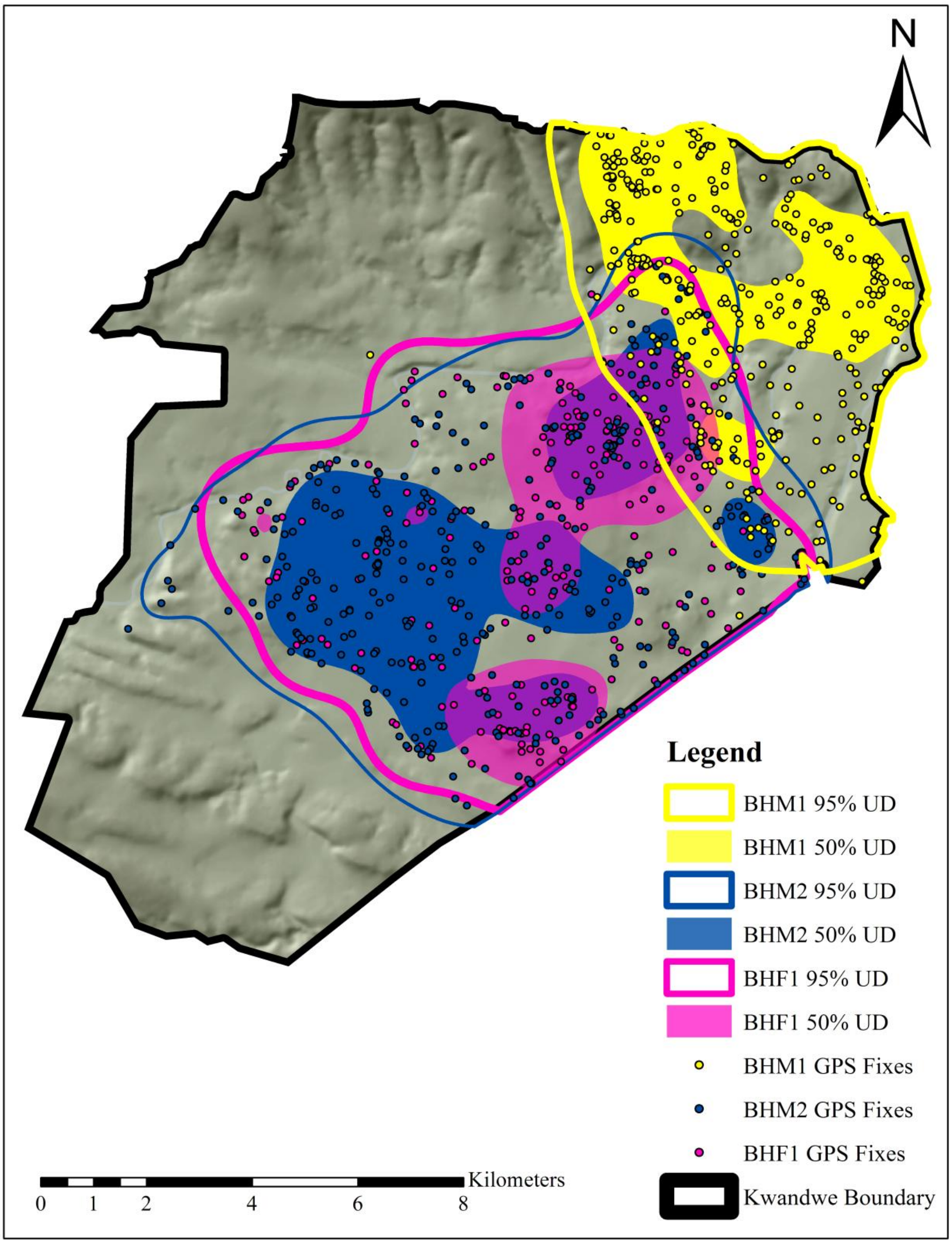


Figure 4.5: 95% and 50% Kernel UD home range estimates for the three collared brown hyaenas. GPS fixes used in the home range analysis are also presented.

Home range sizes calculated using the Brownian bridge method were 59.15km^2 for BHM1, 104.14km^2 for BHM2 and 66.15km^2 for BHF1 (Table 4.1, Figure 4.6). Core areas calculated using the same method were 22.50km^2 for BHM1, 30.76km^2 for BHM2 and 18.65km^2 for BHF1 (Table 4.1, Figure 4.6).

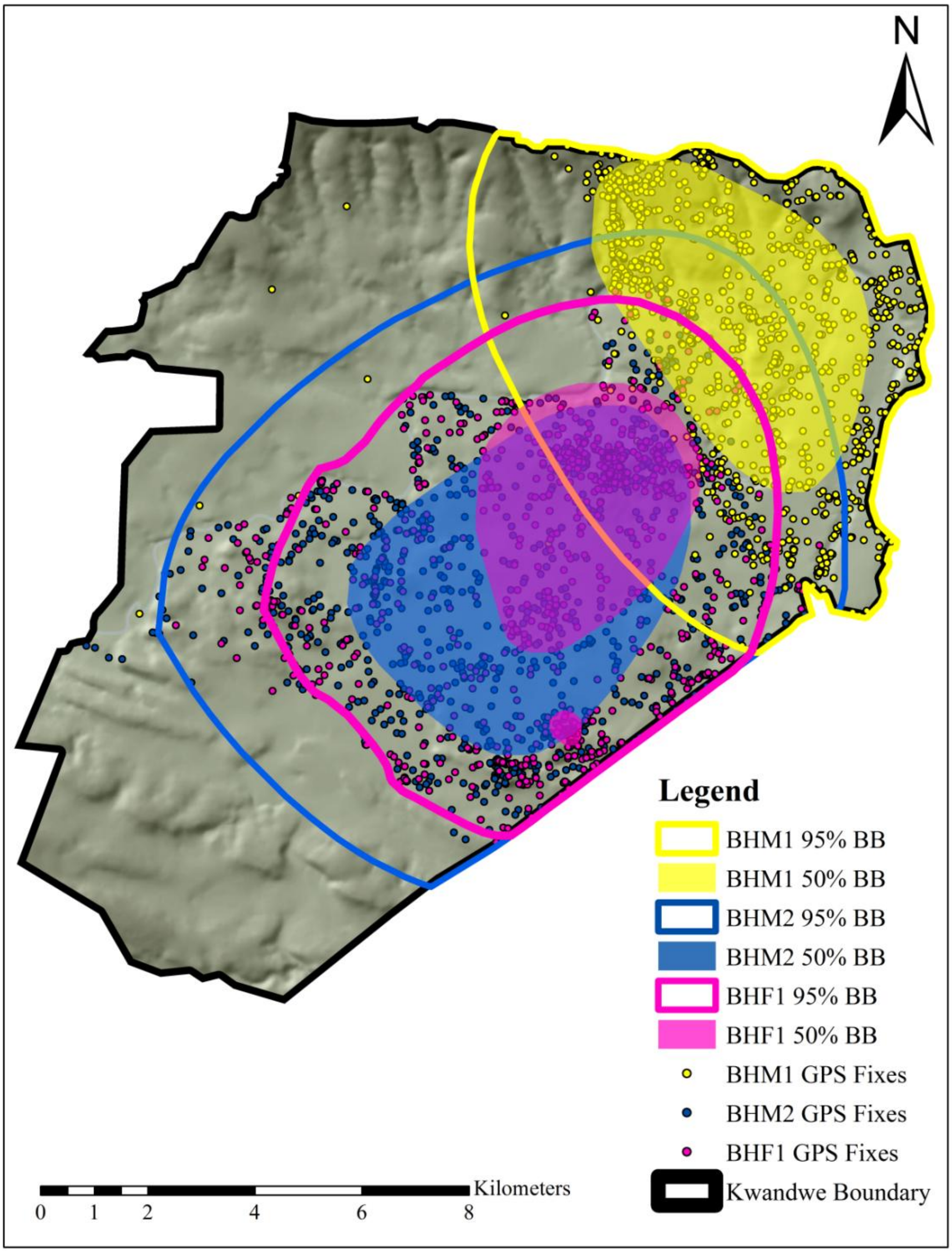


Figure 4.6: 95% and 50% Brownian bridge home range estimates for the three collared brown hyaenas. GPS fixes used in the home range analysis are also presented.

Home range overlap

The home ranges of BHM2 and BHF1 overlapped considerably, with 97.65% of BHF1's home range overlapping with the home range of BHM2 and 88.51% of BHM2's home range overlapping with BHF1 (Table 4.2). Both BHM2 and BHF1 overlapped noticeably less with BHM1, 18.08% and 15.07% respectively. BHM1's home range overlapped with BHM2 by 33.88% and BHF1 by 25.60% (Table 4.2). The same patterns were observed for core areas, where BHM2 and BHF1 overlapped considerably more with each other (55.31% and 36.72%, respectively) than they did with BHM1 (Table 4.2). Core area overlap never exceeded 1.65% between BHM1 with BHM2 and BHF1 (Table 4.2).

Table 4.2: The percentage overlap of each collared brown hyaena's Kernel UD home range and core area. This percentage is a proportion of the 95% and 50% Kernel UD for each brown hyaena.

		95% Kernel			50% Kernel	
	BHM1	BHM2	BHF1	BHM1	BHM2	BHF1
BHM1	-	33.88	25.60	-	0.02	1.65
BHM2	18.08	-	88.51	0.01	-	36.72
BHF1	15.07	97.65	-	1.45	55.31	-

Similar patterns were observed using Brownian bridge home range analysis. The home ranges of BHM2 and BHF1 overlapped extensively, 63.48% and 99.94% respectively (Table 4.3). Both BHM2 and BHF1, once again, overlapped considerably less with BHM1, 34.26% and 32.31%. BHM1's home range overlapped with BHM2 (60.32%) but overlapped noticeably less with BHF1, with only a 36.13% overlap (Table 4.3). There was only core area overlap between BHM2 and BHF1, 46.39% and 76.51% respectively.

Table 4.3: The percentage overlap of each collared brown hyaena's Brownian bridge home range and core area. This percentage is a proportion of the 95% and 50% Brownian bridge for each brown hyaena.

	95% Brownian Bridge			50% Brownian Bridge		
	BHM1	BHM2	BHF1	BHM1	BHM2	BHF1
BHM1	-	60.32	36.13	-	0	0
BHM2	34.26	-	63.48	0	-	46.39
BHF1	32.31	99.94	-	0	76.51	-

Habitat and space use

BHM1's home range was predominantly characterised by thicket vegetation, which made up 63.68% of the home range (Table 4.4). Within this home range BHM1 showed a slight preference for open habitat and water bodies, but this preference was not significant (Table 4.5). BHM2's home range also consisted of mainly thicket vegetation, which comprised 59.30% (Table 4.4). BHM2 showed a very small preference for thicket habitat, but this was not significant (Table 4.5). BHF1's home range was more evenly divided between thicket, which comprised 57.17%, and open vegetation, which comprised 41.69% (Table 4.4). BHF1 showed a significant preference for thicket (Table 4.5).

Table 4.4: Characteristics of the home ranges (95% UD) of individual brown hyaenas in Kwandwe. Data are presented as means ± SD.

	BHM1	BHM2	BHF1
Characteristics			
HR size (km^2)	42.62	79.88	72.40
Vegetation type (%)			
Open	33.97	39.46	41.69
Thicket	63.68	59.30	57.17
Water bodies	2.35	1.24	1.14
Elevation (m)	354.19±94.53	341.86±39.20	354.77±41.68
Slope (°)	5.52±4.65	4.27±4.97	6.73±6.94
Distance (m)			
Drainage lines	122.72±98.83	171.70±147.23	189.64±147.35
Roads	87.37±89.00	78.95±83.05	86.15±84.14

Table 4.5: Home range habitat use by individual brown hyaenas. Observed figures are the actual number of observations per vegetation type. Expected figures were calculated by multiplying the total number of fixes by the percentage of vegetation type occurring within the home range of each individual.

		Open	Thicket	Water bodies	χ^2 Results
BHM1					
	expected	117.98	222.08	6.94	χ^2=2.03, df=2
	observed	124	213	10	P > 0.05
BHM2					
	expected	141.96	214.76	7.28	χ^2=0.20, df=2
	observed	138	219	7	P > 0.05
BHF1					
	expected	108.36	147.06	2.58	χ^2=21.61, df=2
	observed	72	184	2	P < 0.001

When compared to the global RSF, the removal of all individuals resulted in changes to both the coefficient direction and magnitude, and therefore results for each individual hyaena are presented. Resource selection of BHM1 was influenced by distance to drainage lines, distance to roads and elevation (Table 4.6). The probability of hyaena presence decreased with increasing distance from drainage lines (Figure 4.7a), decreased with increasing distance from roads (Figure 4.7b), and increased with increasing elevation (Figure 4.7c).

Table 4.6: The top ranked model for describing resource selection for BHM1 in Kwandwe, between February 2013 and February 2014.

	Coefficient	S.E	Z value	P value
Intercept	-0.0970	0.3479	-0.279	> 0.05
Distance to drainage	-0.0029	0.0007	-4.145	< 0.001
Distance to roads	-0.0031	0.0009	-3.510	< 0.001
Elevation	0.0024	0.0009	2.516	< 0.05

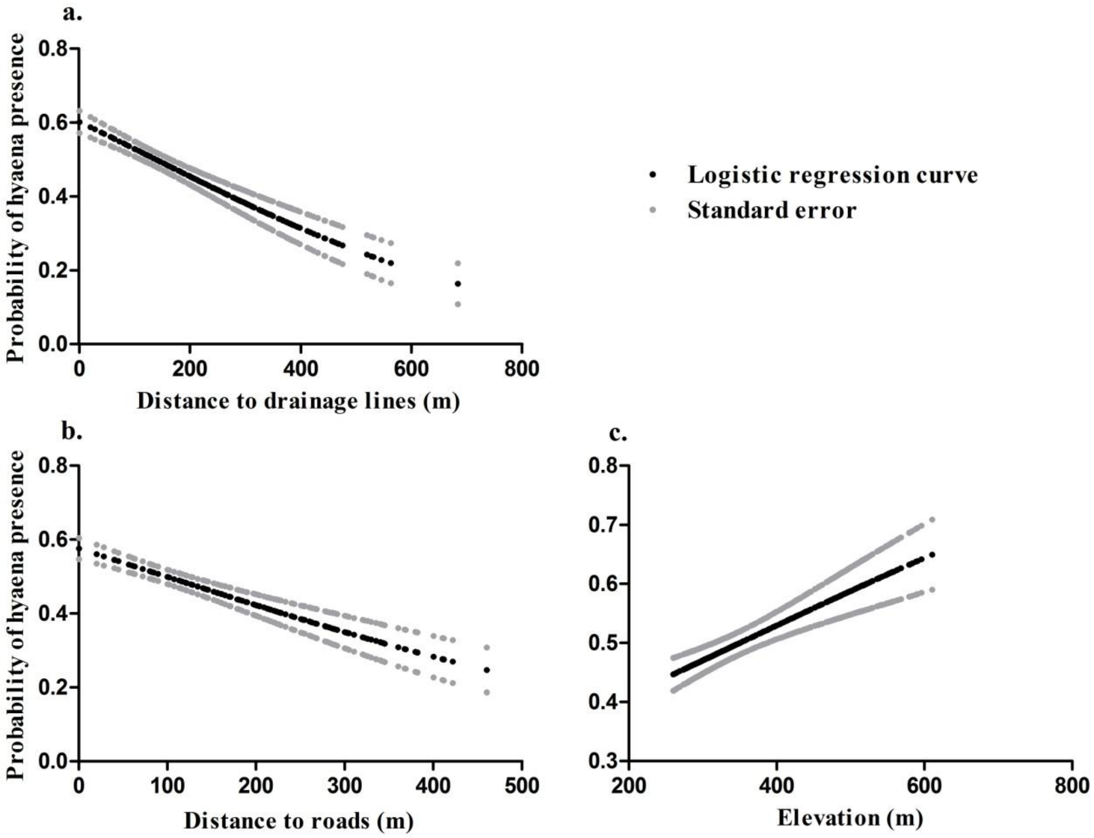


Figure 4.7: The probability of BHM1's presence with relation to a. distance to drainage lines, b. distance to roads, c. elevation, in Kwandwe, between February 2013 and February 2014.

Similarly, resource selection of BHM2 was influenced by the distance to roads, with no influence of elevation or distance to drainage detected (Table 4.7). As was the case for BHM1, the probability of hyaena presence decreased with increasing distance from roads (Figure 4.8).

Table 4.7: The top ranked model for describing resource selection for BHM2 in Kwandwe, between February 2013 and February 2014.

	Coefficient	S.E	Z value	P value
Intercept	0.2349	0.1099	2.137	< 0.05
Distance to roads	-0.0027	0.0009	-2.883	< 0.01

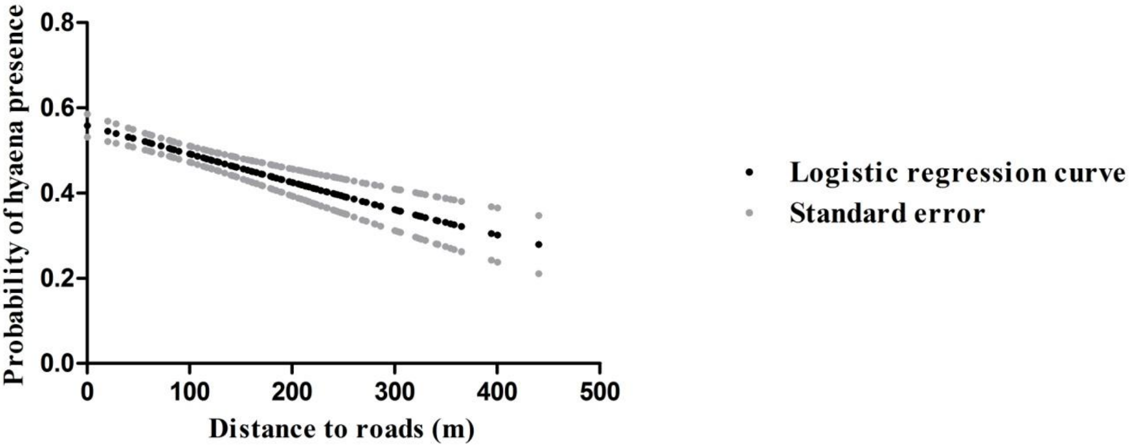


Figure 4.8: The probability of BHM2's presence with relation to distance to roads, in Kwandwe, between February 2013 and February 2014.

Resource selection of BHF1 was influenced by slope, elevation and distance to roads (Table 4.8). The probability of hyaena presence increased with increasing degree of slope (Figure 4.9a), decreased with increasing distance from roads (Figure 4.9b), and increased with increasing elevation (Figure 4.9c).

Table 4.8: The top ranked model for describing resource selection for BHF1 in Kwandwe, between February 2013 and November 2013.

	Coefficient	S.E	Z value	P value
Intercept	-2.2839	0.9175	-2.489	< 0.05
Slope	-0.0856	0.0206	4.161	< 0.001
Elevation	-0.0063	0.0027	2.296	< 0.05
Distance to roads	0.0036	0.0011	-3.161	< 0.01

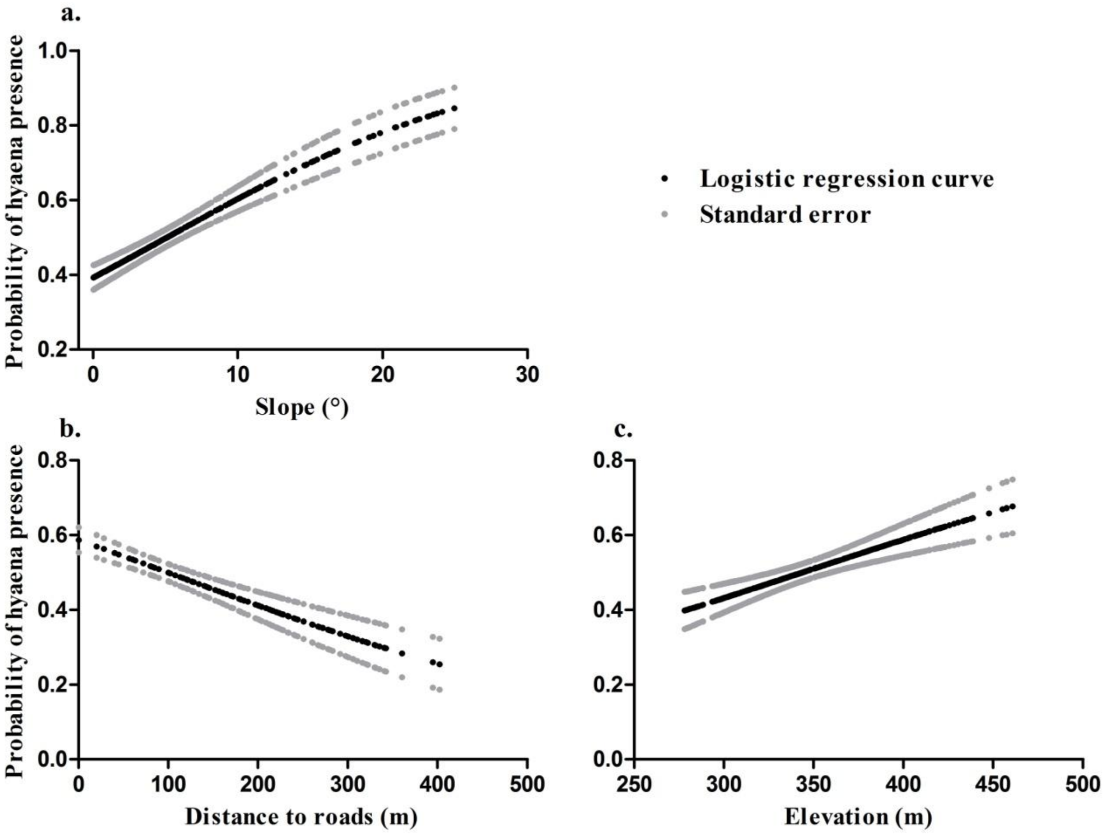


Figure 4.9: The probability of BHF1's presence with relation to a. slope, b. distance to roads, c. elevation, in Kwandwe, between February 2013 and November 2013.

Individual and clan home range estimations using camera data

Home range information for an additional 10 brown hyaenas was collected from camera data and included two males, two females and six unsexed individuals (Figure 4.10). Individual MCP home range data collected from cameras were considerably smaller than MCPs created from collar data (Table 4.9 and Figure 4.11), therefore the camera MCPs represent only a crude estimation of home range, and must be interpreted with caution.

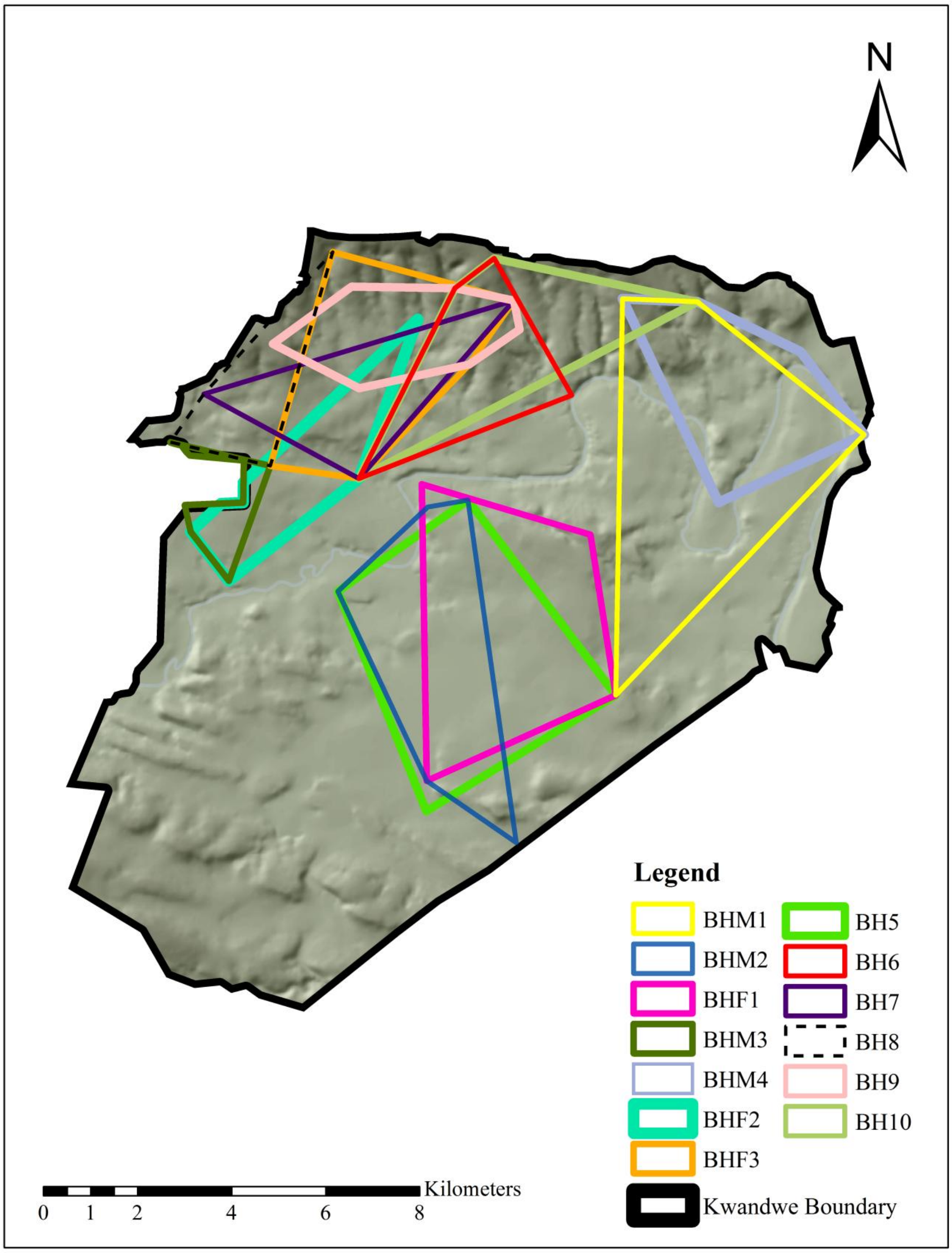


Figure 4.10: Camera MCP home range estimates for the three collared brown hyaenas and an additional ten individuals. MCPs were generated when individuals were captured at four or more different camera locations.

Table 4.9: Crude home range sizes for brown hyaenas captured on camera, with a direct comparison to MCP home range size of the three collared individuals.

Brown Hyaena I.D	Camera data 100% MCP (km^2)	Collar data 95% MCP (km^2)
BHM1	23.97	38.97
BHM2	14.29	66.11
BHF1	18.60	63.00
BHM3	1.95	-
BHM4	11.52	-
BHF2	7.58	-
BHF3	13.89	-
BH5	20.51	-
BH6	9.08	-
BH7	9.21	-
BH8	5.49	-
BH9	7.60	-
BH10	12.47	-

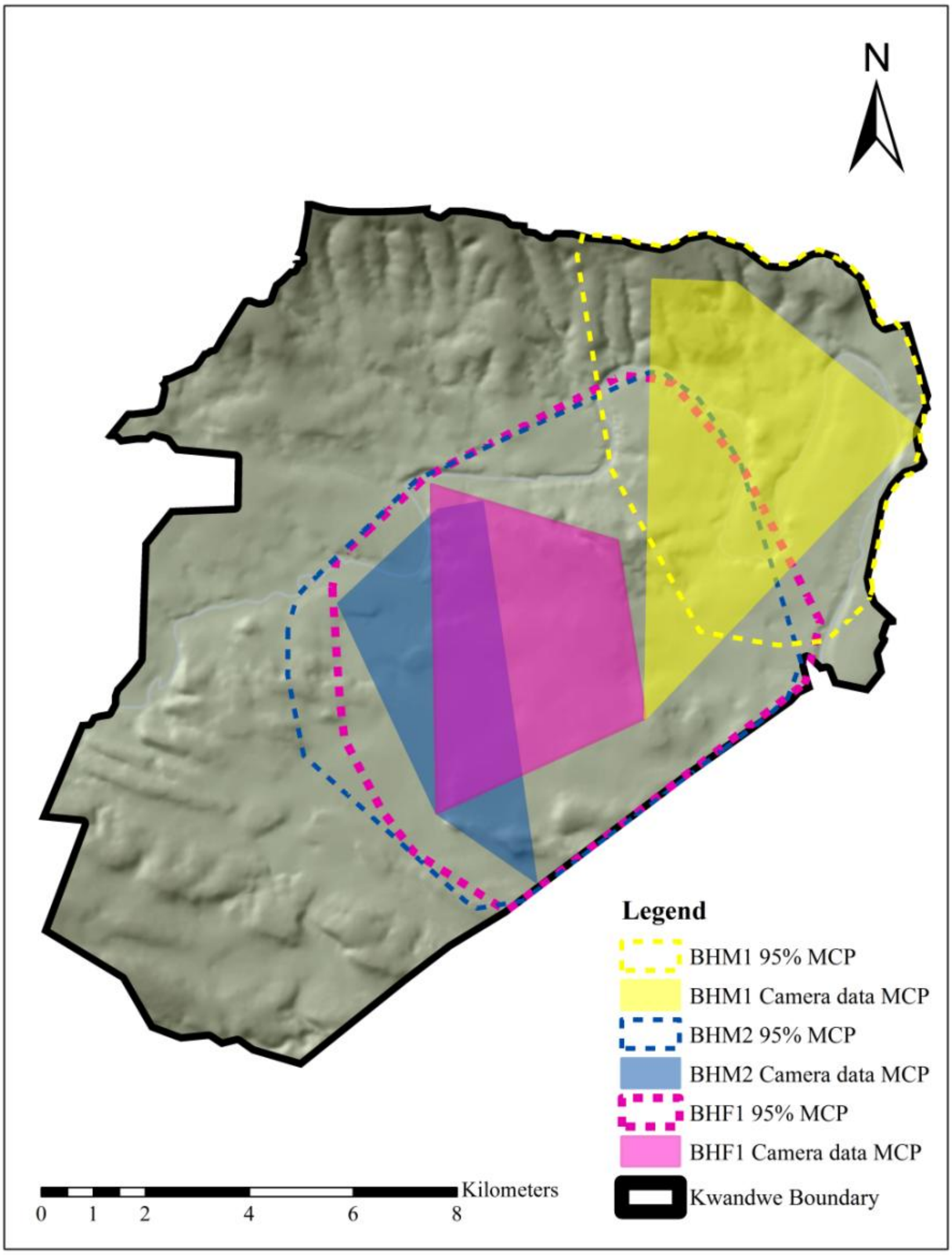


Figure 4.11: A comparison of camera MCPs with collar MCPs, indicating that MCPs calculated using camera data were considerably smaller than the collar MCPs for the same individuals.

There was considerable overlap with eight individuals in the north west of the reserve and this possibly represents one clan (Clan 1, Figure 4.12). One individual overlapped with

BHM2 and BHF1 (Clan 2) and the last individual overlapped with BHM1 (Clan 3), possibly representing a further two clans.

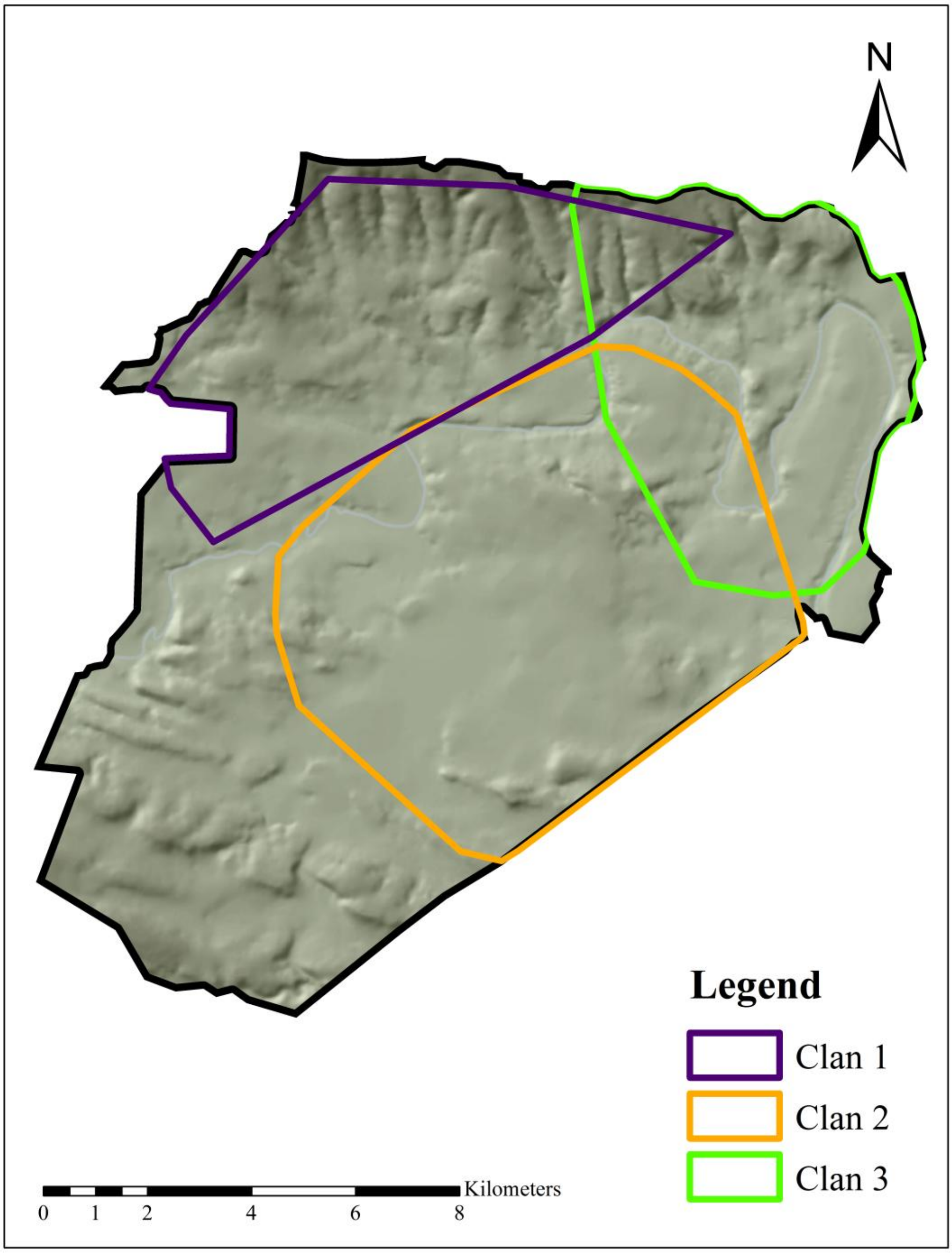


Figure 4.12: Camera MCP home range estimates were constructed from the individual camera MCPs, revealing three distinct clans.

The home range size of Clan 2 was the largest, dominating 65.98km^2 of the reserve (Table 4.10). Both Clan 1 and Clan 3's home range were of very similar sizes, 38.59km^2 and 38.97km^2 respectively, and these clans used opposite ends in the north of the reserve (Table 4.10 and Figure 4.12).

Table 4.10: Home range areas (MCPs) for the three different clans and the number of individual MCPs (from the camera data) used to create clan home range estimates.

	Home Range Area (km^2)	No. of individuals
Clan 1	38.59	8
Clan 2	65.98	3
Clan 3	38.97	2

Based on right-side images, a further four individuals were photographed in the south-west of the reserve where camera traps did not fall into existing clan areas, but there were not enough images to construct MCPs for these individuals.

DISCUSSION

The use of GPS collars in carnivore studies has allowed ecologists to gain insight into aspects of behaviour, space use and inter-specific interactions (Karanth *et al.* 2010). In this study, GPS collars have provided spatial information on three brown hyaenas in Kwandwe Private Game Reserve, a species that, within this reserve, is rarely seen.

Capture and immobilisation

Foot-loop trapping proved to be a successful method of brown hyaena live capture. This method caused minimal stress and injury to the study animals and was quick and efficient, capturing the total number of targeted study animals in just 13 trapping occasions, resulting in one brown hyaena being caught per 4.3 trapping occasions. This method has been successfully used with a number of other species including coyotes (*Canis latrans*) (Nellis 1968), lions (Frank *et al.* 2003), pumas (*Puma concolor*) (Logan *et al.* 1999), and black bears (*Ursus americanus*) (Reagan *et al.* 2002). The method may have been used on brown hyaenas previously, but the capture technique has not been reported in the literature. In previous studies, success using this method has varied, with one lion caught per 1.2 trapping occasions in Kenya (Frank *et al.* 2003), one puma caught per 193 trapping occasions in New Mexico (Logan *et al.* 1999) and one black bear caught per 26.1 trapping occasions in Louisiana (Reagan *et al.* 2002).

Other methods such as cage trapping and free-darting have been used in the live capture of carnivores (Mills 1990; Maude 2005). Free-darting is a suitable method in certain situations and may cause less stress (Smith *et al.* 1983; Mills 1996; Powell 2005), but requires the habituation of animals. Furthermore, with species that have been persecuted free-darting can prove difficult (Frank *et al.* 2003). Cage trapping is commonly used in the live capture of carnivores. These traps usually consist of wire mesh, open at one or both ends (McCarthy *et al.* 2013). They are often associated with injury to the animal, especially trauma to the face, paws and teeth, as the animal attempts to escape (Frank *et al.* 2003; Grant 2012). Species with long tails often get them caught in the trap door causing injury. They also require a large group of people to transport them to trapping areas (Frank *et al.* 2003). Foot-loop trapping is an easy, cheap and efficient way of trapping. It does not require the man-power involved in cage trapping and the risk of injury is far less, as long as the traps are checked regularly. In other brown hyaena studies, both free-darting and cage traps have been used (Mills 1990; Maude 2005; Wiesel 2006). Cage traps were used in the Kalahari, which resulted in a trapping success of one brown hyaena per 3.9 trapping occasions, but this included multiple captures of the same individual (Mills 1990) and where individuals were habituated, free-darting was possible (Maude 2005; Wiesel 2006).

The success of the foot-loop capture method in the current study could be associated with capturing animals in a protected area, and it may be that capture success will be lower in human-carnivore conflict areas. However, recently in the Eastern Cape, a brown hyaena was captured using foot-loop trapping on farmland and therefore outside a protected area (K. Muller pers. comm. 2014). The capture success was as good as in the present study (one brown hyaena per four trapping occasions), indicating that the method could potentially be appropriate in both protected and unprotected areas (K. Muller pers. comm. 2014). It is realised that only one animal was caught and therefore the sample size is small, however it does provide hope for this method outside protected areas. This study therefore recommends foot-loop trapping for situations where animals are not habituated to people or vehicles.

Home range estimation

Previous studies report a diversity of home range sizes for brown hyaenas, ranging from 235km^2 to 481km^2 in the southern Kalahari (Mills 1984), with mean clan territories of 330km^2 (Mills 1990). In the central Kalahari, home ranges varied from 170km^2 to 400km^2 (Owens and Owens 1996). In Botswana home range sizes ranged from 135km^2 to 447km^2 (Maude 2005). An extremely wide range of home ranges has also been observed in Namibia ranging from 31.9km^2 (Skinner *et al.* 1995) to 4370km^2 (Wiesel 2006). All studies used MCPs or Kernels to estimate home ranges. Home range size has been associated with food availability (Mills 1982a; Skinner and van Aarde 1987; Mills 1990), and with the dispersion of food resources; where with more localised food resources home range should be smaller than in cases where food resources are widely dispersed (Mills 1984; Skinner *et al.* 1995;

Wiesel 2006). It has also been suggested that home range size and use of space may be related to cultural inheritance of space, where knowledge of space is acquired from previous generations (Skinner *et al.* 1995).

In this study, home range sizes varied from 42.62km^2 to 79.88km^2 using Kernel UD methods, and from 59.15km^2 to 104.14km^2 using Brownian bridge methods. Despite the differences in the two methods, individual home range sizes in this study were substantially smaller than most previous findings. It is noted that most other studies used MCP home range methods, which sometimes calculate very large home ranges incorporating areas of unused space, however the MCPs calculated in this study (38.97-66.11km^2) were also considerably smaller than in previous studies. The small home range sizes from this study are not surprising given the relatively large number of prey on the reserve. Ungulate species are supplemented on an annual basis and therefore substantial prey numbers are always present on the reserve. The reserve is also a confined area of land and therefore prey items will always be localised within the landscape, which could explain small individual home range sizes. In the Kalahari, territory sizes were observed to decrease in proportion with decreasing distance between prey items (Mills 1982a). Thus, in a reserve with a high density of prey items, such as the study area (see Chapter 2), brown hyaena home ranges would be expected to be comparatively smaller. Both a large availability of prey and limited dispersion are believed to explain the relatively small home range sizes found in this study.

Another factor that could explain the relatively small home range sizes on Kwandwe is that of fresh water. Access to fresh water has been known to influence brown hyaena home range size (Owens and Owens 1978; Skinner and van Aarde 1981; Mills 1987; Wiesel 2006), with individuals extending their home range considerably in dry seasons to access water (Wiesel

2006). All three individuals in the present study had regular access to water, with one individual showing preference for water, and the remaining two individuals showing no preference or avoidance of water. The Great Fish River runs through the centre of the reserve and flows all year round, providing a constant source of fresh water. There are also additional dams that are filled with water throughout the year. The constant and year-round access to water suggests that brown hyaenas do not have to travel far in search of water, as individual home ranges from collar data and clan home ranges all border or intersect the Great Fish River.

Nevertheless, the small home range sizes of the brown hyaena could be no more than an artefact of their existence within an enclosed system. The collared individuals remained within the study area over the duration of the study period, indicating that the population is closed and therefore use of space is restricted. Since brown hyaenas are territorial (Owens and Owens 1979b; Mills *et al.* 1980; Mills 1982a) the restricted space may force territories and home ranges to be small to reduce overlap between neighbouring clans.

Individual brown hyaena home ranges varied slightly in this study, but less than in previous studies. For example, a study in Namibia found that individual home ranges varied between 31.9km^2 and 220km^2 (Skinner *et al.* 1995). A greater variation was observed in the Brownian bridge home range estimates than in the Kernel UD estimates. The two methods produced differing results with respect to the individuals who varied from one another the most. The Brownian bridge home range method indicated that the home range of BHM2 differed most from the other study animals, whereas the Kernel UD home range estimates revealed that BHM1 differed most. The Kernel UD home range estimates appear to give a more accurate representation of results with respect to the GPS observations collected, indicating that the home ranges of BHM2 and BHF1 were of a similar size, and larger than that of BHM1.

The two methods of home range estimation used in this study were reasonably consistent for BHF1, but differed slightly for BHM1 and BHM2, with Brownian bridge estimates being larger than the Kernel estimates. Kernel density estimations were perceived to reveal more representative home range estimates based on GPS observations, whereas Brownian bridge estimates tended to include large areas of unused space.

Brownian bridge home range estimations provide an alternative to Kernel methods where all data, including autocorrelated data and data with telemetry errors can be incorporated into the estimates. In this study, some of the individual home range estimates were larger than expected, based on GPS locations. This is possibly due to the timing intervals between GPS location logs, as Brownian bridge home range methods join individual observations using a conditional random walk model (Horne *et al.* 2007). Increasing the timeframe between observations causes the assumption of random movement between successive locations to be less realistic and therefore movement is calculated with less certainty (Horne *et al.* 2007). When successive locations are separated by a large time interval, movement is more likely to show a biased random walk towards the home range centre (Horne *et al.* 2007). There are currently no recommendations for maximum time intervals between successive points (Horne *et al.* 2007). It is assumed that the large home range estimate of BHM2 was caused by less confidence in the movement pattern for this particular individual and that the time intervals for this study were almost certainly too long for this method. Brownian bridges would perhaps be more applicable in this study if GPS fixes were more closely timed and the subsequent movement of individuals calculated with more confidence. Indeed, this study recommends that carnivore home range studies using Brownian bridges reduce the time intervals between observations in order to calculate more concise home range estimates based on the findings of the present study.

It has been suggested that variation in home range estimates may be related to differences in individual space use and differences in study areas (Börger *et al.* 2006). This study's results must therefore be interpreted with caution, due to the small sample size. These home range estimates may merely reflect individual habits rather than revealing broad patterns. Monitoring more individuals for shorter periods may reveal more pertinent information at the species level than monitoring fewer individuals for longer periods of time (Börger *et al.* 2006).

Home range overlap

Observations made during the study period suggest that BHM2 and BHF1 are members of the same clan, as their home ranges showed considerable overlap. BHM1 represented an individual from a different clan, as his home range overlapped noticeably less. These results are consistent with previous findings, whereby members of the same clan occupy and defend a common territory, and members of different clans occupy different areas and overlap considerably less (Mills 1982a; Mills 1983; Mills 1984; Owens and Owens 1996). Previous research has shown that different clans overlap minimally, usually ≤ 24% (Mills 1983; Skinner *et al.* 1995). This study shows that overlap varies at the individual level and is not as strict as previously described. Using Kernel home range estimates the overlap of both BHM2 and BHF1 with that of BHM1 is consistent with previous findings, and does not exceed 24%; however the home range of BHM1 with both BHM2 and BHF1 was noticeably greater and exceeds 24%. This is most probably a result of space limitation within the reserve. Most areas north of the Great Fish River were additional pieces of land purchased in 2005 and therefore clans in the south could represent groups which established earlier than those in the north. Subsequently, individuals could have migrated and formed clans in the new areas. However, as a result of space limitation and resource availability, these individuals may have to occasionally use areas within the territories of other animals. Brownian bridge home range estimates indicated greater overlap between individuals from differing clans, especially between that of BHM1 and BHM2. This is probably caused by the inflated home range estimates through incorporating areas of unused space, also a result of the long time intervals between fixes.

Habitat and space use

The present investigation represents the first study on brown hyaenas within thicket vegetation and provides information on how they use this habitat type. While most brown hyaena research has been conducted in more arid areas such as the Kalahari and Namibia, the historical range of brown hyaenas stretches well into the Eastern Cape and into areas where thicket vegetation is prevalent (Skead 2007). Therefore, this study provides additional information to our understanding of the species. The effect of vegetation on brown hyaena use of space has also been insufficiently studied. Indeed, vegetation has been identified as a key feature in determining the use of space of other carnivores (Balme *et al.* 2007; Bissett and Bernard 2007; Pettorelli *et al.* 2010). In Tanzania a study combining camera trapping and ecological niche factor analysis observed that the closely related spotted hyaena showed preference for denser acacia communities over more open areas (Pettorelli *et al.* 2010). Additional studies have shown that leopards select dense and moderately dense vegetation types (Bailey 2005; Hayward *et al.* 2006, Balme *et al.* 2007). Dense vegetation has also been found to provide concealment from prey and offer optimal conditions for an ambush hunting technique (Hayward *et al.* 2006). In another study, leopards were found to hunt in vegetation of intermediate density, to provide enough cover for concealment from prey, but present ample space to allow stalking behaviour (Balme *et al.* 2007). At Kwandwe, female cheetahs were found to select denser vegetation and steeper slopes in thicket vegetation for concealment and avoidance of kleptoparasitism (Bissett and Bernard 2007).

It was predicted that brown hyaenas would select thicket vegetation as opposed to more open areas as a form of seclusion from competitively dominant species in this type of environment. All individual home ranges were comprised predominantly of thicket vegetation, but this is probably an artefact of the reserve, having a greater proportion of thicket vegetation available compared to open habitat. Differences were observed at the individual level, with BHM1 showing preference for open habitats, whereas both BHM2 and BHF1 showed preference for thicket vegetation. The logistic regression analysis indicated that vegetation type was not a significant predictor of brown hyaena space use. This may have been because thicket vegetation dominates the reserve; therefore random locations mostly fell into thicket vegetation.

The use of space does not appear to be predictable for brown hyaenas in general, as all individuals varied tremendously in their use of space, with different combinations of variables predicting resource selection. This appears to indicate that in this type of environment brown hyaenas, in general, successfully use a range of landscape features and do not appear to be restricted to certain elevations or degrees of slope. The distance to roads was an exception, where for all three individuals this variable was a significant predictor of space use. Individuals chose to use roads frequently. In a reserve so dominated by thicket vegetation, roads may offer clear foraging routes and territorial boundaries (Mills *et al.*

1980), as latrines and pastings were common along roadsides. Using roads may also reduce energy expenditure as they perhaps offer routes of least resistance when compared to travelling through thick vegetation.

This information appears to indicate that in the Thicket biome, individual brown hyaenas may be generalists and are able to use different habitat types and features. It is, however, recognised that the reserve is small and enclosed and these may be confounding factors; all habitats and features are possibly used as a result of space limitation.

Clans

Previous findings have indicated mean clan home ranges to be 330km^2 in the southern Kalahari (Mills and Mills 1982; Mills 1990) and in the central Kalahari to range from 170km^2 to 400km^2 (Owens and Owens 1996). In this study, clan home ranges were considerably smaller than those quoted in previous studies. Some studies found clan home range size to be larger than the total size of Kwandwe. Thus, the small clan home range sizes could be a direct cause of space restriction. It is also recognised that the methods of calculating clan home range size produce smaller estimates. It does however appear that there are at least four distinct clans on Kwandwe, and population estimates (see Chapter 3) indicate that although home range size is smaller than in more open systems, the population appears to be thriving in this environment.

This study observed that individual brown hyaena home range, for the duration of the study period, was considerably smaller than most previous findings. Both methods of home range estimation produced variable results but Kernel methods are likely to be more appropriate, due to Brownian bridge home range estimates including large areas of unused space. It is believed that small home range size is due to the high abundance and limited dispersion of prey items found within the reserve and as a consequence of it being a small, enclosed system. In this environment, brown hyaenas appear to be generalists, using all habitats and features within the landscape. This study recognises that although the results may be compelling, the small sample size could represent idiosyncrasies at the individual level and therefore further work should be carried out on more individuals to investigate space use. The effects of thicket vegetation on brown hyaena space use is largely unknown and it is recommended that further work be undertaken within this vegetation type to look at the direct effects of this vegetation on the space use of brown hyaenas.

CHAPTER 5.

SYNTHESIS AND CONCLUSIONS

Sunset over Kwandwe

Large carnivores are often described as umbrella or keystone species as they play a pivotal role within ecosystems (Gittleman *et al.* 2001). Understanding aspects of their ecology and behaviour can thus provide information on multiple trophic levels, highlighting the importance of such information for ecosystem management. However, the elusive and wide-ranging behaviour of large carnivores, coupled with their naturally low densities, can mean that conserving these species is challenging (Karanth *et al*. 2004; Balme *et al*. 2009; Efford *et al*. 2009). Conservation of large carnivores is crucial for their survival as they have been persecuted in many parts of the world (Gittleman *et al.* 2001; Linnell *et al.* 2001; Woodroffe 2001). The Eastern Cape of South Africa is no exception. By the beginning of the 20th century in the Eastern Cape, most large carnivores had been extirpated (Skead 2007). Consequently, reintroductions into small, enclosed reserves remains one of the most effective ways to conserve large carnivores (Hayward *et al.* 2007c). Extrapolation of information on species from open systems and from other vegetation types for management purposes is precarious, and therefore the monitoring of reintroduced populations within small, enclosed reserves and within different biomes is critical. Such information can then appropriately inform management decisions, with conservation implications (Mills 1991).

The aims of the present study were to estimate the population size of brown hyaenas within Kwandwe and to provide information on the home range and space use of individuals. The study is among the first of its kind to be conducted in a small enclosed reserve, in contrast to the majority of studies which have been carried out in large open systems. Furthermore, no published information is available on brown hyaenas in the Thicket biome. The findings of this study reveal that Kwandwe supports a large population of brown hyaenas compared to other areas (Mills 1984; 1990; Thorn *et al.* 2009; Kent and Hill 2013). In addition, the brown hyaenas investigated in the present study were shown to have smaller home ranges than those observed in most other areas (Mills 1984; 1990; Maude 2005; Wiesel 2006). As no previous work has been conducted in this environment (enclosed reserve in the Thicket biome) it is unclear whether these results reflect natural densities and space use for brown hyaenas in this habitat.

Home range size has been linked with the abundance and dispersion of potential prey items (Mills 1982a; Skinner and van Aarde 1987; Mills 1990; Skinner *et al.* 1995; Wiesel 2006). The resource dispersion hypothesis correlates the dispersion of resources with home range size (Macdonald 1983). The high numbers and limited dispersion of prey potentially explain the small home range sizes, as individuals have to travel short distances to access resources (Mills 1984). The resource dispersion hypothesis also suggests that the abundance of food can also influence group size, independent of territory size (Macdonald 1983). In this way, areas with more food resources can support higher individual abundances and therefore larger group sizes (Mills 1984). It is therefore suggested that in the present study area, the high numbers of potential prey (Chapter 2) and limited dispersion of these prey items, provide the optimal conditions for the Kwandwe brown hyaena population. As the dispersion of food is low, home range sizes are small and therefore allow for the establishment of a greater number of clans within the reserve. Furthermore, based on the findings of Mills (1984), the high abundance of prey could potentially support an elevated number of individuals per clan. This is, however, currently speculative and further work is needed to quantify the quality of an area and the dispersion of resources.

However, a gap in our understanding of the ecological role of brown hyaenas in small enclosed reserves is that of food resource acquisition. Kwandwe sustains a large number of predators for ecotourism purposes and their densities are higher than those documented elsewhere (Chapter 4; Mills *et al.* 1978; Stander *et al.* 1997; Kleine 2007). As such, prey numbers are also kept high to support the elevated predator numbers (C. Bissett pers. comm. 2013). The high numbers of both predators (lions, leopards and cheetahs) and prey potentially provides greater scavenging opportunities for brown hyaenas (Owens and Owens 1978; Mills 1990). This is supported by a recent study that found high numbers of apex predators lead to higher densities of brown hyaenas through increased scavenging opportunities (Yarnell *et al.* 2013). The thicket vegetation could also provide good cover for the avoidance of competitively dominant carnivores such as lions (Mills 1990). While there is no direct evidence for hunting, brown hyaena individuals have been observed carrying a whole carcass (C. Bissett and K. Muller pers. comm. 2013). Dense and moderately-dense vegetation is preferable for ambush predation (Balme *et al.* 2007; Davidson *et al.* 2012) and could facilitate prey-capture by brown hyaenas.

MANAGEMENT IMPLICATIONS

Considering that large carnivore numbers are declining on a global scale (Weber and Rabinowitz 1996), being able to identify the successes and failures of reintroductions is critical for the future of carnivore conservation (Hayward *et al.* 2007c). The reintroduction of large carnivores into small, enclosed reserves is often a complicated and intensive process (Mills 1991; Hayward *et al.* 2007c) and is usually followed with insufficient monitoring (Breitenmoser *et al.* 2001; Hayward *et al.* 2007b). Reintroductions should be followed with frequent monitoring and peer appraisal in the form of publications, facilitating future reintroduction success through learning (Breitenmoser *et al.* 2001). The primary objective of most reintroductions is for the persistence of populations without human influence; however this is truly achievable only through long-term and continual monitoring (Seddon 1999).

In protected areas, the management of carnivores revolves around two key factors, the influence they have on prey populations and the influence they have on other carnivores (Mills 1991). Although his study did not investigate these factors, the high density of brown hyaenas suggests that these aspects should be considered for future research. It is unclear what impact brown hyaenas have on prey in this environment, since knowledge as to whether they are purely scavenging or actually hunting is non-existent. If they are hunting, additional information is required on how often they hunt, what they hunt, and what sex and age they target, before their effect on prey populations can be established (Mills 1991).

Relationships between carnivores are often complex, and presently the population of brown hyaenas does not appear to have a negative impact on other carnivores. However, if the population continues to grow, the outcome is uncertain, since the feeding behaviour and intra-guild interactions are unknown. Resource limitation is the main driver of predator population control, with food resource limitation often linked to habitat type (White 1978; Morris 1987). Due to the supplementation of food resources in small reserves, this main form of predator control is prevented, enabling predators to reach high densities. Predator carrying capacities should be calculated for small reserves and the availability of prey altered accordingly (Hayward *et al.* 2007a). If predator and prey numbers are artificially high on small reserves, this could influence brown hyaena numbers, causing an increase in numbers through an abundance of resources.

Another consideration is the genetic diversity of a species (Hayward *et al.* 2007c). If populations increase in number from a small founder population, this will often lead to limited genetic diversity within the resulting larger population (Hayward *et al.* 2007c). In larger, open systems genetic variability is naturally maintained through a larger gene pool and out-breeding, whereby individuals avoid mating with closely related individuals (Soulé and Simberloff 1986). Comparatively, in enclosed reserves, small populations are prone to inbreeding depression and a reduction in heterozygosity (Caro 2000). Inbreeding between closely related individuals can result in decreased levels of viability and fecundity, and can cause genetic defects within populations (Soulé and Simberloff 1986). Individuals that are less heterozygous at different loci are associated with decreased levels of fitness, with the ultimate result being an increased risk of mortality associated with periods of stress or environmental change (Soulé and Simberloff 1986). In these circumstances, species require human-mediated intervention to allow for out-breeding. Meta-population management schemes, where individuals are moved from one reserve to another, ensure greater genetic variability within the species and allows for out-breeding, where it cannot occur naturally (Caughley 1994). Thus, populations in their entirety are fitter, and less susceptible to disease and mortality.

The results from this study indicate that if brown hyaenas are introduced into small, enclosed reserves within the Thicket biome with sufficient resources, their population size is likely to increase rapidly. The conditions provided by this type of environment appear to promote brown hyaena survival, and high numbers are able to exist within a relatively small area. Post-release monitoring is vital and un-checked population increases could ultimately result in elevated levels of human-predator conflict if brown hyaenas are able to disperse out of these game reserves. If managers of small reserves in this vegetation type wish to introduce brown hyaenas for ecotourism purposes, contraception may provide a viable mechanism for restricting numbers. This is particularly pertinent for reserves that have elevated numbers of alternate predators and supplemented prey. However, there is currently little information on the use of contraception in brown hyaenas, but contraceptive implants have been successfully used for cheetahs, wild dogs, lions and leopards (Bertschinger *et al.* 2002).

FUTURE RESEARCH

This study has revealed some interesting aspects of brown hyaena ecology; most importantly the high density estimates and small home range sizes. Nevertheless, the study has also highlighted that there is very little known about this species in the Thicket biome and within small enclosed reserves in general. Given this paucity of information, it is unclear whether the results of this study are a consequence of the size of the reserve, the vegetation type, or a combination of the two. It is therefore suggested that further research be conducted in similar reserves, in other habitats and in more open systems in the Thicket biome.

Brown hyaenas are clearly successful generalists in the study area and further studies quantifying this success should be considered. Recommendations for further research within Kwandwe include quantifying the dispersal of prey items and linking this to previous studies that document home range size to be associated with the dispersion of food items. Additionally, studying the feeding behaviour of brown hyaenas should be considered to assess whether they are purely scavenging or if they have adapted to be more successful hunters in this denser vegetation type.

A further possibility would be to investigate litter size and cub survival, to determine whether this could be a contributing factor to the high densities observed in Kwandwe. Indeed, litter size and cub survival is variable for many large and medium-sized carnivores, with numerous factors affecting this aspect of demographic success (Laurenson 1995; Derocher and Stirling 1996; Kelly *et al.* 1998). Although fluctuations in litter size have not been found to influence group size in brown hyaenas, the higher density in Kwandwe suggests it may be a factor worth investigating (Mills 1990). Generally, cub survival is relatively high, with the highest mortality being observed in young sub-adults (Mills 1990). Brown hyaena survival could well be higher across all life-history stages within Kwandwe, which would ultimately lead to elevated population densities, as has been observed in the present study. Furthermore, as the population size has increased to such high numbers from a small founder population, genetic studies would be important to investigate inbreeding depression. If inbreeding depression does occur for brown hyaenas in small reserves, then perhaps a meta-population management scheme could be put in place for small reserves with brown hyaenas.

On a larger scale, this study recommends collaboration with other studies to gather information on many different habitat types for this species. Continuing research on brown hyaenas across their entire range and synthesizing the results will provide information on the integral role they occupy within ecosystems. This information will present conservationists and managers with a greater depth of understanding, allowing for sound future management. As it stands, an extensive proportion of the brown hyaena population in southern Africa lives outside of protected areas and therefore suffers considerable persecution from farmers (Hofer and Mills 1998b; Wiesel *et al.* 2008). Research outside protected areas is extremely important to preserve wild populations and provide ways to mediate human-carnivore conflict. However, small protected areas may provide a valuable option in protecting brown hyaenas, and therefore the need for understanding how the species functions in these types of environments is critical for the management of these populations. If small reserves are to contribute to the conservation of this species, long-term monitoring schemes must be implemented and information must be shared between reserves so that management decisions can be informed.

REFERENCES

AKAIKE, H. 1974. A new look at statistical model identification. *IEEE Transactions on Automatic Control* **19**: 716-723.

AMLANER, C. J. and MACDONALD, D. W. 1980. *A Handbook on Biotelemetry and Radio Tracking.* Pergemon Press, Oxford, UK.

ANCRENAZ, M., HEARN, A. J., ROSS, J., SOLLMANN, R. and WILTING, A. 2012. *Handbook for wildlife monitoring using camera traps*. BBEC II Secretariat, Sabah, Malaysia.

BAILEY, T. N. 2005. *The African Leopard: Ecology and Behaviour of a Solitary Felid. 2nd edn*. Blackburn Press, Caldwell, New Jersey.

BALME, G. A., HUNTER, L. T. B. and SLOTOW, R. 2007. Feeding habitat selection by hunting leopards (*Panthera pardus*) in a woodland savanna: prey catchability versus abundance. *Animal Behaviour* **74**: 589-598.

BALME, G. A., HUNTER, L. T. B. and SLOTOW, R. 2009. Evaluating Methods for Counting Cryptic Carnivores. *Journal of Wildlife Management* **73**: 433-441.

BANGS, E. E. and FRITTS, S. H. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. *Wildlife Society Bulletin* **24**: 402-413.

BART, J., DROEGE, S., GEISSLER, P., PETERJOHN, B. and RALPH, C. J. 2004. Density estimation in wildlife surveys. *Wildlife Society Bulletin* **32**: 1242-1247.

BERGER, K. M. and GESE, E. M. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology* **76**: 1075-1085.

BERLINER, D. and DESMET, P. 2007. *Eastern Cape Biodiversity Conservation Plan: Technical Report*. Department of Water Affairs and Forestry Project No 2005-012, Pretoria, South Africa.

BERTRAND, M. R., DENICOLA, A. J., BEISSINGER, S. R. and SWIHART, R. K. 1996 Effects of parturition on home ranges and social affiliations of female white-tailed deer. *Journal of Wildlife Management* **60**: 899-909.

BERTSCHINGER, H. J., TRIGG, T. E., JÖCHLE, W. and HUMAN, A. 2002. Induction of contraception in some African wild carnivores by downregulation of LH and FSH secretion using the GnRH analogue deslorelin. *Reproduction Supplement (Cambridge, England)* **60**: 41-52.

BESBEAS, P., FREEMAN, S. N., MORGAN, B. J. T. and CATCHPOLE, E. A. 2002. Mark-Recapture-Recovery and Census Data to Estimate Animal Abundance and Demographic Parameters. *Biometrics* **58**: 540-547.

BIRCH, N. V. E. 2000. The vegetation potential of natural rangelands in the mid-fish river valley, Eastern Cape, South Africa: Towards a sustainable and acceptable management system. PhD thesis, Rhodes University, Grahamstown, South Africa.

BISSETT, C. 2004. The feeding ecology, habitat selection and hunting behaviour of re-introduced cheetah on Kwandwe Private Game Reserve, Eastern Cape Province. Msc thesis, Rhodes University, Grahamstown, South Africa.

BISSETT, C. 2007. The feeding and spatial ecologies of the large carnivore guild on Kwandwe Private Game Reserve. PhD thesis, Rhodes University, Grahamstown, South Africa.

BISSETT, C. and BERNARD, R. T. F. 2007. Habitat Selection and feeding ecology of the cheetah (*Acinonyx jubatus*) in thicket vegetation: is the cheetah a savannah specialist? *Journal of Zoology* **271**: 310-317.

BLAKE, S. and HEDGES, S. 2004. Sinking the Flagship: the Case of Forest Elephants in Asia and Africa. *Conservation Biology* **18**: 1191-1202.

BORCHERS, D. L. and EFFORD, M. G. 2008. Spatially Explicit Maximum Likelihood Methods for Capture-Recapture Studies. *Biometrics* **64**: 377-385.

BÖRGER, L., FRANCONI, N., DE MICHELE, G., GANTZ, A., MESCHI, F., MANICA, A., LOVARI, S. and COULSON, T. 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology* **75**: 1393-1405.

BOYDSTON, E. E., KAPHEIM, K. M., SZYKMAN, M. and HOLEKAMP, K. E. 2003a. Individual variation in space use by female spotted hyenas. *Journal of Mammalogy* **84**: 1006-1018.

BOYDSTON, E. E., KAPHEIM, K. M., WATTS, H. E., SZYKMAN, M. and HOLEKAMP, K. E. 2003b. Altered behavior in spotted hyenas associated with increased human activity. *Animal Conservation* **6**: 207-219.

BREITENMOSER, U., BREITENMOSER-WÜRSTEN, C., CARBYN, L. N. and FUNK, S. M. 2001. Assessment of carnivore reintroductions In: *Carnivore conservation*, (eds) J. L. Gittleman, S. M. Funk, D. Macdonald and R. K. Wayne, pp. 241-281. Cambridge University Press, Cambridge.

BROWN, J. S., KOTLIER, B. P. and VALONE T. J. 1994. Foraging under predation: A comparison of energetic and predation costs in rodent communities of the Negev and Sonoran Deserts. *Australian Journal of Zoology* **42**: 435-448.

BURNHAM, K. P. and OVERTON, W. S. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* **65**: 625-633.

BURNHAM, K. P., ANDERSON, D. R. and HUYVAERT, K. P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations and comparisons. *Behavioural Ecology and Sociobiology* **65**: 23-35.

BURT, W. H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* **24**: 346-352.

BYRNE, M. E., MCCOY, J. C., HINTON, J. W., CHAMBERLAIN, M. J. and COLLIER, B. A. 2014. Using dynamic Brownian bridge movement modeling to measure temporal patterns of habitat selection. *Journal of Animal Ecology*. DOI:10.1111/1365-2656.12205.

CARO, T. 2000. Controversy over behaviour and genetics in cheetah conservation. In: *Behaviour and Conservation*, (eds) L. M. Gosling and W. J. Sutherland, pp. 221-237. Cambridge University Press, Cambridge.

CARO, T. M. 2003. Umbrella species: critique and lessons from East Africa. *Animal Conservation* **6**: 171-181.

CAUGHLEY, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* **63**: 215-244.

CHAO, A. and HUGGINS, R. M. 2005. Modern closed capture-recapture models. In: *Handbook of capture-recapture analysis*, (eds) S. C. Amstrup, T. L. Mcdonald and B. F. J. Manly, pp. 58-87. Princeton University Press, New Jersey.

CHAPMAN, S. and BALME, G. 2010. An estimation of leopard population density in a private reserve in KwaZulu-Natal, South Africa, using camera-traps and capture-recapture models. *South African Journal of Wildlife Research* **40**: 114-120.

CROOKS, K. R. and SOULÉ, M. E. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* **400**: 563-566.

CUSHMAN, S. A., CHASE, M. and GRIFFIN, C. 2005. Elephants in space and time. *Oikos* **109**: 331-341.

DAVIDSON, Z., VALEIX, M., LOVERIDGE, A. J., HUNT, J. E., JOHNSON, P. J., MADZIKANDA, H. and MACDONALD, D. W. 2012. Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. *Journal of Mammalogy* **93**: 677-685.

DE SOLLA, S. R., BONDURIANSKY, R. and BROOKS, R. J. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology* **68**: 221-234.

DELLINGER, J. A., PROCTOR, C., STEURY, T. D., KELLY, M. J. and VAUGHAN, M. R. 2013. Habitat selection of a large carnivore, the red wolf, in a human-altered landscape. *Biological Conservation* **157**: 324-330.

DEROCHER, A. E. and STIRLING, I. 1996. Aspects of survival in juvenile polar bears. *Canadian Journal of Zoology* **74**: 1246-1252.

DEVAULT, T. L., RHODES, O. E. and SHIVIK, J. A. 2003. Scavenging by vertebrates: behavioural, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* **102**: 225-234.

DI BITETTI, M. S., PAVIOLO, A. and DE ANGELO, C. 2006. Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones, Argentina. *Journal of Zoology* **270**: 153-163.

DONCASTER, C. P. 1992. Testing the role of intraguild predation in regulating hedgehog populations. *Proceedings of the Royal Society of London* **249**: 113-117.

DONCASTER, C. P. and WOODROFFE, R. 1993. Den site can determine shape and size of badger territories: implications for group-living. *Oikos* **66**: 88-93.

EBERHARDT, L. L. 1990. Using Radio-Telemetry for Mark-Recapture Studies with Edge Effects. *Journal of Applied Ecology* **27**: 259-271.

EFFORD, M. 2004. Density Estimation in Live-Trapping Studies. *Oikos* **106**: 598-610.

EFFORD, M. G., DAWSON, D. K. and ROBBINS, C. S. 2004. DENSITY: software for analysing capture-recapture data from passive detector arrays. *Animal Biodiversity and Conservation* **27**: 217-228.

EFFORD, M. G., WARBURTON, B., COLEMAN, M. C. and BARKER, R. J. 2005. A Field Test of Two Methods for Density Estimation. *Wildlife Society Bulletin* **33**: 731-738.

EFFORD, M. G., DAWSON, D. K. and BORCHERS, D. L. 2009. Population density estimated from locations of individuals on a passive detector array. *Ecology* **90**: 2676-2682.

ELMHAGEN, B. and RUSHTON, S. P. 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters* **10**: 197-206.

ESTES, J. A., TINKER, M. T., WILLIAMS, T. M. and DOAK, D. F. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282**: 473-476.

ESTES, J., CROOKS, K. and HOLT. R. 2001. Predation and diversity. In: *Encyclopedia of Biodiversity* (ed) S. Levin, pp. 857-878. Academic Press, San Diego, California.

ESTES, J. A., TERBORGH, J., BRASHARES, J. S., POWER, M. E., BERGER, J., BOND, W. J., CARPENTER, S. R., ESSINGTON, T. E., HOLT, R. D., JACKSON, J. B. C., MARQUIS, R. J., OKSANEN, T., PAINE, R. T., PIKITCH, E. K., RIPPLE, W. J., SANDIN, S. A., SCHEFFER, M., SCHROENER, T. W., SHURIN, J. B., SINCLAIR, A. R. E., SOULÉ, M. E., VIRTANEN, R. and WARDLE, D. A. 2011. Trophic downgrading of Planet earth. *Science* **333**: 301-306.

EWER, R. E. 1973. *The carnivores.* Cornell University Press, Ithaca, New York.

FOREMAN, D. 1993. Developing a regional wilderness recovery plan. *Wild Earth (The Wildlands Project special issue)*: 26-29.

FOSTER, R. J., HARMSEN, B. J. and DONCASTER, C. P. 2010. Habitat use by sympatric jaguars and pumas across a gradient of human disturbance in Belize. *Biotropica* **42**: 724-731.

FOSTER, R. J. and HARMSEN, B. J. 2012. A Critique of Density Estimation from Camera-Trap Data. *The Journal of Wildlife Management* **76**: 224-236.

FRANK, L., SIMPSON, D. and WOODROFFE, R. 2003. Foot snares: An effective method for capturing African lions. *Wildlife Society Bulletin* **31**: 309-314.

FULLER, T. K. and SIEVERT, P. R. 2001. Carnivore demography and the consequences of changes in prey availability. In: *Carnivore Conservation*, (eds), J. L. Gittleman, S. M. Funk, D. Macdonald and R. K. Wayne, pp. 163-178. Cambridge University Press, Cambridge.

GERBER, B., KARPANTY, S. M., CRAWFORD, C., KOTSCHWAR, M. and RANDRIANANTENAINA, J. 2010. An assessment of carnivore relative abundance and density in the eastern rainforests of Madagascar using remotely-triggered camera traps. *Oryx* **44**: 219-222.

GERBER, B. D., KARPANTY, S. M. and KELLY, M. J. 2012. Evaluating the potential biases in carnivore capture-recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. *Population Ecology* **54**: 43-54.

GESE, E. M. 2001. Monitoring of terrestrial carnivore populations. In: *Carnivore conservation*, (eds) J. L. Gittleman, S. M. Funk, D. Macdonald and R. K. Wayne, pp. 372-396. Cambridge University Press, Cambridge.

GHANI, I. M. M. and AHMAD, S. 2010. Stepwise multiple regression method to forecast fish landing. *Procedia Social and Behavioral Sciences* **8**: 549-554.

GIBBONS, J. W. and ANDREWS, K. M. 2004. PIT tagging: simple technology at its best. *Bioscience* **54**: 447-454.

GILLINGHAM, M. P. and PARKER, K. L. 2008. The importance of individual variation in defining habitat selection by moose in northern British Columbia. *Alces* **44**: 7-20.

GITTLEMAN, J. L., FUNK, S. M., MACDONALD, D. and WAYNE, R. K. 2001. Why ‘carnivore conservation’? In: *Carnivore conservation*, (eds) J. L. Gittleman, S. M. Funk, D. Macdonald and R. K. Wayne, pp. 1-7. Cambridge University Press, Cambridge.

GRANT, T. 2012. Leopard population density, home range size and movement patterns in a mixed landuse area of the Mangwe District of Zimbabwe. MSc thesis, Rhodes University, Grahamstown, South Africa.

GRAY, T. N. E. and PRUM, S. 2012. Leopard Density in Post-Conflict Landscape, Cambodia: Evidence from Spatially Explicit Capture-Recapture. *Journal of Wildlife Management* **76**: 163-169.

GROS, P. M., KELLY, M. J. and CARO, T. M. 1996. Estimating carnivore densities for conservation purposes: indirect methods compared to baseline demographic data. *Oikos* **77**: 197-206.

GUSSET, M. and BURGENER, N. 2005. Estimating larger carnivore numbers from track counts and measurements. *African Journal of Ecology* **43**: 320-324.

HARIHAR, A., GHOSH, M., FERNANDES, M., PANDAV, B. and GOYAL, S. P. 2009. Use of photographic capture-recapture sampling to estimate density of Striped Hyena (*Hyaena hyaena*): implications for conservation. *Mammalia* **74**: 83-87.

HARMSEN, B. J., FOSTER, R. J., DONCASTER, C. P. 2011. Heterogeneous capture rates in low density populations and consequences for capture–recapture analysis of camera-trap data. *Population Ecology* **53**: 253-259.

HARRIS, S., CRESSWELL, W. J., FORDE, P. G., TREWHELLA, W. J., WOOLLARD, T. and WRAY, S. 1990. Home-range analysis using radio-tracking data: a review of the problems and techniques particularly as applied to the study of mammals. *Mammal Review* **20**: 97-123.

HAYWARD, G. D., MIQUELLE, D. G., SMIRNOV, E. N. and NATIONS, C. 2002. Monitoring Amur tiger populations: characteristics of track surveys in snow. *Wildlife Society Bulletin* **30**: 1150-1159.

HAYWARD, M. W. 2006. Prey preferences of the spotted hyaena (*Crocuta crocuta)* and degree of dietary overlap with the lion (*Panthera leo*). *Journal of Zoology* **270**: 606-614.

HAYWARD, M. W., HENSCHEL, P., O'BRIEN, J., HOFMEYR, M., BALME, G. and KERLEY, G. I. H. 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* **270**: 298-313.

HAYWARD, M. W., O'BRIEN, J., and KERLEY, G. I. H. 2007a. Carrying capacity of large African predators: predictions and tests. *Biological Conservation* **139**: 219-229.

HAYWARD, M. W., ADENDORFF, J., O'BRIEN, J., SHOLTO-DOUGLAS, A., BISSETT, C., MOOLMAN, L. C., BEAN, P., FOGARTY, A., HOWARTH, D., SLATER, R. and KERLEY, G. I. H. 2007b. The reintroduction of large carnivores to the Eastern Cape, South Africa: an assessment. *Oryx* **41**: 205-214.

HAYWARD, M. W., ADENDORFF, J., O'BRIEN, J., SHOLTO-DOUGLAS, A., BISSETT, C., MOOLMAN, L. C., BEAN, P., FOGARTY, A., HOWARTH, D., SLATER, R. and KERLEY, G. I. H. 2007c. Practical considerations for the reintroduction of large, terrestrial, mammalian predators based on reintroductions to South Africa's Eastern Cape Province. *Open Conservation Biology Journal* **1**:1-11.

HEBBLEWHITE, M., WHITE, C. A., NIETVELT, C., MCKENZIE, J. M., HURD, T. E., FRYXELL, J. M., BAYLEY, S. and PAQUET, P. C. 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology* **86**: 2135-2144.

HEILBRUN, R. D., SILVY, N. J., TEWES, M. E. and PETERSON, M. J. 2003. Using automatically triggered cameras to individually identify bobcats. *Wildlife Society Bulletin* **31**: 748-755.

HEMSON, G., JOHNSON, P., SOUTH, A., KENWARD, R., RIPLEY, R. and MACDONALD, D. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *Journal of Animal Ecology* **74**: 455-463.

HENSCHEL, P. and RAY, J. 2003. *Leopards in African Rainforests: Survey and Monitoring Techniques*. Wildlife Conservation Society Report, Global Carnivore Program, New York, USA.

HEWSON, R. 1986. Distribution and density of fox breeding dens and the effects of management. *Journal of Applied Ecology* **23**: 531-538.

HEYDON, M. J., REYNOLDS, J. C. and SHORT, M. J. 2000. Variation in abundance of foxes (*Vulpes vulpes*) between three regions of rural Britain, in relation to landscape and other variables. *Journal of Zoology* **251**: 253-264.

HOARE, D. B., MUCINA, L., RUTHERFORD, M. C., VLOK, J. H. J., EUSTON-BROWN, D. I. W., PALMER, A. R., POWRIE, L. W., LECHMERE-OERTEL, R. G., PROCHEŞ, Ş. M., DOLD, A. P. and WARD, R. A. 2006. Albany Thicket Biome. In: *The Vegetation of South Africa, Lesotho and Swaziland,* (eds) L. Mucina and M. C. Rutherford, pp. 540-567. South African National Biodiversity Institute, Pretoria, South Africa.

HOFER, H. and MILLS, G. 1998a. Worldwide Distribution of Hyaenas. In: *Hyaenas: status survey and conservation action plan*, (eds) M. G. L. Mills and H. Hofer, pp. 39-63. IUCN, Gland, Switzerland and Cambridge, UK.

HOFER, H. and MILLS, G. 1998b. Population Size, Threats and Conservation Status of Hyaenas. In: *Hyaenas: status survey and conservation action plan*, (eds) M. G. L. Mills and H. Hofer, pp. 64-79. IUCN, Gland, Switzerland and Cambridge, UK.

HOFMEYR, M., DAVIES, R., NEL, P. and DELL, S. 2003. Operation Phoenix - the introduction of larger mammals to Madikwe Game Reserve. In: *Madikwe Game Reserve: A Decade of Progress*, (ed.) M. Brett, pp. 8-20. North West Parks and Tourism Board, Rustenberg, South Africa.

HORNE, J. S., GARTON, E. O., KRONE, S. M. and LEWIS, J. S. 2007. Analyzing animal movements using Brownian bridges. *Ecology* **88**: 2354-2363.

HORNE, J S. and GARTON. E. O. 2009. Animal Space Use 1.3. Available from: <http://www.cnr.uidaho.edu/population_ecology/animal_space_use>.

HOSMER, D. W. and LEMESHOW, S. 2000. *Applied logistic regression*. John Wiley and Sons, New York.

HUCK, M., DAVISON, J. and ROPER, T. J. 2008. Comparison of two sampling protocols and four home-range estimators using radio-tracking data from urban badgers *Meles meles*. *Wildlife Biology* **14**: 467-477.

JACKSON, R. M., ROE, J. D., WANGCHUK, R. and HUNTER, D. O. 2006. Estimating Snow Leopard Population Abundance Using Photography and Capture-Recapture Techniques. *Wildlife Society Bulletin* **34**: 772-781.

JACQUES, C. N., JENKS, J. A. and KLAVER, R. W. 2009. Seasonal movements and home-range use by female pronghorns in sagebrush-steppe communities of western South Dakota. *Journal of Mammalogy* **90**: 433-441.

JANEČKA, J. E., MUNKHTSOG, B., JACKSON, R. M., NARANBAATAR, G., MALLON, D. P. and MURPHY, W. J. 2011. Comparison of noninvasive genetic and camera-trapping techniques for surveying snow leopards. *Journal of Mammalogy* **92**: 771-783.

JENKS, S. and WERDELIN, L. 1998. Taxonomy and systematics of living hyaenas (family Hyaenidae). In: *Hyaenas: status survey and conservation action plan*, (eds) M. G. L. Mills and H. Hofer, pp. 8-17. IUCN, Gland, Switzerland and Cambridge, UK.

JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**: 65-71.

JORDAN, M. J., BARRETT, R. H. and PURCELL, K. L. 2011. Camera trapping estimates of density and survival of fishers *Martes pennanti*. *Wildlife Biology* **17**: 266-276.

KALLE, R., RAMESH, T., AURESHI, Q. and SANKAR, K. 2011. Density of tiger and leopard in a tropical deciduous forest of Mudamalai Tiger Reserve, southern India, as estimated using photographic capture-recapture sampling. *Acta Theriologica* **56**: 335-342.

KARANTH, K. U. 1995. Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture models. *Biological Conservation* **71**: 333-338.

KARANTH, K. U. and NICHOLS, J. D. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* **79**: 2852-2862.

KARANTH, K. U. and NICHOLS, J. D. 2002. *Monitoring tigers and their prey: a manual for researchers, managers and conservationists in tropical Asia.* Centre for Wildlife Studies: Bangalore.

KARANTH, K. U., NICHOLS, J. D., SEIDENSTICKER, J., DINERSTEIN, E., DAVID SMITH, J. L., MCDOUGAL, C., JOHNSINGH, A. J. T., CHUNDAWAT, R. S. and THAPAR, V. 2003. Science deficiency in conservation practice: the monitoring of tiger populations in India. *Animal Conservation* **6**: 141-146.

KARANTH, K. U., CHUNDAWAT, R. S., NICHOLS, J. D. and KUMAR, N. S. 2004. Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture–recapture sampling. *Animal Conservation* **7**: 285-290.

KARANTH K. U., FUNSTON, P. and SANDERSON, E. 2010. Many ways of skinning a cat: tools and techniques for studying wild felids. In: *Biology and Conservation of Wild Felids*, (eds.) D. W. Macdonald and A. J. Loveridge, pp: 197-216. Oxford University Press, Oxford, UK.

KAWANISHI, K. and SUNQUIST, M. E. 2004. Conservation status of tigers in a primary rainforest of Peninsular Malaysia. *Biological Conservation* **120**: 329-344.

KEATING, K. A. and CHERRY, S. 2004. Use and interpretation of logistic regression in habitat selection studies. *Journal of Wildlife Management* **68**: 774-789.

KELLY, M. J., LAURENSON, M. K., FITZGIBBON, C. D., COLLINS, D. A., DURANT, S. M., FRAME, G. W., BERTRAM, B. C. R. and CARO, T. M. 1998. Demography of the Serengeti cheetah (*Acinonyx jubatus*) population: the first 25 years. *Journal of Zoology* **244**: 473-488.

KELLY, M. J. 2003. Jaguar monitoring in the Chiquibul Forest, Belize. *Caribbean Geography* **13**: 19-32.

KELLY, M. J., NOSS, A. J., DI BITETTI, M. S., MAFFEI, L., ARISPE, R. L., PAVIOLO, A., DE ANGELO, C. D. and DI BLANCO, Y. E. 2008. Estimating Puma Densities from Camera Trapping across Three Study Sites: Bolivia, Argentina, and Belize. *Journal of Mammalogy* **89**: 408-418.

KENT, V. T. and HILL, R. A. 2013. The importance of farmland for the conservation of the brown hyaena *Parahyaena brunnea. Oryx* **47**: 431-440.

KENWARD, R. E. 1987. *Wildlife Radio Tagging: Equipment, Field Techniques, and Data Analysis.* Academic Press, London, UK.

KÉRY, M., GARDNER, B., STOECKLE, T., WEBER, D. and ROYLE, J. A. 2011. Use of Spatial Capture-Recapture Modeling and DNA Data to Estimate Densities of Elusive Animals. *Conservation Biology* **25**: 356-364.

KIE, J. G. and BOROSKI, B. B. 1996 Cattle distribution, habitats, and diets in the Sierra Nevada of California. *Journal of Range Management* **49**: 482-488.

KIE, J. G., BOWYER, R. T., BOROSKI, B. B., NICHOLSON, M. C. and LOFT, E. R. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. *Ecology* **8**: 530-544.

KIE, J. G., MATTHIOPOULOS, J., FIEBERG, J., POWELL, R. A., CAGNACCI, F., MITCHELL, M. S., GAILLARD, J-M. and MOORCROFT, P. R. 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society B* **365**: 2221-2231.

KLAR, N., FERNÁNDEZ, N., KRAMER-SCHADT, S., HERRMANN, M., TRINZEN, M., BÜTTNER, I. and NIEMITZ, C. 2008. Habitat selection models for European wildcat conservation. *Biological Conservation* **141**: 308-319.

KLEINE, R. 2007. Status report for the cheetah in Botswana. In: *The Status and Conservation Needs of the Cheetah in Southern Africa*, (eds) C. Breitenmoser, and S. M. Durant, pp. 14-21. CAT news special edition, December.

KOK, A. D., PARKER, D. M. and BARKER, N. P. 2012. Life on high: the diversity of small mammals at high altitude in South Africa. *Biodiversity and Conservation* **21**: 2823-2843.

KREEGER, T. J. and ARNEMO, J. M. 2007. *Handbook of Wildlife Chemical Immobilization 3rd ed*. Wheatland, Wyoming, USA.

KRUUK, H. 1998. Role and Management of Hyaenas in Protected areas. In: *Hyaenas: status survey and conservation action plan*, (eds) M. G. L. Mills and H. Hofer, pp. 80-83. IUCN, Gland, Switzerland and Cambridge, UK.

KUHN, B. F., WIESEL, I. and SKINNER, J. D. 2008. Diet of brown hyaenas (*Parahyaena brunnea*) on the Namibian coast. *Transactions of the Royal Society of South Africa* **63**: 150-159.

LAURENSON, M. K. 1995. Implications of high offspring mortality for cheetah population dynamics. In: *Serengeti II: dynamics, management and conservation of an ecosystem,* (eds) A. R. E. Sinclair and P. Arcese, pp. 385-399. University of Chicago, Chicago, USA.

LAVER, P. N. and KELLY, M. J. 2008. A critical review of home range studies. *Journal of Wildlife Management* **72**: 290-298.

LEGENDRE, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* **74**: 1659-1673.

LIMA, S. L. and DILL, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**: 619-640.

LINNELL, J. D. C., SWENSON, J. E. and ANDERSEN, R. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favorable. *Animal Conservation* **4**: 345-349.

LINK, W. A. 2003. Nonidentifiability of Population Size from Capture-Recapture Data with Heterogeneous Detection Probabilities. *Biometrics* **59**: 1123-1130.

LINKIE, M., CHAPRON, G., MARTYR, D. J., HOLDEN, J. and LEADER-WILLIAMS, N. 2006. Assessing the viability of tiger subpopulations in a fragmented landscape. *Journal of Applied Ecology* **43**: 576-586.

LOGAN, K. A., SWEANOR, L. L., SMITH, J. F. and HORNOCKER, M. G. 1999. Capturing pumas with foot-hold snares. *Wildlife Society Bulletin* **27**: 201-208.

MACDONALD, D. W. 1983. The ecology of carnivore social behaviour. *Nature* **301**: 379-384.

MACE, G. M., COLLAR, N., GASTON, K. J., HILTON-TAYLOR, C., AKÇAKAYA, H. R., LEADER-WILLIAMS, N., MILNER-GULLAND, E. J. and STUART, S. N. 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology* **22**: 1424-1442.

MADDOCK, A. H. 1993. Analysis of brown hyaena (*Hyaena brunnea*) scats from the central karoo, South Africa. *Journal of Zoology* **231**: 679-683.

MANLY, B. F. J., MCDONALD, L. L., THOMAS, D. L., MCDONALD, T. L. and ERICKSON, W. P. 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Kluwer Academic Publishers, Norwell, Massachusetts, USA

MANNING, J. A. and GOLDBERG, C. S. 2010. Estimating population size using capture-recapture encounter histories created from point-coordinate locations of animals. *Methods in Ecology and Evolution* **1**: 389-397.

MARKER, L. L., DICKMAN, A. J., MILLS, M. G. L., JEO, R. M. and MACDONALD, D. W. 2008. Spatial ecology of cheetahs on north-central Namibian farmlands. *Journal of Zoology* **274**: 226-238.

MARLTON, J. 2008. Estimating the population size of brown hyaenas (*Hyaena brunnea*) and relative abundances of nocturnal mammals in Kwandwe Private Game Reserve, South Africa, using a photographic mark-recapture sampling protocol. Unpublished Honours Project, Rhodes University, Grahamstown, South Africa.

MARNEWICK, K., FUNSTON, P. J. and KARANTH, K. U. 2008. Evaluating camera trapping as a method for estimating cheetah abundance in ranching areas. *South African Journal of Wildlife Research* **38**: 59-65.

MAUDE, G. 2005. The Comparative Ecology of the Brown Hyaena, (*Hyaena brunnea*) in Makgadikgadi National Park and a Neighbouring Community Cattle Area in Botswana. MSc thesis, University of Pretoria, Pretoria, South Africa.

MAUDE, G. and MILLS, M. G. L. 2005. The comparative feeding ecology of the brown hyaena in a cattle area and a national park in Botswana. *South African Journal of Wildlife Research* **35**: 201-214.

MCCARTHY, J. L., BELANT, J. L., BREITENMOSER-WÜRSTEN, C., HEARN, A. J. and ROSS, J. 2013. Live trapping carnivores in tropical forests – tools and techniques to minimise efficacy. *Raffles Bulletin of Zoology* **28**: 55-66.

MILLER, S. D., WHITE, G. C., SELLERS, R. A., REYNOLDS, H. V., SCHOEN, J. W., TITUS, K., BARNES, V. G. JR., SMITH, R. B., NELSON, R. R., BALLARD, W. B. and SCHWARTZ, C. C. 1997. Brown and Black Bear Density Estimation in Alaska Using Radiotelemetry and Replicated Mark-Resight Techniques. *Wildlife Monologues* **133**: 1-55.

MILLER, B., DUGELBY, B., FOREMAN, D., MARTINEZ DEL RIO, C., NOSS, R., PHILLIPS, M., READING, R., SOULÉ, M. E., TERBORGH, J. and WILCOX, L. 2001. The Importance of Large Carnivores to Healthy Ecosystems. *Endangered Species Update* **18**: 202-210.

MILLS, M. G. L. and MILLS, M. E. J. 1978. The Diet of the Brown Hyaena *Hyaena brunnea* in the Southern Kalahari. *Koedoe* **21**: 125-149.

MILLS, M. G. L., WOLFF, P., LE RICHE, E. A. N. and MEYER, I. J. 1978. Some population characteristics of the lion *Panthera leo* in the Kalahari Gemsbok National Park. *Koedoe* **21**: 163-171.

MILLS, M. G. L., GORMAN. M. L. and MILLS, M. E. J. 1980. The scent marking behaviour of the brown hyaena *Hyaena brunnea*. *South African Journal of Zoology* **15**: 240-248.

MILLS, M. G. L. 1981. The Socio-ecology and social behaviour of the brown hyaena, *Hyaena brunnea* Thunberg, 1820 in the southern Kalahari. DSc thesis, University of Pretoria, South Africa.

MILLS, M. G. L. 1982a. Factors affecting group size and territory size of the brown hyaena, *Hyaena brunnea* in the southern Kalahari. *Journal of Zoo1ogy* **198**: 39-51.

MILLS, M. G. L. 1982b. The Mating System of the Brown Hyaena, *Hyaena brunnea* in the Southern Kalahari. *Behavioral Ecology and Sociobiology* **10**: 131-136.

MILLS, M. G. L. 1982c. Notes on Age Determination, Growth and Measurements of Brown Hyaenas *Hyaena brunnea* from the Kalahari Gemsbok National Park. *Koedoe* **25**: 55-61.

MILLS, M. G. L. and MILLS, M. E. J. 1982. Factors affecting the movement patterns of brown hyaena, *Hyaena brunnea*, in the southern Kalahari. *South African Journal of Wildlife Research* **12**: 111-117.

MILLS, M. G. L. 1983. Behavioural Mechanisms in territory and group maintenance of the Brown Hyaena, *Hyaena brunnea*, in the southern Kalahari. *Animal Behaviour* **31**: 503-510.

MILLS, M. G. L. 1984. The Comparative behavioural Ecology of the Brown Hyaena (*Hyaena brunnea*) and The Spotted Hyaena (*Crocuta crocuta*) in The Southern Kalahari. *Koedoe* (Supplement): 237-247.

MILLS, M. G. L. 1987. Behavioural adaptations of brown and spotted hyaenas in the Southern Kalahari. *South African Journal of Science* **83**: 595-598.

MILLS, M. G. L. 1990. *Kalahari hyaenas: Comparative behavioural ecology of two species*. Unwin Hyman, London, UK.

MILLS, M. G. L. 1991. Conservation management of large carnivores in Africa. *Koedoe* **34**: 81-90.

MILLS, M. G. L. 1996. Methodological advances in capture, census, and food habits studies of large African carnivores. In: *Carnivore Behavior, Ecology and Evolution Volume II,* (ed) J. L. Gittleman, pp. 223-242. Cornell University Press, Ithaca, New York, USA.

MILLS, M. G. L. 1998a. Brown hyaena *Hyaena (Parahyaena) brunnea* (Thunberg, 1820) In: *Hyaenas: status survey and conservation action plan,* (eds) M. G. L. Mills and H. Hofer, pp. 26-29. IUCN, Gland, Switzerland and Cambridge, UK.

MILLS, G. 1998b. Hyaenas Living Close to People: Predator Control, Attacks on People and Translocations. In: *Hyaenas: status survey and conservation action plan,* (eds) M. G. L. Mills and H. Hofer, pp. 84-87. IUCN, Gland, Switzerland and Cambridge, UK.

MILLS, M. G. L., BROOMHALL, L. S. and DU TOIT, J. T. 2004. Cheetah *Acinonyx jubatus* feeding ecology in the Kruger National Park and a comparison across African savanna habitats: is the cheetah only a successful hunter on open grassland plains? *Wildlife Biology* **10**: 177-186.

MIZUTANI, F. and JEWELL, P. A. 1998. Home-range and movements of leopards (*Panthera pardus*) on a livestock ranch in Kenya. *Journal of Zoology* **244**: 269-286.

MORRIS, D. W. 1987. Ecological Scale and Habitat Use. *Ecology* **68**: 362-369.

NEGRÕES, N., SARMENTO, P., CRUZ, J., EIRA, C., REVILLA, E., FONSECA, C., SOLLMANN, R., TÔRRES, N. M., FURTADO, M. M., JÁCOMO, A. T. A. and SILVEIRA, L. 2010. Use of camera-trapping to estimate puma density and influencing factors in Central Brazil. *Journal of Wildlife Management* **74**: 1195-1203.

NELLIS, C. H. 1968. Some methods for capturing coyotes alive. *Journal of Wildlife Management* **32**: 402-405.

NEWDICK, M. T. 1983. The behavioural ecology of urban foxes, *Vulpes vulpes*, in Oxford. PhD thesis, University of Oxford, Oxford, UK.

NOSS, A. J., GARDNER, B., MAFFEI, L., CUÉLLAR, E., MONTAÑO, R., ROMERO-MUÑOZ, A., SOLLMANN, R. and O'CONNELL, A. F. 2012. Comparison of density estimation methods for mammal populations with camera traps in the Kaa-lya del Gran Chaco landscape. *Animal Conservation* **15**: 527-535.

NOWELL, K. and JACKSON, P. 1996. *Wild Cats: Status survey and conservation action plan*. IUCN/SSC Cat Specialist Group, Switzerland.

NÚÑEZ-PÉREZ, R. 2011. Estimating jaguar population density using camera-traps: a comparison with radio-telemetry estimates. *Journal of Zoology* **285**: 39-45.

OTIS, D., BURNHAM, K., WHITE, G. and ANDERSON, D. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* **62**: 1-135.

OTIS, D. L. and WHITE, G. C. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. *Journal of Wildlife Management* **63**: 1039-1044.

OWENS, M. J. and OWENS, D. D. 1978. Feeding ecology and its influence on social organization in brown hyaenas (*Hyaena brunnea*, Thunberg) of the Central Kalahari Desert. *East African Wildlife Journal* **16**: 113-36.

OWENS, D. and OWENS, M. 1979a. Communal denning and clan associations in brown hyenas (*Hyaena brunnea*, Thunberg) of the central Kalahari Desert. *African Journal of Ecology* **17**: 35-44.

OWENS, D. and OWENS, M. 1979b. Notes on Social Organization and Behavior in Brown Hyaenas (*Hyaena brunnea*). *Journal of Mammalogy* **60**: 405-408.

OWENS, D. D. and OWENS, M. J. 1984. Helping behaviour in brown hyenas. *Nature* **308**: 843-845.

OWENS, D. and OWENS, M. 1996. Social dominance and reproductive patterns in brown hyaenas, *Hyaena brunnea*, of the central Kalahari desert. *Animal Behaviour* **51**: 535-551.

PAINE, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. The Third Tansley Lecture. *Journal of Animal Ecology* **49**: 667-685.

PETTORELLI, N., HILBORN, A., BROEKHUIS, F. and DURANT, S. M. 2009. Exploring habitat use by cheetahs using ecological niche factor analysis. *Journal of Zoology* **277**: 141-148.

PETTORELLI, N., LOBORA, A. L., MSUHA, M. J., FOLEY, C. and DURANT, S. M. 2010. Carnivore biodiversity in Tanzania: revealing the distribution patterns of secretive mammals using camera traps. *Animal Conservation* **13**: 131-139.

POLIS, G. A. and STRONG D. R. 1996. Food web complexity and community dynamics. *American Naturalist* **147**: 813-846.

POWELL, R. A. 2000. Animal Home Ranges and Territories and Home Range Estimators. In: *Research techniques in Animal Ecology*, (eds.) L. Boitani and T. K. Fuller, pp. 65-110. Columbia University Press, New York, USA.

POWELL, R. A. 2005. Evaluating welfare of American black bears (*Ursus americanus*) captured in foot snares and in winter dens. *Journal of Mammalogy* **86**: 1171-1177.

RAY, J. C., REDFORD, K. H., STENECK, R. S. and BERGER, J. 2005. *Large Carnivores and the Conservation of Biodiversity*. Island Press, Washington, DC, USA.

REAGAN, S. R., ERTEL, J. M., STINSON, P., YAKUPZACK, P. and ANDERSON, D. 2002. A passively triggered foot snare design for American black bears to reduce disturbance by non-target animals. *Ursus* **13**: 317-320.

REXSTAD, E. A. and BURNHAM, K. P. 1992. *User's Guide for Interactive Program CAPTURE: Abundance Estimation of Closed Animal Populations*. Colorado Cooperative Fish and Wildlife Research Unit, Colorado, USA.

RIPPLE, W. J., ESTES, J. A., BESCHTA, R. L., WILMERS, C. C., RITCHIE, E. G., HEBBLEWHITE, M., BERGER, J., ELMHAGEN, B., LETNIC, M., NELSON, M. P., SCHMITZ, O. J., SMITH, D. W., WALLACH, A. D. and WIRSING, A. J. 2014. Status and ecological effects of the world's largest carnivores. *Science* **343**: DOI:10.1126/science.1241484.

RITCHIE, E. G. and JOHNSON, C. N. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* **12**: 982-998.

RODGERS, A. R. and KIE, J. G. 2011. *HRT: Home Range Tools for ArcGIS®, Version 1.1, June 2007. Draft User's Manual, Draft June 2*. Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources.

ROYLE, J .A. and YOUNG, K. V. 2008. A Hierarchical Model for Spatial Capture-Recapture Data. *Ecology* **89**: 2281-2289.

ROYLE, J. A., NICHOLS, J. D., KARANTH, K. U. and GOPALASWAMY, A. M. 2009. A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology* **46**: 118-127.

SADLIER, L. M. J., WEBBON, C. C., BAKER, P. J. and HARRIS, S. 2004. Methods of monitoring red foxes *Vulpes vulpes* and badgers *Meles meles*: are field signs the answer? *Mammal Review* **34**: 75-98.

SCHMITZ, O. J., BECKERMAN, A. P. and O'BRIEN, K. M. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* **78**: 1388-1399.

SCHWARZ, C. J. and SEBER, G. A. F. 1999. Estimating animal abundance: Review III. *Statistical Science* **14**: 427-456.

SEAMAN, D. E. and POWELL, R. A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* **77**: 2075-2085.

SEDDON, P. J. 1999. Persistence without intervention: assessing success in wildlife reintroductions. *Trends in Research of Ecology and Evolution* **14**: 503.

SHAFFER, M. L. 1981. Minimum Population Sizes for Species Conservation. *BioScience* **31**: 131-134.

SIKES, R. S., GANNON, W. L., AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* **92**: 235-253.

SILVEIRA, L., JÁCOMO, A. T. A., ASTETE, S., SOLLMANN, R., TÔRRES, N. M., FURTADO, M. M. and MARINHO-FILHO, J. 2010. Density of the Near Threatened jaguar *Panthera onca* in the caatinga of north-eastern Brazil. *Oryx* **44**: 104-109.

SILVER, S. C., OSTRO, L. E. T., MARSH, L. K., MAFFEI, L., NOSS, A. J., KELLY, M. J., WALLACE, R. B., GÓMEZ, H. and AYALA, G. 2004. The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx* **38**: 148-154.

SIMS-CASTLEY, R., KERLEY, G. I. H., GEACH, B. and LANGHOLZ, J. 2005. Socio-economic significance of ecotourism-based private game reserves in South Africa’s Eastern Cape Province. *Parks* **15**: 67-77.

SKEAD, C. J. 2007 *Historical incidence of the larger land mammals in the broader eastern cape 2nd edn.* (eds A. F. Boshoff, G. I. H. Kerley and P. H. Lloyd). Nelson Mandela Metropolitan University Bukani Print, Port Elizabeth, South Africa.

SKINNER, J. D. and VAN AARDE, R. J. 1981. The distribution and ecology of the brown hyaena *Hyaena brunnea* and spotted hyaena *Crocuta crocuta* in the central Namib Desert. *Madoqua* **12**: 231-239.

SKINNER, J. D. and VAN AARDE, R. J. 1987. Range use by brown hyaenas *Hyaena brunnea* relocated in an agricultural area of the Transvaal. *Journal of Zoology* **212**: 350-352.

SKINNER, J. D., VAN AARDE, R. J. and GOSS, R. A. 1995. Space and resource use by brown hyaenas *Hyaena brunnea* in the Namib Desert. *Journal of Zoology* **237**: 123-131.

SMITH, J. L. D., SUNQUIST, M. E., TAMANG, K. M. and RAJ, P. B. 1983. A technique for capturing and immobilizing tigers. *The Journal of Wildlife Management* **47**: 255-257.

SOISALO, M. K. and CAVALCANTI, S. M. C. 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture-recapture sampling in combination with GPS radio-telemetry. *Biological Conservation* **129**: 487-496.

SOLLMANN, R., FURTADO, M. M., GARDNER, B., HOFER, H., JÁCOMO, A. T. A., TÔRRES, N. M. and SILVEIRA, L. 2011. Improving density estimates for elusive carnivores: Accounting for sex-specific detection and movements using spatial capture-recapture models for jaguars in central Brazil. *Biological Conservation* **144**: 1017-1024.

SOULÉ, M. E. and SIMBERLOFF, D. 1986. What do genetics and ecology tell us about the design of nature reserves? *Biological Conservation* **35**: 19-40.

SPONG, G. 2002. Space use in lions, *Panthera leo*, in the Selous Game Reserve: social and ecological factors. *Behavioral Ecology and Sociobiology* **52**: 303-307.

STANDER, P. E., HADEN, P. J., KAQECE, H. and GHAU, H. 1997. The ecology of asociality in Namibian leopards. *Journal of Zoology* **242**: 343-364.

STANDER, P. E. 1998. Spoor counts and indices of large carnivore populations: the relationship between spoor frequency, sampling effort and true density. *Journal of Applied Ecology* **35**: 378-385.

STEPHENS, P. A., ZAUMYSLOVA, O. Y., MIQUELLE, D. G., MYSLENKOV, A. I., and HAYWARD, G. D. 2006. Estimating population density from indirect sign: track counts and the Formozov-Malyshev-Pereleshin formula. *Animal Conservation* **9**: 339-348.

STONE, A. W., WEAVER, A. B. and WEST, W. O. 1998. Climate and weather. In: *Field guide to the Eastern and Southern Cape coasts,* (eds) R. Lubke and I. de Moor, pp. 41-49. University of Cape Town Press, Cape Town, South Africa.

SUNQUIST, M. and SUNQUIST, F. 2002. The essence of cats. In: *Wild cats of the world,* (eds) M. Sunquist and F. Sunquist, pp. 11-13. The University of Chicago Press, Chicago, USA.

SUTHERLAND, W. J., PULLIN, A. S., DOLMAN, P. M. and KNIGHT, T. M. 2004. The need for evidence-based conservation. *Trends in Ecology and Evolution* **19***:* 305-308.

SWIHART, R. and SLADE, N. 1985. Testing for independence of observations in animal movements. *Ecology* **66**: 1176-1184.

SYMONDS, M. R. E. and MOUSSALLI, A. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioural Ecology and Sociobiology* **65**: 13-21.

TERBORGH, J., ESTES, J. A., PAQUET, P., RALLS, K., BOYD-HEGER, D., MILLER, B. J. and NOSS, R. F. 1999. The role of top carnivores in regulating terrestrial ecosystems. In: *Continental conservation: scientific foundations of regional reserve networks,* (eds) M. E. Soulé and J. Terborgh, pp. 39-64. Island Press, Washington, DC, USA.

TERBORGH, J., LOPEZ, L., NUÑEZ, P., RAO, M., SHAHABUDDIN, G., ORIHUELA, G., RIVEROS, M., ASCANIO, R., ADLER, G. H., LAMBERT, T. D. and BALBAS, L. 2001. Ecological meltdown in predator-free forest fragments. *Science* **294**: 1923-1926.

TEW, T. E. 1989. The behavioural ecology of the wood mouse, *Apodemus sylvaticus,* in the cereal field ecosystem. PhD thesis, University of Oxford, Oxford, UK.

THORN, M., SCOTT, D. M., GREEN, M., BATEMAN, P. W. and CAMERON, E. Z. 2009. Estimating brown hyaena occupancy using baited camera traps. *South African Journal of Wildlife Research* **39**: 1-10.

THORN, M., GREEN, M., BATEMAN, P. W., WAITE, S. and SCOTT, D. M. 2011. Brown hyaenas on roads: estimating carnivore occupancy and abundance using spatially auto-correlated sign survey replicates. *Biological Conservation* **144**: 1799-1807.

TOBLER, M. W. and POWELL, G. V. N. 2013. Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies. *Biological Conservation* **159**: 109-118.

TROLLE, M. and KÉRY, M. 2003. Estimation of ocelot density in the Pantanal using capture-recapture analysis of camera-trapping data. *Journal of Mammalogy* **84**: 607-614.

VAN SICKLE, J. 1996. *GPS for Land Surveyors*. Ann Arbor Press, Michigan, USA.

VAN WINKLE, W. 1975. Comparison of several probalistic home-range models. *Journal of Wildlife Management* **39**: 118-123.

WALLACE, R., GOMEZ, H., AYALA, G. and ESPINOZA, F. 2003. Camera trapping for jaguar (*Panthera onca*) in the Tuichi Valley, Bolivia. *Journal of Neotropical Mammalogy* **10**: 133-139.

WEBER, W. and RABINOWITZ, A. 1996. A global perspective on large carnivore conservation. *Conservation Biology* **10**: 1046-1054.

WESTERN, D. 1979. Size, life history and ecology in mammals. *African Journal of Ecology* **17**: 185-204.

WHITE, T. C. R. 1978. The Importance of a Relative Shortage of Food in Animal Ecology. *Oecologia* **33**: 71-86.

WHITE, G. C., ANDERSON, D. R., BURNHAM, K. P. and OTIS, D. L. 1982. *Capture-recapture and removal methods for sampling closed populations*. Los Alamos National Laboratory Publication LA-8787-NERP. Los Alamos, New Mexico, USA.

WIESEL, I. 2006. Predatory and Foraging Behaviour of Brown Hyenas (*Parahyaena brunnea* (Thunberg, 1820)) at Cape Fur Seal (*Arctocephalus pusillus pusillus* Schreber, 1776) Colonies. PhD thesis, University of Hamburg, Hamburg, Germany.

WIESEL, I., MAUDE, G., SCOTT, D. and MILLS, G. 2008. *Hyaena brunnea*. In: 2008 IUCN Red List of Threatened Species; http://www.iusnredlist.org, Gland.

WILLIAMS, B. K., NICHOLS, J. D. and CONROY, M. J. 2002. *Analysis and Management of animal populations: modeling, estimation, and decision making.* Academic Press, London, UK.

WILSON, K. R. and ANDERSON, D. R. 1985. Evaluation of Two Density Estimators of Small Mammal Population Size. *Journal of Mammalogy* **66**: 13-21.

WILSON, D. E., COLE, F. R., NICHOLS, J. D., RUDRAN, R. and FOSTER, M. S. 1996. *Measuring and Monitoring Biological Diversity: Standard Methods for Mammals.* Smithsonian Institution Press, Washington, DC, USA.

WILSON, E. E. and WOLKOVICH, E. M. 2011. Scavenging: how carnivores and carrion structure communities. *Trends in Ecology and Evolution* **26**: 129-135.

WOODROFFE, R. 2001. Strategies for carnivore conservation: lessons from contemporary extinctions. In: *Carnivore conservation*, (eds) J. L. Gittleman, S. M. Funk, D. Macdonald and R. K. Wayne, pp. 61-92. Cambridge University Press, Cambridge, UK.

WORTON, B. J. 1987. A review of models of home range for animal movement. *Ecological Modelling* **38**: 277-298.

WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**: 164-168.

WORTON, B. J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimates. *Journal of Wildlife Management* **59**: 794-800.

YARNELL, R. W., PHIPPS, W. L., BURGESS, L. P., ELLIS, J. A., HARRISON, S. W. R., DELL, S., MACTAVISH, D., MACTAVISH, L. M. and SCOTT, D. M. 2013. The influence of large predators on the feeding ecology of two African mesocarnivores: the black-backed jackal and the brown hyaena. *South African Journal of Wildlife Research* **43**: 155-166.

APPENDICES

Appendix I: List of mammals found in Kwandwe Private Game Reserve

ORDER PRIMATE
chacma baboon *Papio ursinus*
vervet monkey *Cercopithecus aethiops*

ORDER LAGOMORPHA
scrub hare *Lepus saxatilis*
Smith's red rock rabbit *Pronolagus rupestris*

ORDER RODENTIA
springhare *Pedetes capensis*
greater canerat *Thryonomys swinderianus*
Cape porcupine *Hystrix africaeaustralis*
pouched mouse *Saccostomus campestris*
Namaqua rock mouse *Micaelamys namaquensis*
four striped mouse *Rhabdomys pumilio*
pygmy mouse *Mus minutoides*
multimammate mouse *Mastomys coucha*
vlei rat *Otomys irroratus*

ORDER HYRACOIDEA
rock hyrax *Procavia johnstoni*

ORDER EULIPOTYPHLA
Southern African hedgehog *Atelerix frontalis*

ORDER MACROSCELIDEA
round-eared elephant-shrew *Macroscelides proboscideus*

ORDER CHIROPTERA
Egyptian free-tailed bat *Tadarida aegyptiaca*
Egyptian fruit bat *Rousettus aegyptiacus*
straw-coloured fruit bat *Eidolon helvum*
Wahlberg’s epauletted fruit bat *Epomophorus wahlbergi*
Cape horse-shoe bat *Rhinolophus capensis*
African yellow house bat *Scotophilus dinganii*
Schreibers' long-fingered bat *Miniopterus schreibersii*
Cape serotine bat *Neoromicia capensis*
common silt-faced bat *Nycteris thebaica*
Mauritian tomb bat *Taphozous mauritianus*

ORDER TUBULIDENTATA

aardvark *Orycteropus afer*

ORDER PERISSODACTYLA

Plains zebra *Equus quagga*

ORDER PROBOSCIDEA

elephant *Loxodonta africana*

ORDER ARTIODACTYLA

warthog *Phacochoerus aethiopicus*
bushpig *Potamochoerus porcus*
giraffe *Giraffa camelopardalis*
bushbuck *Tragelaphus scriptus*
greater kudu *Tragelaphus strepsiceros*
eland *Tragelaphus oryx*
buffalo *Syncerus caffer*
waterbuck *Kobus ellipsiprymnus*
gemsbok *Oryx gazella*
mountain reedbuck *Redunca fulvorufula*
red hartebeest *Alcelaphus buselaphus*
nyala *Tragelaphus angasii*
black wildebeest *Connochaetes gnou*
steenbok *Raphicerus campestris*
common duiker *Sylvicapra grimmia*
impala *Aepyceros melampus*
springbok *Antidorcas marsupialis*
Cape grysbok *Raphicerus melanotis*

ORDER CARNIVORA

Cape grey mongoose *Galerella pulverulenta*
yellow mongoose *Cynictis penicillata*
water mongoose *Atilax paludinosus*
white tailed mongoose *Ichneumia albicauda*
suricate *Suricata suricatta*
large spotted genet *Genetta tigrina*
small spotted genet *Genetta genetta*
striped polecat *Ictonyx striatus*
Cape clawless otter *Aonyx capensis*
Cape fox *Vulpes chama*
bat-eared fox *Otocyon megalotis*
aardwolf *Proteles cristatus*
black-backed jackal *Canis mesomelas*
caracal *Felis caracal*
African wildcat *Felis libyca*
small spotted cat *Felis nigripes*
cheetah *Acinonyx jubatus*
serval *Felis serval*

leopard *Panthera pardus*
lion *Panthera leo*
brown hyaena *Hyaena brunnea*
honey badger *Mellivora capensis*

Appendix II: Example of capture matrix for brown hyaenas (left-side images) captured during the camera survey. Numbers 1-28 represent sampling occasions and BH01-BH28 represent individuals captured. ‘1’ represents that an individual was captured and ‘0’ represents that an individual was not captured.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
BH01	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BH02	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
BH03	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BH04	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BH05	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
BH06	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0
BH07	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
BH08	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
BH09	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
BH10	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BH11	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
BH12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
BH13	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
BH14	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
BH15	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BH16	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
BH17	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
BH18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
BH19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
BH20	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BH21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
BH22	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BH23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
BH24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
BH25	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
BH26	0	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
BH27	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BH28	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

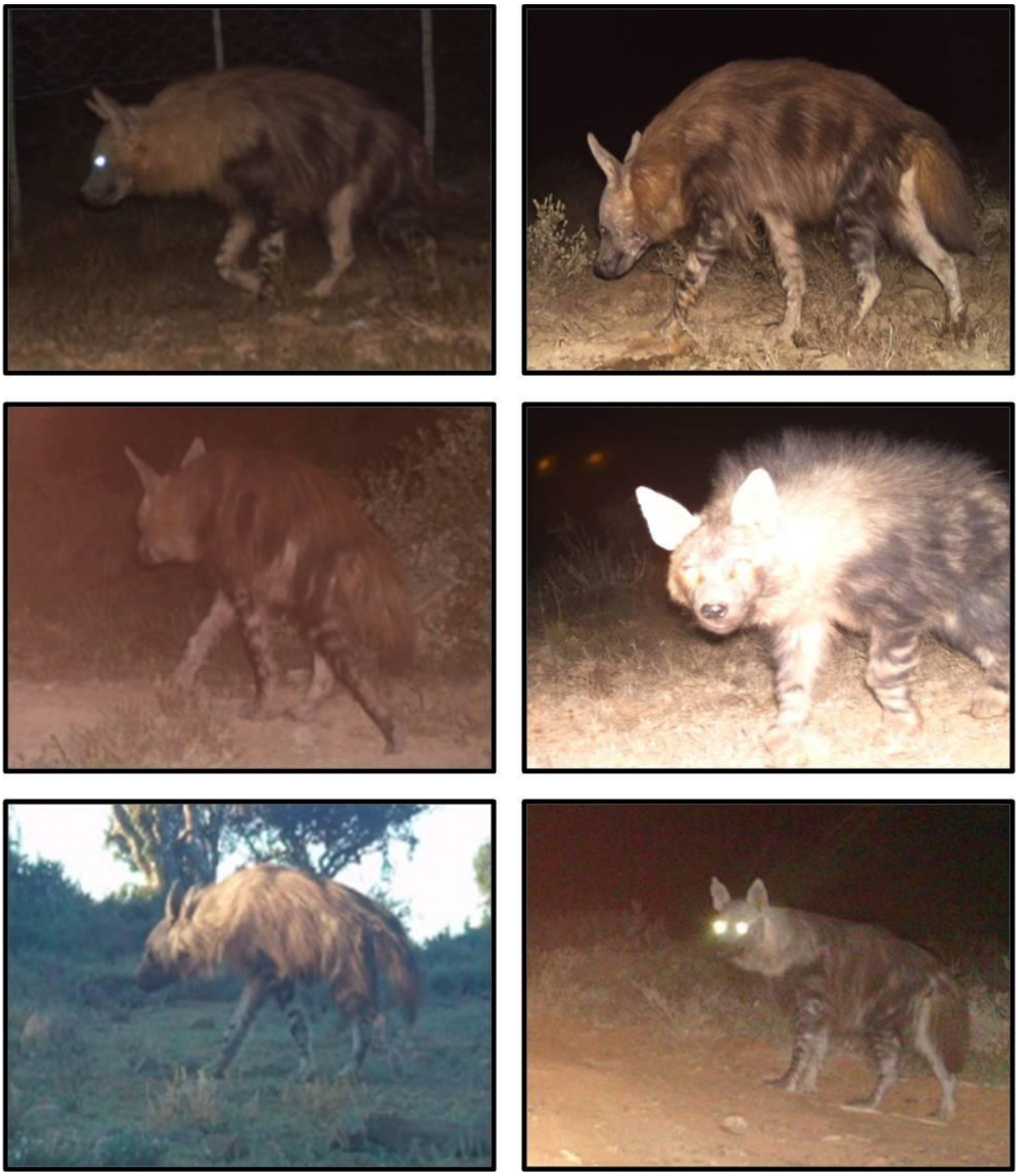
Appendix III: Example of trap layout file used in DENSITY 5.0. Table shows the trap ID and associated X and Y co-ordinates. Numbers 1-20 represent sampling occasions. ‘1’ represents if a camera was active and ‘0’ represents if a camera was inactive.

TRAP ID	X_Coord	Y_Coord	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
B7	41697	-3670961	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
B8	41914	-3673221	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
B9	42854	-3674837	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
C7	44475	-3670829	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
C8	44126	-3672690	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
C9	44233	-3674542	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
D7	46557	-3670735	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
D8	46065	-3673073	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
D9	45864	-3674944	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
E7	48352	-3670724	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
E8	47776	-3671931	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
E9	47336	-3674292	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
F7	49584	-3670032	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
F8	50255	-3672034	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
G7	51478	-3671010	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
B6	42504	-3669149	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C4	45025	-3664023	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C5	44143	-3666469	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C6	43817	-3668438	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D5	46461	-3666694	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D6	46318	-3668502	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E5	49349	-3665995	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E6	49042	-3668505	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
F5	50684	-3666683	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
F6	49940	-3667950	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G5	52607	-3666563	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix IV: Example of DENSITY 5.0 input file showing brown hyaena capture details (highlighting a section of results used in right-side analyses), the number of sessions (only 1 as this example does not contain pooled data), animal ID, sampling occasion the individual was caught and the trap ID where the individual was captured.

SESSION	ANIMAL ID	SO	TRAP ID
1	BH29	43	B6
1	BH29	28	B6
1	BH29	31	B6
1	BH29	34	C6
1	BH30	31	C4
1	BH30	32	C5
1	BH30	54	D4
1	BH31	31	C4
1	BH31	65	D1
1	BH31	73	D1
1	BH31	77	D1
1	BH31	62	D3
1	BH31	62	E2
1	BH32	62	E2
1	BH32	57	E3
1	BH32	61	E3
1	BH32	55	F2
1	BH32	57	F2
1	BH32	58	F2
1	BH33	66	D3
1	BH33	56	D3
1	BH33	57	D3
1	BH34	86	B3
1	BH34	93	C3
1	BH34	30	C4
1	BH34	72	D1
1	BH34	64	E2
1	BH35	95	B4
1	BH35	47	C5
1	BH36	80	C2
1	BH36	54	D2
1	BH36	64	D3
1	BH36	59	E2
1	BH36	77	F2
1	BH37	60	D4
1	BH37	69	E2
1	BH37	72	E2
1	BH37	62	H2
1	BH37	69	F1
1	BH38	73	G2
1	BH38	69	H2
1	BH38	76	H2

Appendix V: Side profiles of individual brown hyaenas (profiles used in left- and right-side analyses are shown).











Appendix VI: Data sheet with individual brown hyaena capture information and morphological measurements.

Measurements	**BHM1**	**BHM2**	**BHF1**
Trapping site	S33.12135, E26.59573	S33.16478, E26.52911	S33.11651, E26.57289
Weight (kg)	42	56	50
Age	Young adult	Adult	Adult
Darting:			
Dart-in time	0050h	2340h	2350h
Dart site	Right shoulder	Left shoulder	Below base of tail
Animal downtime (mins)	46	72	60
Trapping foot	Front right	Front left	Front right
Dosage:			
Zoletil dart dosage (mg)	40	30	20
Medetomidine dart dosage (mg)	4	2	2
Reversal Atipamezole dosage (mg)	20	10 (IV) + 10 (IM)	10
Morphological measurements (cm):			
Nose to tail tip	144.5	152	147.5
Tail length	20	23	23.5
Stomach size	85	91	94.5
Skull width	19	21.5	22
Skull length	30.5	28.5	28.5
Chest girth	85	84	87
Chest depth	41	42	44.5
Neck girth	58.5	57	58
Shoulder height (leg bent)	55	66.5	63.5
Shoulder height (leg straight)	62	72.5	71
Canines:			
Top right	3	3	2.5
Bottom right	3	3	3
Top left	3	2.75	3
Bottom left	3	2.5	3
Distance between top tips	6	5.5	6.5
Distance between bottom tips	4	4.5	4.5
Front paw length	13	15.5	13
Back paw length	12	12.5	10
Front paw width	11	11	11
Back paw width	9	8.5	7.5