FEEDING AND SPATIAL ECOLOGY OF BROWN HYAENA (*HYAENA BRUNNEA*) IN THE PRESENCE OF A VULTURE RESTAURANT ON MOGALE'S GATE BIODIVERSITY CENTRE, GAUTENG PROVINCE, SOUTH AFRICA

by

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Declaration

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Abstract

Initial studies of brown hyaena occurred mainly in relatively large and arid systems, such as in the Namib Desert, the Kalahari region of southern Africa and savanna regions of Botswana and northern South Africa. In recent years studies on this species have focused on smaller areas, and in different habitats and land use types. My study investigated the feeding and spatial ecology of brown hyaena in the presence of a long-standing supplementary feeding site (vulture restaurant) on the Mogale's Gate Biodiversity Centre, a small (3060 ha) protected area in the Gauteng province of South Africa. Vulture restaurants have, for decades, been used globally to facilitate conservation by increasing survival and reproduction in local vulture populations. As little is known about the potential impact of vulture restaurants on other scavengers the main objective of my study was to ascertain how the presence of a long-standing vulture restaurant influences aspects of brown hyaena feeding ecology, home range and population estimates. Scat analysis was used to determine the seasonal diet of brown hyaena. Brown hyaena have access to a regular supply of carrion at the vulture restaurant which during my study contributed 43% to their overall diet. The remaining 28% was made up of smaller prey items, and 9% plant material. Population data were collected by camera traps placed across the property over a 15-month period, in which time 5 independent capturerecapture surveys were done. In order to test for population closure and to select the best models for capture probability, the Program CAPTURE was used. The program DENSITY 5.0. was used to run non-spatial capture-recapture analyses. Over the 15-month survey period abundance estimates ranged from 4 to 6 individuals per three-month capture period, resulting in density estimates of 13 to 20 individuals per 100 km². The density estimates obtained from my study are higher than those calculated for brown hyaenas in arid areas, but similar to those of small reserves in the Eastern Cape province of South Africa. Home range estimates were calculated by using satellite collar data in QGIS V2.18 and generated using the adehabitatHR package (version 0.4.1.9) (Calenge 2006) in program R 3.5.0 (R Core Team 2018). Two methods for home range estimates were used and compared - Kernel Utilisation Distribution and Minimum Convex Polygons. Two of the three collared, hyaena were found to make regular use of the vulture restaurant and their home ranges were smaller than that reported elsewhere. The relatively small home ranges may suggest that there are sufficient resources available within Mogale's Gate for these brown hyaenas. The results from my study indicate that food resources provided by a permanent vulture restaurant influences the diet, population density, and home range size of individual brown hyaenas. It is suggested that in an area such as the Magaliesberg Biosphere Reserve, where large predators such as lion, cheetah and wild dog no longer occur, the vulture restaurants in the region act as an alternative food source for brown hyaenas, maintaining potentially viable populations and thus acting as a buffer to local extinction for this species.

Keywords

Vulture restaurant, domestic livestock, hunting offal, urban development, camera traps, kernel density estimates, minimum convex polygons, scat analysis.

Opsomming

Voorheen is studies oor die bruin hiëna meestal gedoen in taamlik uitgestrekte en droë stelsels soos die Namibwoestyn, die Kalahari in suidelike Afrika en die savannas van Botswana en die noorde van Suid-Afrika. In die laaste jare is studies oor hierdie hiënaspesie egter in kleiner gebiede, ander habitatte en gebiede met ander grondgebruike gedoen. Ek het die voedingsgewoontes en ruimtelike ekologie van die bruin hiëna in 'n klein, beskermde gebied (3 060 ha), genaamd die Mogale's Gate Biodiversity Centre, in die Gauteng provinsie in Suid-Afrika bestudeer. Na aanleiding van 'n aanvanklike studie oor die teenwoordigheid van spesies wat 'n aanvullende voedselbron gebruik, was die doel van hierdie studie om vas te stel of die langdurige teenwoordigheid van 'n voerplek vir aasvoëls op die eiendom enigsins 'n uitwerking op bruin hiënas se voedingsekologie, tuisveld en geskatte bevolking het. Die seisoenale dieet van bruin hiënas is aan die hand van 'n SCATontleding bepaal. Die aas wat hulle gereeld by die aasvoëlvoerplek kry, het in die studie tydperk 47% van die bruin hiënas se dieet uitgemaak. Soogdier prooi, plant materiaal en voël reste het die oorblywende 53% uitgemaak. Die bevolkings data is oor 15 maande versamel met behulp van kameras wat oral op die eiendom versteek is. In hierdie tydperk is vyf onafhanklike vang-hervang opnames gedoen. Om vir bevolkings digtheid te toets en die mees geskikte modelle vir vangswaarskynlikheid te kies, is die CAPTURE-program gebruik. Die nieruimtelike vang-hervang ontleding is met behulp van die DENSITY 5.0.-program gedoen. In die 15-maande tydperk is vier tot ses individue elke drie maande gevang. Gevolglik is die bevolkings digtheid op 13 tot 20 individue per 100 km² geskat. Ofskoon die bevolkingsdigtheidskattings in hierdie studie hoër is as dié vir bruin hiënas in droë gebiede, stem dit ooreen met dié van bruin hiënas in klein reservate in die Oos-Kaap provinsie van Suid-Afrika. Die oppervlakte van tuisvelde is met satelliet halsband data in QGIS V2.18 geskat, en met die adehabitatHR-pakket (0.4.1.9weergawe) (Calenge 2006) in die program R 3.5.0 (R Core Team 2018) gegenereer. Kernel Utilisation Distribution en Minimum Convex Polygons, die twee metodes waarvolgens die oppervlakte van tuisvelde geskat is, is met mekaar vergelyk. Twee van die drie hiënas met halsbande het die aasvoëlvoerplek gereeld

besoek, en hulle tuisvelde was kleiner as dié wat elders opgemerk is. Hulle betreklik klein tuisvelde kan beteken dat daar by Mogale's Gate genoegsame voedsel vir hierdie bruin hiënas is. Ek het in hierdie studie gevind dat die voedsel by die permanente aasvoël voerplek die dieet, bevolkings digtheid en grootte van sommige bruin hiënas se tuisveld beïnvloed. Daar word aanbeveel dat die aasvoël voerplekke in gebiede soos die Magaliesberg-biosfeerreservaat, waar groot predatore soos leeus, jagluiperds en wildehonde nie langer voorkom nie, as alternatiewe voedselbron vir lewensvatbare bevolkings van bruin hiënas aangewend word om hierdie spesie van uitsterwing te red.

Setsopolwa

Dinyakišišo tša peleng ka ga phiri ye tsooto di dirilwe kudu ka mafelong a magolo a komelelo, a go swana le ka Leganateng la Namib, ka dileteng tša ka Kalahari tša borwa bja Afrika le ka mafelong a mehlare ye mentši a ka Botswana le ka leboa la Afrika Borwa. Mo mengwageng ye e sa tšwago go feta, dinyakišišo tše di dirilwego ka ga mehuta ye di lebeletše kudu mafelo a mannyane le ka madulong a diphoofolo a mehutahuta le ka go mehuta ya tšhomišo ya naga. Dinyakišišo tša ka di nyakišišitše mabapi le go fepa le phedišano le diphedi tše dingwe ga phiri ye tsooto mo lefelong le lennyane leo le šireleditšwego (la dihekthara tše 3060), e lego lefelo laMogale's Gate Biodiversity Centre, ka Phrobentsheng ya Gauteng ya ka Afrika Borwa. Ka morago ya dinyakišišo tše di dirilwego peleng mabapi le go ba gona ga mehuta ye ka go diriša mothopo wa dijo wa tlaleletšo, maikemišetšomagolo e bile go tseba ka fao go ba gona ga lefelo la go fepela manong leo e lego kgale le le gona mo lefelong le go huetšago mabaka mabapi le go iphepa ka phiri ye tsooto ge e dutše e phedišana le diphedi tše dingwe, lefelong leo e dulago go lona le dikakanyo mabapi le palo ya tšona. Tshekatsheko ya Scate šomišitšwe ka go nyaka go tseba seo phiri ye tsooto e se jago ka dihla tše dingwe. Phiri ye tsooto e kgona go fihlelela kabo ya kgafetšakgafetša ya ditopo tša diphoofolo ka lefelong la go fepela manong,gomme se se bile le seabe sa 47% go dijo tša tšona ka kakaretšo ka nakong yeo ke bego ke nyakišiša ka yona. 53% ye e šetšego yona ke ya ge e eja diphoofolo tša diamuši, dimela le mašaledi a dinonyana. Tshedimošo ka ga palo ya tšona e ile ya tšewa ka molaba wa setšeadiswantšho seo se beilwego go ralala le lefelo le mo lebakanakong la dikgwedi tše 15, gomme ka yona nako yeo go ile gwa dirwa diphatišišo ka go tšea diswantšho leboela makga a mahlano ka fao go ikemego.Ka nepo ya go dira teko ya go felela ga palo ya tšona le go kgetha mekgwa ye mekaone ya koonagalo ya go tšea diswantšho, Lenaneo la CAPTUREle ile la šomišwa. Lenaneo laDENSITY 5.0.le ile la šomišwa go dira tshekatsheko ya go tšea diswantšho leboelela. Mo nakong ya dikgwedi tše 15 ya dinyakišišo, dikakanyo tša bontši bja tšona go thomile go tše nne go fihla go tše tshela ka nako ya go tšea diswantšho ya dikgwedi tše tharo, gomme se sa feletša ka dikakanyo tša bontši bja tše 13 go fihla go tše 20 kadisekwerekhilometara (km²) tše 100. Kakanyo ya bontši

bja tšona yeo e hweditšwego go dinyakišišo tša ka e godimo go feta yeo e hlakantšwego ya phiri ye tsooto ka mafelong a komelelo, eupša go swana le tšeo di dulago ka mafelong a bolotaphoofolo a mannyane ka phrobentsheng ya Kapa Bohlabela ya Afrika Borwa. Dikakanyo mabapi le mehuta ya mafelo ao di dulago go ona di hlakantšwe ka go šomiša tshedimošo ya sathalaete ka goQGIS V2.18 gomme tshedimošo ye ya tšweletšwa ka go šomiša mohuta wa adehabitatHR (bešene ya 0.4.1.9) (Calenge 2006) ka go lenaneo la R 3.5.0 (R Core Team 2018). Mehuta ye mebedi ya go nyakišiša ka ga madulo a tšona e ile ya šomišwa le go bapetšwa:e lego Kernel Utilisation Distribution and Minimum Convex Polygons. Tše pedi tša diphiri tše tharo tšeo di bapeditšwego go hweditšwe gore di fela di šomiša lefelo la go fepela manong gomme mehuta ya mafelo ao di dulago gona go hweditšwe e le a mannyane go fetwa ke ka fao go begilwego go gongwe. Madulo ao a lego a mannyane kudu a ka be a šišinya gore go na le methopo ye e lekanego ya dijo ye e hwetšagalago ka lefelong la Mogale's Gateyeo e fepago phriri ye tsooto. Dipoelo go tšwa dinyakišišong tša ka di laetša gore methopo ya dijo yeo e abjago ke lefelo la go fepela manong la sa ruri le huetša mehuta ya dijo, bontši bja tšona le bogolo bja lefelo leo phiri ye tsooto nngwe le ye nngwe e dulago go lona. Go akanywa gore ka lefelong la go swana lela Bolotaphoofolo la Magaliesberg Biosphere Reserve, fao dibata tše kgolo tša go swana le tau, lengau le lehlalerwa di sa hlwego di hwetšagala, mafelo a go fepela manong ka mo lefelong le a šoma bjalo ka mothopo wa dijo wa boikgethelo wa phiri ye tsooto, gomme se se tšwetša pele go ba gona ka bontši ga tšona gomme sa šoma bjalo ka seo se thibelago gore mohuta wo wa diphiri o se ke wa hwelela.

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Chapter 1

General Introduction



"The cats are certainly cool and the wild dog is wild, but the hyenas are heroes."¹ -D. Mills

¹ Illustration by Dr. K. Williams

INTRODUCTION

The order Carnivora consists of 245 terrestrial species (Hunter 2011), of which 66 occur in Africa (Estes 1991). Carnivores are widely distributed across the world, have lower population numbers than herbivores (Ripple *et al.* 2014) and play an important role in regulating ecosystems (Prugh *et al.* 2009). The idea that an apex predator can affect an ecosystem and have far-reaching impacts on multiple trophic levels is termed trophic cascades (Estes *et al.* 2011; Welch 2014). Predators have been shown to affect prey species directly through predation (Orrock *et al.* 2010; Welch 2014), and through non-consumptive effects such as influencing various behavioural traits in the prey species (Brown *et al.* 1994; Orrock *et al.* 2010). For example, prey may change their behaviour by changing the times they are active and what they eat (Miller *et al.* 2001; Welch 2014). The degree and type of predator impacts on prey populations are influenced by the predator's size, density, metabolic demands and hunting tactics (Ripple *et al.* 2014).

Mesopredators are defined as predators normally competitively inferior to apex predators (Prugh *et al.* 2009; Welch 2014). Normally large apex predators influence the numbers of mesopredators in an ecosystem through competition and direct intraguild predation (Ritchie and Johnson 2009; Prugh *et al.* 2009; Welch 2014). In addition, apex predators also provide foraging opportunities for facultative and obligate scavengers such as jackals and vultures (Braack 1987; Yarnell *et al.* 2013). Mesopredator populations increase when large, dominant apex predators are absent, resulting in the potential decline of populations of small prey species (Crooks and Soule 1999; Prugh *et al.* 2009). For example, in southern California, the decline of apex predator, the coyote (*Canis latrans*) resulted in increased population sizes of smaller, native predators such as striped skunk (*Mephitis mephitis*), grey fox (*Urocyon cinereo argenteus*), and Virginia opossum (*Didelphis virginiana*), leading to increased mortalities of prey species (Crooks and Soule 1999).

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At least 77% of large predators have declining populations and 61% are classified by the International Union for the Conservation of Nature (IUCN) as being threatened and are at risk of local or total extinction (Ripple *et al.* 2014; Wolf and Ripple 2016). Range loss is seen as a dominant factor in this decline, with many species having lost large parts of their historical distribution ranges. Lions, tigers (*Panthera tigris*), Ethiopian and red wolves (*Canis lupus rufus*) have lost more than 90%, whilst grey wolves (*Canis lupus*) now occupy 26% of their original ranges; collectively hyaenas have lost 22% of their historical ranges (Wolf and Ripple 2017).

Protected land allocated for the conservation of large predator species often means that many other species are afforded protection in the same area (Foreman 1993). Nevertheless, protected areas are often relatively small and large predators require large ranging areas to meet their resource demands. This means large predators often incorporate unprotected areas into their home range (Winterbach *et al.* 2013). Although protected areas remain crucial to the continuance of many predator populations, mortality most often occurs when predators move beyond protected area boundaries, where they are killed either accidentally or deliberately by people (Castley *et al.* 2002; Schwartz *et al.* 2006; Loveridge *et al.* 2007).

Worldwide human-predator conflict is on the increase due to fragmented natural landscapes, habitat destruction, urbanisation, large spatial requirements and low population densities of predators (Cardillo *et al.* 2004; Balme *et al.* 2010; Ripple *et al.* 2014; Loveridge *et al.* 2017). As a result, many predators are thus particularly vulnerable to extinction. Some of the most endangered species are carnivores, such as the Ethiopian wolf (*Canis simensis*) which is the world's rarest canid with fewer than 500 animals remaining (Kennedy *et al.* 2011; Richmond-Coggan 2014). As the human population grows, the rate at which it consumes resources leads to habitat loss, inevitably bringing people and wildlife in closer proximity to each other (Richmond-Coggan 2014). Predator populations are impacted either directly or indirectly by human interference and anthropogenic threats (Burton *et al.* 2012), overexploited for bush meat and medicinal purposes (Lindsey *et al.* 2013), and killed

in response to livestock losses (Treves and Karanth 2003). In Southern Africa conflict has been shown to be extreme in relation to cats of medium-to-large size, in particular caracal (*Caracal caracal*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), and lion (*Panthera leo*) (Inskip and Zimmermann 2009; Richmond-Coggan 2014).

In the Gauteng province of South Africa, many free-ranging species have become locally extinct, with at least twenty large mammal species, including the African lion being eradicated from the Magaliesberg area during the last 150 years (Carruthers 2007). Urbanisation on the Highveld has resulted in one in five-people occurring within 100 km of the Magaliesberg mountain range and is expected to double by the year 2027 (Carruthers 2007). The remaining natural areas within the Magaliesberg are therefore under great pressure in terms of human development. Free roaming medium-to-large predators remaining in the Magaliesberg are brown hyaena (*Hyaena brunnea*), leopard, caracal, black-backed jackal (*Canis mesomelas*), and serval (*Leptailurus serval*) (Carruthers 2007).

Endemic to southern Africa the brown hyaena occurs in the arid countries of Namibia, Zimbabwe, Botswana and South Africa (Yarnell *et al.* 2016). In South Africa the brown hyaenas' historical distributional range has decreased significantly since the 18th century (Mills and Hofer 1998; Mills 2013) (Figure 1.1).

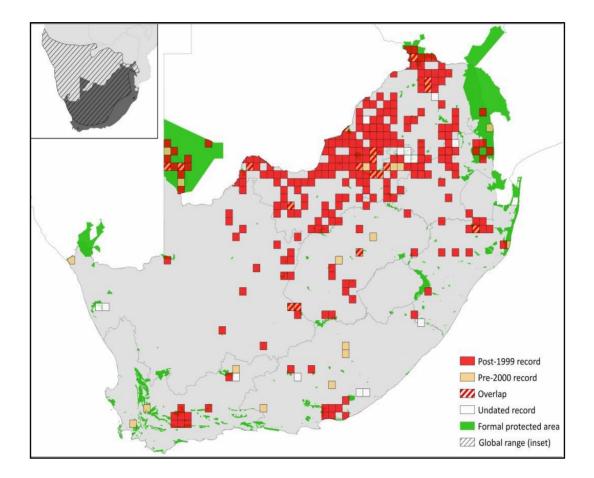


Figure 1.2. Distribution records for the brown hyaena (*Hyaena brunnea*) in South Africa, according to South African National Biodiversity Institute and the Endangered Wildlife Trust, 2016 (Yarnell *et al.* 2016).

Brown hyaenas are currently classified as Near-Threatened by the IUCN (Wiesel 2015; Williams 2017). With almost 90% of the brown hyaena population occurring in Botswana (an estimated 4642 animals; Winterbach *et al.* 2017), the total population size of brown hyaenas is estimated between 5000 to 8000 individuals (Wiesel 2015). In South Africa, in 1998 the population was estimated to be 1700 with a range of 800 to 2200 individuals, but more recent studies suggest that this estimate is too low (Yarnell *et al.* 2016). Although the range of the brown hyaena may be expanding it is probable that the number of mature individuals outside of protected areas is still declining, thus the species retains its Near-Threatened status as a precautionary measure (Yarnell *et al.* 2016). The persecution of brown hyaenas due to the perception that they kill domestic livestock is one of the major threats to their survival outside of protected areas (Maude 2005; Wiesel 2015; Williams 2017).

Brown hyaena are poisoned, trapped and killed due to ignorance and / or intolerance of livestock farmers in South Africa, Zimbabwe and Namibia (Wiesel *et al.* 2008). Additional anthropogenic threats such as vehicle collisions, hunting, snaring and the killing of brown hyaenas for 'muti' (traditional medicine) also seem to be on the increase (Williams 2017). Despite many threats to this species, brown hyaenas adapt well to areas with human activity and appear to tolerate land-use changes (Mills and Hofer 1998; Kent and Hill 2013; Williams 2017). Therefore, with the increase in habitat fragmentation, destruction of natural areas and increase of small fenced protected areas, non-protected areas are becoming more important in conserving brown hyaenas (Kent and Hill 2013).

STUDY SPECIES

Fossil hyaenids dating from the Miocene (23 to 25 million years ago) have been found in North and East Africa, making the *Hyaena* genus the longest existing genera of Carnivora recorded (Savage 1978; Skinner and Chimimba 2005). Hyaenids are represented in Africa today by three genera and four species, namely, the striped hyaena (*Hyaena hyaena*), which occurs from central Tanzania northwards into the Middle East and India; the brown hyaena, which is limited to the southern African sub-region (Mills and Hoffer 1998), the spotted hyaena (*Crocuta crocuta*), which has a wider distribution occurring south of the Sahara and into the northern and eastern regions of southern Africa (Estes 1991), and the aardwolf (*Proteles cristata*), which is distributed in east, north-eastern and southern Africa (Skinner and Chimimba 2005).

The brown hyaena is medium-sized, with strong forequarters and sloping back (Mills and Hofer 1998). The coat is shaggy with a dark brown to black colour, with under parts that are light coloured. Adult brown hyaenas weigh on average 40 kg, with small differences between the sexes (Mills and Mills 1982). Males weigh between 40 - 44 kg, whereas females weigh around 38 - 40 kg (Edwards 2019).

Brown hyaenas are primarily scavengers, playing an important ecological role by feeding on and thus removing carrion from the landscape (Kruuk 1998). However, brown hyaena will also opportunistically consume fruits, insects, reptiles, bird's eggs and small vertebrates (Mills and Mills 1978; Stuart and Stuart 2000; Burgener and Gusset 2003; Maude 2005). Brown hyaenas are not efficient hunters and will rarely hunt (Maude and Mills 2005), but when they do, small-sized prey such as springhare (Pedetes capensis), korhaan (Eupodotis sp) and bat-eared fox (Otocyon megalotis) are examples of prey hunted (Mills and Mills 1978). In the southern Kalahari, only 4.2% of the diet consisted of vertebrate prey that the brown hyaena caught themselves (Mills 1990). On the south-west coast of Namibia, Cape fur seal pups (Arctocephalus pusillus pusillus) are hunted and scavenged by brown hyaenas as their primary food source (Wiesel 2006; Kuhn et al. 2008). In areas where other large predators such as lion, cheetah and leopard occur the remains left from the hunting of large prey species are the most important food items in the brown hyaena's diet (Burgener and Gusset 2003; Slater and Müller 2014; Comley 2016). Brown hyaena also kleptoparasitise, particularly from cheetah (Owens and Owens) 1978) and leopard (Williams 2017).

In protected areas where there are no large apex predators, such as lion and cheetah, the majority of the brown hyaenas' diet will consist of hunted small mammals, fruit, and occasional opportunistic carcasses (Yarnell *et al.* 2013; Comley *et al.* 2018). Furthermore, in areas with no large apex predators to provide regular sources of carrion, brown hyaena population densities are expected to be smaller than in areas where large apex predators are present (Yarnell *et al.* 2013).

The brown hyaena's home range size is largely influenced by how food is distributed, while aspects of social organisation, such as clan (family group) size are determined by the quantity and amount of food resources available (Mills and Mills 1982). A plentiful food supply potentially reduces the mean distance between food 'patches', resulting in an increased density of brown hyaenas in that area and a decrease in home range sizes of individuals (Maude 2005).

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Brown hyenas coexist with each other as members of a clan or are nomadic (Owens and Owens 1979). Clans are generally composed of a dominant male and a dominant female (Knowles *et al.* 2009), with the rest of the clan comprising of adults, sub-adults and cubs of both sexes, with the size of the clan varying between four and fourteen individuals (Mills and Mills 1982; Owens and Owens 1996). Members of a clan will defend their territories, which usually includes a communal den site, satellite dens and the feeding grounds used by the clan (Owens and Owens 1979; Skinner and Chimimba 2005). While the females tend to stay in social bonded groups and defend a common territory and dens (Owens and Owens 1978), most males become nomadic (Mills and Mills 1982).

Nomadic male hyenas are not affiliated with a particular clan, are not territorial (Owens and Owens 1978; Mills and Mills 1982) and make up about 33% of adult male brown hyaenas. Although nomadic males are not permanent members of a clan, they do mate with clan females and assist with food provision for cubs (Mills and Mills 1982; Owens and Owens 1996). Brown hyaena cubs are born in a den, and for the first three months are fed by their lactating mothers (Mills and Mills 1982). All females in the clan will provide non-parental assistance at the communal den, including nursing each other's young (Owens and Owens 1979). Cubs remain close to the den until they are about 15 months old, during which time they eat carrion brought to the den by clan members from foraging sessions (Mills and Mills 1982; Owens and Owens 1996) (Figure 1.2).



Figure 1.2. Brown hyaena cub coming out of the den to feed on carrion brought to den by adult hyaena. (Source: Camera trap image of maternal den on Mogale's Gate Biodiversity Centre.)

Unlike spotted hyaena, brown hyaenas are not very vocal and instead use scent as their primary form of communication (Mills 1990; Edwards 2019). Paste marks are produced by the anal gland, and placed on grass and bush stalks, with this scent marking individuals convey information to other members of the clan regarding individual activity within the clan's territory and to maintain some sort of territorial communication (Mills and Mills 1978; Gorman and Mills 1984). Pastings are scattered mainly within the interior of the territory, in areas the hyaenas spend the majority of their time (Gorman and Mills 1984). Communal latrines, which are distinctive collections of white faeces (Edwards 2019), are found mostly along territory boundaries (Mills *et al.* 1980). Throughout their geographical range brown hyaenas have shown a strong preference towards the utilisation of the road networks within their home range areas (Mills 1990; Thorn *et al.* 2009; Hulsman *et al.* 2010), using this infrastructure to patrol and defecate (latrines), thereby marking their territorial boundaries (Mills 1990; Thorn *et al.* 2009; Richmond-Coggan 2014).

Many of the pioneering studies on brown hyaena took place in Namibia and the Kalahari region of Botswana (Owens and Owens 1978; Mills and Mills 1982; Maude and Mills 2005; Wiesel 2006; Knowles *et al.* 2009). More recently, there have been several studies in regions of southern Africa, investigating brown hyaena ecology in a variety of habitats and land use types (Kent and Hill 2013; Welch 2014; Richmond-Coggan 2014; Comley 2016; Williams 2017; Müller 2020). As food resources influence home range size, population density and social organisation (Mills 1984; Maude and Mills 2005; Welch 2014), studies on brown hyaena home range sizes and utilisation in areas faced with increasing urban and farming developments are important. Furthermore, studies focusing on brown hyaena range use and food resource acquisition in small (<400 km²) fenced reserves are lacking. With increasing habitat fragmentation and urban spread, these small, fenced reserves may become increasingly important population source areas for brown hyaena in the future (Welch and Parker 2016).

With increasing evidence that large areas of brown hyaena home ranges fall outside of protected areas, human influences such as artificial food resources like rubbish dumps (Skinner and van Aarde 1987) and altered land-use types such as livestock farming (Maude 2005), could impact on the dispersion of brown hyaena food resources, and thus home range sizes. In support of the above the comparison between brown hyaena feeding ecology in Makgadikgadi National Park and surrounding unprotected areas, home range sizes decreased for brown hyaenas living near pastoralists (Maude 2005). The death of livestock through predation, disease and drought in the areas near human habitation and the discarding of food waste by people, provided hyaenas with an abundant, reliable food source (Maude 2005). Anthropogenic activity and the predictability of resources have also been found to have a strong influence on home range size, movement patterns, and aspects of space utilisation of canids such as red foxes (Vulpes vulpes; Contesse et al. 2004), coyotes (Atwood et al. 2004) and golden jackals (Canis aureus; Rotem et al. 2011). Although, Yarnell et al. (2014) reported an increase in the local abundance of brown hyaenas and black-backed jackals following the introduction of supplementary vulture feeding sites (vulture restaurants) on the Mankwe Wildlife

Reserve (North-West province, South Africa), the effect of vulture restaurants on the diet and home range size of brown hyaenas is currently unknown.

Due to the decline in vulture numbers globally (Markandya *et al.* 2008; Ogada *et al.* 2011), vulture restaurants have been used as a conservation tool for 40 years (Piper 2005). Such feeding schemes increase the survival and reproduction of local vulture populations (Meretsky and Mannan 1999) and the establishment of vulture restaurants are advocated on the basis of five main advantages: the provision of extra food and dietary supplements; provision of poison-free food; providing a safe place for birds to feed; to raise awareness amongst landowners and the general public; and to act as an eco-tourism tool (Piper 2005).

No large predators such as lion, cheetah or spotted hyaena remain in the Magaliesberg area, to provide natural carcasses on which vultures can feed and provide bone fragments to growing chicks (Anderson and Anthony 2005). Endemic to southern Africa, the Cape vulture (*Gyps coprotheres*) is currently listed as endangered, with current populations declining (IUCN Red List of Threatened Species, 2020). Hence, the Cape vultures in the Magaliesberg area are highly dependent on the provision of carcasses at vulture restaurants to meet their nutritional requirements (Anderson and Anthony 2005).

As in other regions where vultures occur, the establishment of vulture restaurants, in the Magaliesberg area has seen Cape vulture numbers increasing and the reestablishment of old, abandoned breeding colonies on the cliffs of the Magaliesberg range (Monadjem *et al.* 2014). Wildlife reserves, conservationists, and provincial environmental authorities have turned the vulture restaurant philosophy into an important conservational tool, with this modern concept now involving the research and close monitoring of these birds.

However, despite the success of vulture restaurants in increasing vulture population numbers, concerns have been raised about the provisioning of regular food at fixed sites (Yarnell *et al.* 2014). Regular supplies of carrion at one site increases the

occurrence of other scavenger species such as domestic dogs and black-backed jackal, can potentially lead to changing the foraging ecology of species, increase competitive interactions, and potentially lead to an increase in the spread of diseases such as rabies (Monello and Gompper 2011).

The relatively high spatial and temporal predictability of supplementary feeding sites, such as vulture restaurants, make this food resource easier to access compared to natural sources (Cortes-Avizanda *et al.* 2012; Oro *et al.* 2013). The decreased foraging time consequently improves fitness components, including individual breeding performance (Oro *et al.* 2013).

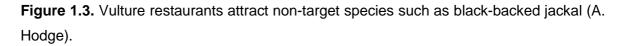
Some facultative scavengers such as foxes (*Vulpes* spp.) (Oro *et al.* 2013) and black-backed jackals (Yarnell *et al.* 2014) have benefitted from supplementary food sources, resulting in increased numbers, which may lead to an 'overabundant' population, potentially causing changes in food webs and ecosystems (Oro *et al.* 2013). Impacts on individuals can vary as age, gender, and personality differences may affect supplementary food source use (Oro *et al.* 2013). Predictable food sources can also improve the survival prospects of individuals in poor condition due to genetic weakness or old age, hence relaxing selection pressures (Genovart *et al.* 2010).

Although a direct relationship between the availability of a predictable food resource and population growth rate is difficult to determine, several studies have demonstrated that these food resources increase population density. For example, the density of coyotes (*Canis latrans*) and golden jackals (*Canis aureus*) is higher where predictable food resources occur, hence leading to a reduction of home range for individuals foraging at these feeding sites (Fedriani *et al.* 2001).

Although, vulture restaurants may have multiple negative impacts such as increased predation rates on herbivores, and increased spread of pathogens, they also have the potential as a management tool in conservation (Oro *et al.* 2013). Feeding sites can be used to redistribute species, reduce human-wildlife conflicts,

and can limit population declines of endangered species when natural food sources are diminished (Kaplan *et al.* 2011; Oro *et al.* 2013). In the Gauteng province the brown hyaena may be a species of conservation concern that could benefit locally from the provisioning of supplementary carcasses at vulture restaurants.





The long-term provisioning of food at a vulture restaurant, the absence of large apex predators and the protected status of the Mogale's Gate Biodiversity Centre (Mogale's Gate) within a landscape surrounded by increasing human development, provided an opportunity to investigate brown hyaenas in the context of diet, home range and population estimates.

The aim of this study was therefore to investigate the feeding and spatial ecology of brown hyaenas in the presence of a regular food source on Mogale's Gate. With the information obtained from this study an important contribution to the understanding of brown hyaena ecology in small-protected areas with regular food resources and threatened by urbanisation will be made. Furthermore, to date, no known studies on the ecology of brown hyaenas in the Magaliesberg region have been published.

OBJECTIVES

The objectives of this study were to:

- Determine the seasonal diet of brown hyaena using faecal scat analysis
- Estimate the abundance of brown hyaena on Mogale's Gate using images from camera traps
- Determine the home range sizes of three collared brown hyaenas
- Determine how habitats within the study area are utilised in proportion to their availability

Research questions

From the above objectives, the following research questions relating to brown hyaenas on Mogale's Gate were devised:

- What is the seasonal diet of brown hyaena?
- How many brown hyaenas are estimated to occur on Mogale's Gate?
- What are the seasonal home ranges sizes of collared brown hyaenas?
- What is the habitat utilisation of brown hyaenas on Mogale's Gate?

The collection of samples, and the capture and handling of brown hyaena during this study, were done under the auspices of UNISA-CAES Animal Research Ethics Committee (Permit 2013/CAES/132) (Appendix 1).

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Chapter 2

Study area



"Geology, climate and nature combine to create spectacular scenery..." -V. Carruthers

INTRODUCTION

The Magaliesberg region has a rich biodiversity, reflecting many aspects of evolution, biodiversity and geology (Magaliesberg Biosphere Management Plan 2011). The scenery, climate, and proximity to large cities such as Johannesburg, Pretoria and Rustenburg make it especially suitable for outdoor recreational activities and residential development (Magaliesberg Biosphere Management Plan 2011). There are also many challenges facing this area with increasing development pressures from expanding mining endeavours and the impacts of bordering the most developed commercial metropolitan area in Africa (Magaliesberg Biosphere Management Plan 2011). During 1975 in response to environmentalists campaigning for the area to be legally protected and future intense developments be restricted, the Magaliesberg Protection Association was established (Carruthers 2007). However, as the demands for tourism activities and accommodation increased so did road networks, alien vegetation, unchallenged illegal developments, and changes in municipal boundaries occurred, which subsequently hindered conservation efforts (Carruthers 2007). Due to this increased pressure on the area's natural and heritage resources, key stakeholders in government, private landowners and interest groups had the Magaliesberg declared an internationally recognised Biosphere Reserve. Being declared a Biosphere Reserve facilitates the promotion of conservation of the landscape, socio-cultural and ecological sustainable developments (Magaliesberg Biosphere Management Plan 2011).

The Magaliesberg Biosphere Reserve was proclaimed in 2015, covering an area of 357 870 ha between the cities of Rustenburg and Pretoria (UNESCO 2017). Within the biosphere there are three core conservation areas, totalling 58 212 ha: the Kgaswane Nature Reserve, the Magaliesberg Protected Environment, and the Cradle of Humankind World Heritage Site (UNESCO 2017). Surrounding the above core areas are buffer zones totalling 109 561 ha, which are adjoining areas between the strictly conserved core areas and the unprotected transition zone (190 097 ha).

Some forms of sustainable development and extraction of natural resources are allowed within the buffer zones (Magaliesberg Biosphere Management Plan 2011).

Mogale's Gate is a 3060 ha protected area, comprised of five converted agricultural and cattle farms (Tuckett 2013). With an approximate centre point of -25.96040S; 27.63498E, Mogale's Gate is situated in the buffer zone to the west of the Cradle of Humankind, 20 km north of the city of Krugersdorp, and 15 km east of the town of Magaliesburg, in the Gauteng province of South Africa (Figure 2.1). The prominent land-use types in the immediate surroundings of Mogale's Gate include commercial and non-commercial livestock and crop farming.

Mogale's Gate was purchased by its current corporate owners during the 1980's and was transformed into a game reserve. The improvement and conservation of biodiversity is a key component of the Mogale's Gate ecological management plan (Tuckett 2013). The main aims of Mogale's Gate are the promotion of sustainable resources through low impact tourism activities, including environmental education programs, the hosting of university field courses, research, and small corporate events (Tuckett 2013).

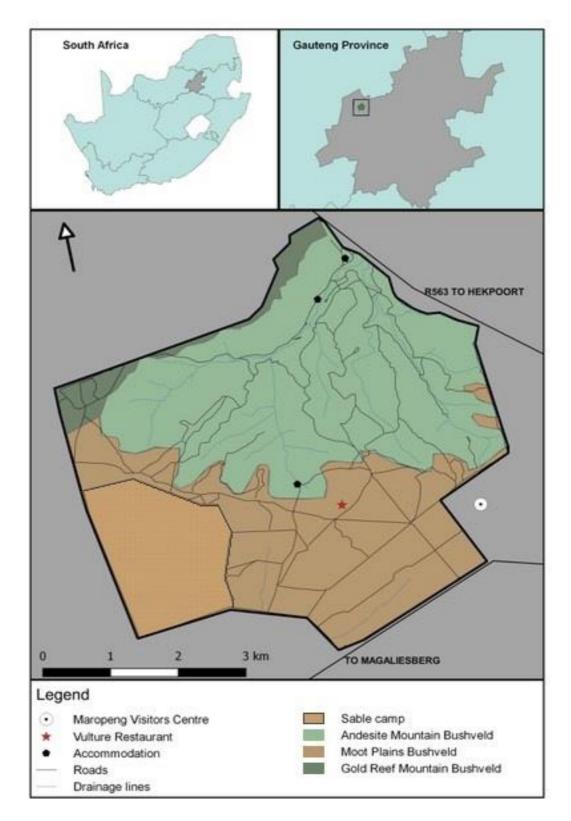


Figure 2.7. Mogale's Gate, Gauteng province, South Africa. The map depicts the main vegetation types, infrastructure, and road network on Mogale's Gate.

VEGETATION AND TERRAIN

Mogale's Gate is situated on the southern slopes of the Witwatersrand mountain range, which runs parallel to the prominent Magaliesberg mountain range to the north. The two ranges separate the Highveld grasslands from the bushveld savanna, each of which has its own unique faunal and floral composition (Carruthers 2007). The altitude on Mogale's Gate varies from 1390 m.a.s.l. to 1675 m.a.s.l. with a difference of 285 m in altitude from the lowest to the highest points (Tuckett 2013).

The vegetation on Mogale's Gate fall within the Moot Plains Bushveld, Gold Reef Mountain Bushveld and Andesite Mountain Bushveld vegetation types (Mucina and Rutherford 2006). Twelve plant communities have been identified within these three broad vegetation types (Tuckett 2013). The southern half of Mogale's Gate falls within the Moot Plains Bushveld vegetation type, described by Mucina and Rutherford (2006), as an open to closed, often thorny, savanna dominated by *Senegalia* and *Vachellia* spp. There are woodlands of varying heights and densities, and grasses dominate the herbaceous layer. On Mogale's Gate, this vegetation type consists predominantly of plant communities dominated by grasslands (Figure 2.2) and wetlands. Only small patches (3.61% of the study area) of woody vegetation occur in the higher lying western and eastern portions of the reserve. A variety of grass species, including *Themeda triandra, Loudetia simplex, Sporobolus africana, Hyparrhenia hirta* and *Cynodon dactylon,* and wetland forbs such as *Schoenoplestus corymbosus* and *Hemarthria altissima* can be found in the plant communities of the Moot Plains Bushveld.



Figure 2.8. An example of a grassland plant community within the Moot Plains Bushveld vegetation type, of Mogale's Gate (H. Moolman).

The central to northern area of Mogale's Gate consists of Andesite Mountain Bushveld and has undulating hills with dense, medium-tall thorny bushveld and a well-developed grass layer (Mucina and Rutherford 2006). Covering 44.89% of the reserve, a mosaic of grassland and woodland species are found in this section of the reserve (Figure 2.3). Grasses such as *Setaria sphacelata* and *Hyparrhenia tamba*, and shrub species such as *Ziziphus zeyheriana* and *Diospyros austroafricana* dominate the mid slopes. Lower down in the valley's (Figure 2.3) woody species such as *Ziziphus mucronata*, *Olea europea*, *Celtis africana* and *Euclea crispa* dominate (Tuckett 2013). Altitude varies in this plant community ranging from 1405 to 1640 m.a.s.l resulting in a variety of woody and herbaceous plant species.



Figure 2.9. Examples of plant communities found within the Andesite Mountain Bushveld vegetation type: (a) the central mid slope and (b) the valley bottom areas of Mogale's Gate (C. Kruger).

Small portions of the northern section of the reserve located on the Witwatersberg mountain range fall within the Gold Reef Mountain Bushveld, which is characterised by rocky hills and ridges, with variable tree cover and a herbaceous layer dominated by grasses (Mucina and Rutherford 2006) (Figure 2.4). On Mogale's Gate, the dominant plant species in this vegetation type include *Senegalia caffra, Protea caffra, Loudetia simplex, Panicum natalense, Schizachyrium sanguineum* and *Trachypogon spicatus.* Rocky crests, scarps and mid slopes occur in this veld type, with slopes varying from flat to 5% on the exposed northern high points, to mid slopes which vary from 10-100% in gradient (Tuckett 2013).



Figure 2.10. Gold Reef Mountain Bushveld, making up the northern boundary of Mogale's Gate, is characterised by rocky ridges and steep slopes (C. Kruger).

CLIMATE

The climate in the northern areas of the Gauteng province, in which Mogale's Gate is situated, is warm and temperate with summer rainfall and cold winters. Weather data from onsite weather stations indicated a mean annual temperature of 17° C over a six-year period (2010 to 2016). During my study, which took place during 2014 to 2016, the highest temperature reached was 38° C in January 2016, whilst the minimum temperature was -6° C in July 2014 (Figure 2.5). Annual rainfall ranges from 635 to 826 mm with the wet season occurring from November to April, and the dry season from May to October (²A. Tuckett pers. comm.). During the study period, the total rainfall was 2052 mm (Figure 2.5).

²Mr Alistair Tuckett, Operations director, Mogale's Gate Biodiversity Centre.

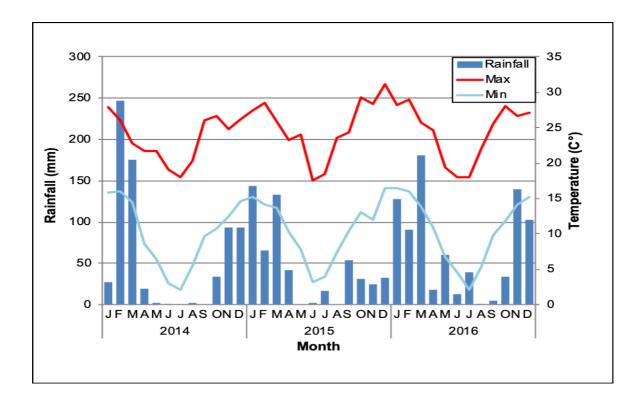


Figure 2.11. Mean maximum and minimum temperatures (blue and red lines respectively), and total monthly rainfall from January 2014 to December 2016. (Source: Mogale's Gate on site weather stations).

FAUNA

There are 58 known mammal species on Mogale's Gate (Appendix 2). Twenty large herbivore species, including threatened or protected species, such as black wildebeest (*Connochaetes gnou*) and oribi (*Ourebia ourebi*) occur on the reserve. Carnivores make up thirteen of the mammal species occurring naturally on the reserve including *inter alia*, brown hyaena, caracal, serval and black-backed jackal. Several amphibian species, including the near threatened bull frog (*Pyxicephalus aspersus*), 32 reptile and over 270 bird species have been recorded (Tuckett 2013), as well as over 1000 invertebrate species (Hausmann 2012; Tuckett 2013).

Mogale's Gate operates a vulture feeding site (vulture restaurant) located in the southern section of the reserve (Figure 2.1). It is one of the three original, official vulture restaurants established in South Africa to provide supplementary food for the cape vultures breeding in the Magaliesberg mountains and has been active for more than 30 years (³K. Wolter pers. comm.). The Mogale's Gate vulture restaurant is supplied regularly with livestock and game carcasses throughout the year. Varying amounts of livestock (mostly pig carcasses supplied by a neighbouring commercial piggery) are dropped off at the vulture restaurant (Figure 2.6). Other livestock carcasses disposed of at the site include cattle, sheep, and donkeys. Game carcass offal from Mogale's Gate culling operations are also deposited at the vulture restaurant (Estimated annual game count numbers for 2014 and 2015 are provided in Appendix 3). The amount of carrion available to the brown hyaenas at the vulture restaurant depends on the number and size of carcasses delivered, as well as the number of other scavengers present before the brown hyaenas arrive at the carcasses to feed. No provisioning rates of carrion at the vulture restaurant were available, as deposits at the vulture restaurant are not recorded by management. Although the camera trap at the vulture restaurant recorded what was deposited at the site, it was not possible to determine biomass from images. Scavengers such as vultures and jackals feed during the day at the site, so to determine how much carrion was available to brown hyaenas was not feasible. A number of species other than vultures have been recorded feeding off the carrion at the Mogale's Gate vulture restaurant (Slater and Kruger in prep), but the ecological impact on these other species is unknown.

³Kerri Wolter - CEO and founder of VulPro (Vulture Programme for the Conservation of Vulture Species in southern Africa)



Figure 2.12. The vulture restaurant on Mogale's Gate established for the supplementary feeding of vultures, with domestic pig being the main food source (C. Kruger).

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Chapter 3

Diet of brown hyaena



"Although spending time near humans is dangerous for brown hyaenas, the benefits of a ready food source may outweigh the threats..." - Dr. K. Williams

INTRODUCTION

Information on the diet of predators contributes significantly to the understanding of their behaviour, activity patterns and spatial ecology (Mills 1992; Breuer 2005). A predator's diet reflects whether it is an opportunist or specialist, the availability of food sources and the animal's physiological adaptations (Kok and Nel 2004; Slater and Müller 2014). As there is potentially competition between predators and subsequent impacts on prey populations, dietary studies might have implications for the development of conservation management plans (Klare et al. 2011). Brown hyaenas are predominantly scavengers as well as opportunistic feeders, eating a variety of foods, including invertebrates, reptiles, birds, fruits, mammals and carrion (Owens and Owens 1978; Mills 1990; Burgener and Gusset 2003; Slater and Müller 2014), which can vary across their geographic range (Maude and Mills 2005; Wiesel 2006; Williams et al. 2018). Brown hyaenas are not efficient hunters and will rarely hunt (Mills and Mills 1978; Maude and Mills 2005). Although medium to large mammals such as kudu (Tragelaphus strepsiceros), red hartebeest (Alcelaphus caama), gemsbok (Oryx gazella), and bushbuck (Tragelaphus scriptus) have been found in the diet of brown hyaena this is believed to be the result of scavenging kills from other predators such as lion, leopard and cheetah (Mills and Mills 1978; Yarnell et al. 2013; Slater and Müller 2014; Comley et al. 2018; Williams et al. 2018). Where apex predators are present brown hyaenas have sufficient food for scavenging and do not need to hunt (Slater and Muller, 2014; Williams 2017). It was predicted that brown hyaenas on Mogale's Gate obtain food from the vulture restaurant on a regular basis and therefore species that are frequently deposited at the vulture restaurant will dominate the brown hyaenas' diet. When a particular food source is readily available, the breadth of the brown hyaena's diet decreases (Williams 2017), hence I predicted that domestic livestock would dominate the diet as represented in the scats of brown hyaenas on Mogale's Gate.

Whether deliberately consumed or ingested whilst feeding on carcasses, invertebrates have been found in the scats of brown hyaena (Mills and Mills 1978; Burgener and Gusset 2003; Slater and Müller 2014; Faure *et al.* 2019). Plant matter

such as seeds, berries, and melons are found in brown hyaena scats especially in arid areas, possibly playing a role in meeting the animal's water requirements (Owens and Owens 1978; Mills and Mills 1978; Mills 1992). In areas where there are permanent water sources available the presence of plant material in the diet is not as high, suggesting that brown hyaenas have less of a need to consume plant material to gain moisture (Williams 2017; Faure *et al.* 2019).

Human dominated farmlands and pastoral areas such as the Ghanzi farm block and wildlife management areas bordering the Makgadikgadi National Park in Botswana, offer easy feeding opportunities for brown hyaenas, as they scavenge on livestock carcasses of animals that have died from old age, predation or disease (Maude 2005; Kent and Hill 2013). Although perceived as regular stock killers there are no published studies reporting conclusive evidence that living livestock is considered a naturally hunt able and dominant food source for brown hyaenas (Faure *et al.* 2019).

Being nocturnal, elusive scavengers, direct feeding observations of brown hyaenas are impractical and, therefore faecal analysis remains a primary technique used to assess what this species consumes (Mills and Mills 1978; Maude 2005; Wiesel 2006; Klare *et al.* 2011; Slater and Müller 2014; Comley 2016; Williams 2017; Comley *et al.* 2018). Faecal analysis of carnivore scats is an indirect, cost effective and non-invasive method whereby diet is inferred from the identification of indigestible food remains such as hair, bone, hooves, insect remains, plant material and feathers (De Marinis and Asprea 2006; Wachter *et al.* 2012).

The percentage occurrence and the relative percentage occurrence of items in analysed scat are commonly used calculations to quantify not only what a species feeds on, but also the importance of the identified food items relative to other consumed food items (Brassine 2011). Although results of occurrences are often used in studies (Corbett 1989), there are drawbacks as scat analysis is often not accurate in accounting for rare and very small food items (Klare *et al.* 2011). Furthermore, the importance of some prey items may be overestimated due to

unequal digestion times of individual items (Murie 1946). O'Gara (1986) concluded in a study of coyote diets that large prey is generally underrepresented when using scat analysis as large quantities of meat and fat are consumed, and that the reliability of scat analysis in determining diet varies with carnivore species and circumstances.

The feeding ecology of brown hyaena has been well described on tracts of protected and unprotected land, and across a variety of habitats (Mills and Mills 1978; Wiesel 2006; van der Merwe *et al.* 2009; Stein *et al.* 2013; Slater and Müller 2014; Williams 2017; Comley *et. al.* 2018). There is however limited data available on brown hyaena diet in small, protected areas within a semi-urban context. Furthermore, the presence of a permanent vulture restaurant on Mogale's Gate presented an additional opportunity to evaluate how a regular food source influences the feeding ecology of brown hyaena.

The aim of this chapter was to determine the seasonal diet of brown hyaena on Mogale's Gate over a one-year period.

Research questions

- What is the seasonal diet of brown hyaenas on Mogale's Gate?
- To what degree does the vulture restaurant contribute to the diet of the brown hyaenas?

METHODS

Scat collection

Like many other carnivores, brown hyaena often use roads and game paths to travel (Gusset and Burgener 2005; Thorn *et al.* 2011; Williams 2017) and consequently brown hyaena latrine sites are often situated on the side of roads (Hulsman *et al.* 2010). As the existing road network (98 km) on Mogale's Gate is quite extensive across the reserve (see Figure 2.1 in chapter 2), I used roads to search for scats and active latrines. Using a map of Mogale's Gate, I divided the reserve into a 21-cell grid with each cell measuring approximately 143 ha in size (Appendix 4). During each sampling period, I surveyed all accessible roads on Mogale's Gate by either driving or walking and attempts were made during sampling to find scats within each grid cell, to avoid biased sampling of only some areas of the reserve.

I collected scat samples twice a month (every two weeks) from May 2014 to April 2015 and included one dry (May - October) and one wet season (November - April) for analyses. As latrines play an important role in brown hyaena olfactory communication (Hulsman *et al.* 2010) only ±50% of each fresh scat found was collected using braai tongs and placed into individual brown paper bags. Each bag was numbered, dated, and the GPS location of the collected scat was recorded. A description of where the scat was found, such as a latrine, road verge or game path was also recorded. Collected scats were air dried until processing.

If latrines only contained old, white and crumbly scats, they were recorded as being inactive, but still checked during subsequent sampling sessions for any new scats. To ensure that the contents of the scats were representative of the time of the year at which they were collected, I only collected scats less than approximately two weeks of age for analysis. Fresh scat is mostly wet and greenish (Stuart and Stuart 2013) but can also be dark green to black in colour (Burgener and Gusset 2003). As the scat ages, it changes to a creamish colour before drying and eventually becoming completely white and crumbly (Stuart and Stuart 2013). To facilitate the determining of the approximate age of scats, I collected ten fresh brown hyaena

scats and monitored their change in colour, wetness, structure and appearance over twenty days at the study site. I took photographs of these scats daily to observe the changes in colour and appearance (Figure 3.1).



Figure 3.1. Aging of brown hyaena scat: a fresh scat in a latrine, and the same scat sample 2, 4 and 19 days later (C. Kruger).

Scat analysis

In preparation, for analyses of the scat content, I placed each scat sample into a piece of nylon stocking tied securely at both ends and submerged it into warm water for about 20 minutes to soften. Whilst still in the stocking I crushed the scat by hand and rinsed under running water until the water ran clear, thus indicating that all the digestive debris had been removed. The remaining contents of the scat were spread onto newspaper to air dry for two days and then manually sorted and separated into the following broad categories: hair, bone, bird remains, anthropogenic items (e.g., plastic, paper, rubber), plant material (seeds, fruit, leaves, sticks, grass), stones and invertebrate remains (Figure 3.2). I recorded any other items that could not be identified as unidentified.



Figure 3.2. Manual sorting of a brown hyaena scat sample into categories of hair, bird remains, anthropogenic items, plant material, stones, invertebrates, and bone (C. Kruger).

The sorted contents of each scat were stored in ziplock bags, labelled with the sample number, date of collection, and GPS co-ordinates. I classified the items identified in the scats as either dietary (ingested for nutritional purposes) or non-dietary (ingested incidentally whilst feeding or for no obvious nutritional gain). The following categories were regarded as dietary: hair, bird remains and fruit / seed. Non-dietary items included bone fragments, invertebrates, stones, anthropogenic items, leaves, sticks, grass, and unidentified items. Invertebrate remains found in the scat belonged to the family Trogidae (hide or carrion beetles) were considered to be the result of incidental consumption, and not included in analyses. Bone fragments were regarded as non-dietary, as they could not be identified and were considered to have already been represented in the diet by the hair (Chase-Grey 2011; Williams 2017). Although brown hyaena are known to be cannibalistic (Mills and Mills 1978; Brain 1981), for the purpose of this study, brown hyaena hair in scats was categorised as a non-dietary item and assumed to be due to allo-grooming (Mills 1983; Burgener and Gusset 2003).

Hairs that I found in the samples were used to identify the mammal species ingested by brown hyaenas. Counting and microscopically identifying all the hairs found in each scat sample is impractical, and therefore I selected a sub-sample of hairs (Brassine 2011). Using the technique as described in Maude (2005) I examined all hairs within a scat sample and then selected a representative sub-sample of 20 hairs of different size, thickness, colour and length for identification. In addition, I selected very small hairs from the samples to increase the probability of identifying small mammal species such as small rodents (Maude 2005). I identified individual mammal hairs by their physical appearance and microscopic traits, including cuticular scale imprints and cross-sections (Perrin and Campbell 1980; Keogh 1983; van der Merwe 2009).

I made cuticular scale imprints by placing each hair onto a glass microscope slide covered with a mixture of liquid gelatine and green food colouring. The slide was placed into a fridge for about 12 hours to ensure that the gelatin set completely. I then pulled each hair from the slide leaving the imprint of the hair's scale pattern in the gelatin (Perrin and Campbell 1980). Once I had removed the hairs from the gelatin, the hairs from each scat were stored together in a marked (with scat sample number) ziplock bag until used to make cross sections. Notes were made on each hair's outward appearance, i.e., colour, size and thickness, to use when I had both imprint and cross section in front of me for identification.

I made cross sections of the hairs by placing the sample of 20 hairs from each scat, used to make the cuticular imprints, into a 2.5 to 3 cm length of a plastic drinking straw. Using a wooden block stand, marked with each of the scat sample numbers, the straw pieces were stood upright and the hairs placed into each straw using tweezers. I melted a mixture of paraffin wax (90%) and depilatory wax (10%) together and then syringed the mixture into each straw section containing the hair samples. The wooden block with samples was placed in a fridge to cool and solidify the wax. Once the wax had solidified, I cut each straw into thin slices (<0.1 mm) using a sharp minor® razor blade. At least ten cross sections of each straw were made and then glued to a microscope slide using clear glue (Boast *et al.* 2016). Each slide was labelled with the sample number and stored in individual ziplock bags.

I identified hairs under 100x and 400x magnification using a microscope by comparing both their cross-sections and cuticular scale patterns to reference libraries of local mammals compiled by myself, and published reference lists (Perrin and Campbell 1980; Keogh 1983; Buys and Keogh 1984; Wade 2016). I compiled a reference library of hairs from wild and domestic animals, by opportunistically sampling from animals killed on roads or through hunting operations. Where possible I collected hairs from different parts of the animals' body, as although the structure of the hairs is the same there can be visual differences seen in the hairs (Bhatpara and Kindlmann 2012; Williams 2017). I used the same procedure outlined for making cuticular imprints and cross sections described above to prepare reference slides for each species and photographed each slide using a microscope camera. The benefit of using a reference library compiled by myself was that the samples and references could be prepared and viewed under the same conditions

and magnification, increasing the identification certainty (Melville *et al.* 2004) (Figure 3.3).

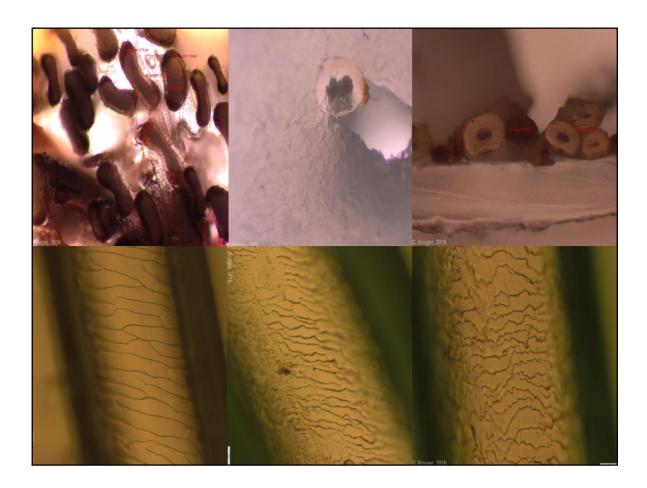


Figure 3.3. Examples of hair cross sections at 100x magnification (top row) and cuticular imprints at 400x magnification (bottom row). From left to right - blesbok, domestic pig, and brown hyaena (C. Kruger).

Macroscopic features such as colour, size and thickness of the hair, and reexamining the scat content for other remains (e.g., hoof; claws or other identifying characteristics) was done to improve the probability of identification. If I could still not identify the species from which the hair originated, the hair was recorded as unknown. Hair samples were identified to the lowest taxonomic level possible.

Prey species identified from the hairs were categorised into size classes as per Mills and Mills (1978): very small (<1 kg), small (1 - 15 kg), medium (16 - 50 kg) and large (>50 kg) mammals based on using the mean mass of a live adult female (Skinner

and Chimimba 2005). For the purposes of my study, domestic livestock, was considered to have originated from the carcasses provided at the vulture restaurant and was placed into its own category.

The large mammal category (>50 kg) was divided into two groups: non-provisioned, i.e., sable antelope (*Hippotragis niger*) and bushpig (*Potamochoerus larvatus*), which were not hunted or culled as part of the Mogale's Gate management plan, and provisioned, i.e., those species that were considered available to the brown hyaenas as by-products of hunting or culling as their remains were deposited at the vulture restaurant.

Data analysis

To determine if I had analysed sufficient scats to provide an accurate representation of the brown hyaena's diet on Mogale's Gate, I constructed species accumulation curves using EstimateS 9.1.0 (Colwell 2013). Here the number of species identified as food are plotted against the number of scats collected. Once the curve reaches an asymptote, the identification of any additional species in further scats collected is very unlikely (Braczkowski *et al.* 2012). Only mammal species that could be identified by the hairs found in the scats were used in the construction of the species accumulation curves.

Due to variation in the digestion and passage rates of ingested food (Melville *et al.* 2004; Glen and Dickman 2006) quantifying the actual amount of prey species ingested by brown hyaneas through faecal analysis is problematic (Mills and Mills 1978). The amount of prey items that is ingested varies depending on the species and what part of the prey is consumed (Mills and Mills 1978), and currently there is no known baseline data on food intake to scat volume ratios for brown hyaena (Klare *et al.* 2011; Williams 2017). Therefore, an attempt to quantify the dietary composition of the brown hyaena scats was made by calculating the percentage occurrence and the relative percentage occurrence of food items. The percentage occurrence (PO) of each food item in the sampled scats was calculated by taking

the number of scats containing a particular food item and dividing it by the total number of scats x 100 (Burgener and Gusset 2003; Loveridge and MacDonald 2003; Slater and Müller 2014). The relative percentage of occurrence (RPO), which provides an indication of how important a food item or species is in relation to all other items fed on (Ackerman *et al.* 1984), was calculated by taking the number of times a specific food item was identified in the scat samples divided by the total number of occurrences of all food items x 100 (Burgener and Gusset 2003; Loveridge and MacDonald 2003; Slater and Müller 2014). A 95% confidence interval for both the percentage of occurrences and the relative percentage occurrences were generated from 1000 bootstrap simulations (Andheria *et al.* 2007; Slater and Müller 2014).

The Chi square test of independence (Fisher 1922) was used to test for differences in the occurrence of the non-dietary and the dietary items between the dry and wet seasons. Whilst the t-test for independent samples was used to determine if there was a significant difference between the occurrence of non-dietary items versus dietary items in the diet of the brown hyaenas. The Chi square test of independence was used to determine if there were significant contributions of each of the mammal size classes to the dry and wet season diets. The t-test for independent samples was used to determine if there was a larger contribution to the season diets of domestic livestock versus the other dietary items found.

RESULTS

Between May 2014 and April 2015, 141 scats were collected and analysed. Of these, 85 were collected during the dry season (May to October) and 56 collected during the wet season (November to April). Of the 141 scats, 121 (86%) were from the Andesite Mountain Bushveld areas, 18 (13%) from the Moot Plains Bushveld, and two (1%) from the Gold Reef Mountain Bushveld areas of Mogale's Gate (Figure 3.4).

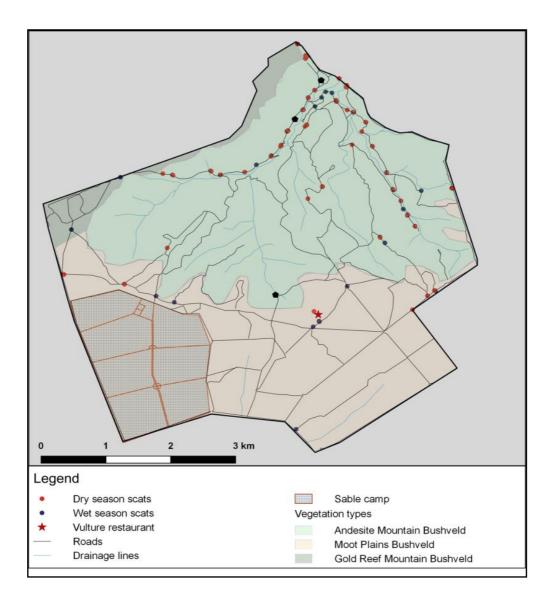


Figure 3.4. Locations of collected scat samples found on Mogale's Gate for the period May 2014 to April 2015.

I collected a mean of 11±6 scats per month (range 4-21). Most scats (60%; n=85) were collected during the dry season as there were no dung beetles (*Scarabaeus* spp) removing the scat or rain washing the scat away during this period. The lowest number of scats (n=4) were collected during December 2014, and the highest number in April 2015 (n=21) (Figure 3.5).

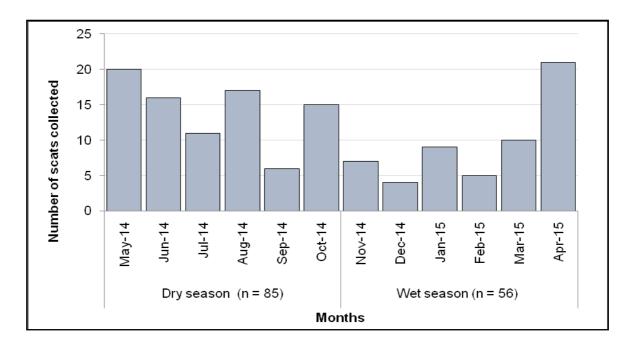


Figure 3.5. The number of scats collected per month, over the course of the study period (May 2014 - April 2015).

I collected the majority (89%; n=125) of scats from latrines, whilst the remainder were found along roadsides and game paths. Although attempts were made to collect samples from each of the 21 designated sampling cells, only 15 of the cells had fresh scat, which could be used for analyses. Five of the six cells where no scats were found were located in grasslands in the south west of the reserve, with two of the cells (numbers 14 and 20) being in the sable camp, which is fenced off, thereby presumably restricting hyaena movement through this area. One cell (number 7) was situated in the northwest section of the property on the border between plant communities Andesite Mountain Bushveld areas and Moot Plains Bushveld.

The species accumulation curve for both seasons combined reached an asymptote at 79 samples suggesting that 141 samples were representative of diet of brown hyaena on Mogale's Gate during the study period. An asymptote was reached at 76 samples for the dry season (Figure 3.6a), and at 50 samples for the wet season (Figure 3.6b), indicating that the samples collected were seasonally representative of the diet in these periods.

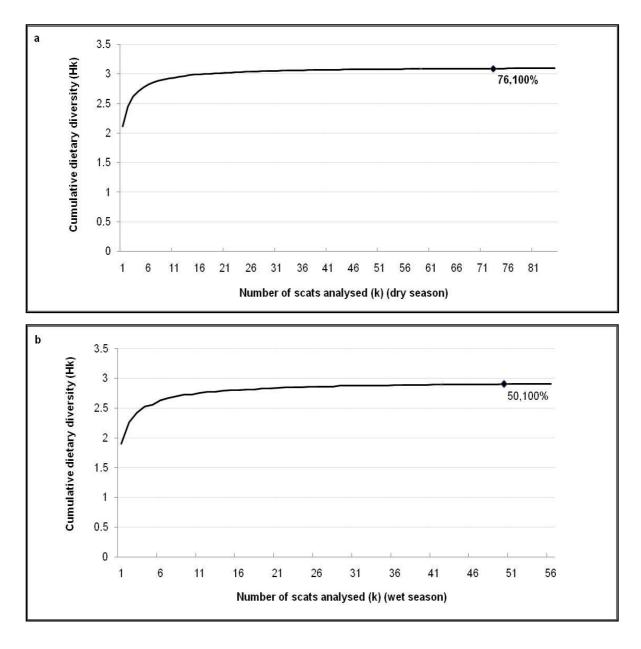
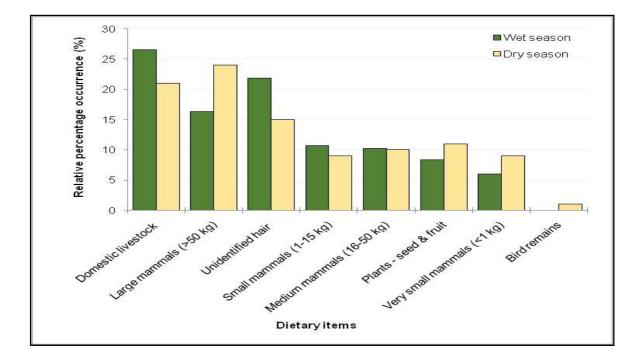


Figure 3.6. Species accumulation curves for brown hyaena diet on Mogale's Gate as determined for the (a) dry and (b) wet seasons.

I found 709 items in the 85 scat samples collected during the dry season, and 461 items in the 56 scat samples collected during the wet season. The dry season scat samples consisted of 58% dietary items (n=413) and 42% non-dietary items (n=296) whereas the wet season scats consisted of 47% dietary (n=215) and 53% non-dietary items (n=246). I found no significant difference in the occurrence of dietary items between the wet and the dry seasons ($\chi^2 = 10.4$, p = 0.11). However, there were significantly more non-dietary items in the dry season scats than the wet season scats ($\chi^2 = 36.4$, p < 0.001). When the difference between dietary and non-dietary items per season was compared, there was no significant difference in occurrence (dry season: t = 0.50, df = 11, p = 0.62; wet season: t = 1.23, df =11, p = 0.24).

I found hair in all the sampled scats and identified 34 species as food items (Table 3.1). The relative percentage occurrence (RPO) (Figure 3.7) of identified mammalian hair accounted for 71% of all dietary items found in scats, followed by unidentified hair (19%), seeds and fruits (10%), and bird remains (1%).



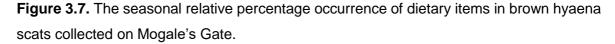


Table 3.1. The percentage occurrence and relative percentage of occurrence of all ingested items (dietary and non-dietary items) found in scats of brown hyaena on Mogale's Gate (n=141 scats).

Category			Contribution to diet					
		Dry season (n = 85)			Wet season (n = 56)		Dry season	Wet season
Dietary food Items	Frequency	PO(%) (Range)	RPO(%) (Range)	Frequency	PO(%) (Range)	RPO(%) (Range)	RPO(%) (Range)	RPO(%) (Range)
		RPO (%) - Rel	ative percentage occurr	ence, PO (%) -	Percentage occurrence	е	-	
Very small mammals (<1 kg)								
Pouched mouse (Saccostomus campestris)	13	15.29 (8.2-23.5)	1.83 (1.7-1.9)	7	12.50 (5.4-21.4)	1.51 (1.4-1.6)	3.15 (1.5-4.8)	3.26 (0.9-5.8)
Multimammate mouse (<i>Mastomys</i> sp)	10	11.76 (5.9-18.8)	1.41 (1.3-1.5)	6	10.71 (3.6-19.6)	1.30 (1.2-1.4)	2.42 (0.8-3.3)	2.79 (0.9-5.1)
Woodland dormouse (Graphiurus murinus)	5	5.88 (1.2-10.6)	0.70 (0.6-0.8)	0	-	-	1.21 (0.2-2.4)	-
Lesser musk shrew (Crocidura sp)	5	5.88 (1.2-10.6)	0.70 (0.6-0.8)	0	-	-	1.21 (0.2-2.4)	-
Striped grass mouse (Lemniscomys rosalia)	4	4.71 (1.2-9.4)	0.56 (0.5-0.8)	0	-	-	0.97 (0.2-1.9)	-
Small mammals (1-15 kg)								
Rock hyrax (<i>Procavia capensis</i>)	24	28.24 (19.4-37.6)	3.38 (3.3-3.5)	14	25.00 (14.3-37.5)	3.03 (2.9-3.2)	5.81 (2.9-6.7)	6.51 (3.2-1.0)
Scrub hare (<i>Lepus saxatilis</i>)	6	7.06 (2.4-12.9)	0.84 (0.7-1.0)	0	-	-	1.45 (0.4-2.2)	-
Black-backed jackal (Canis mesomelas)	4	4.71 (1.2-9.4)	0.56 (0.5-0.8)	2	3.75 (0.0-8.9)	0.43 (0.3-0.6)	0.97 (0.2-1.9)	0.93 (0.0-2.3)
Aardwolf (Proteles cristatus)	2	2.35 (0.0-5.9)	0.28 (0.2-0.4)	0	-	-	0.48 (0.0-1.0)	-
Water mongoose (Atilax paludinosus)	0	-	-	4	7.14 (1.8-14.3)	0.86 (0.7-1.0)	-	1.86 (0.5-3.7)
Vervet monkey (Chlorocebus pygerythrus)	0	-	-	1	1.79 (0.0-5.4)	0.21 (0.1-0.3)	-	0.47 (0.0-1.4)
Porcupine (Hystrix africaeustralis)	0	-	-	1	1.79 (0.0-5.4)	0.21 (0.1-0.3)	-	0.47 (0.0-1.4)
Steenbuck (Raphicerus campestris)	0	-	-	1	1.79 (0.0-5.4)	0.21 (0.1-0.3)	-	0.47 (0.0-1.4)
Medium mammals (16-50 kg)								
Bushbuck (Tragelaphus scriptus)	10	11.76 (5.9-18.8)	1.41 (1.3-1.5)	6	10.71 (3.6-19.6)	1.30 (1.2-1.4)	2.42 (0.8-3.3)	2.79 (0.9-5.1)
Grey duiker (<i>Sylvicapra grimmia</i>)	10	11.76 (5.9-18.8)	1.41 (1.3-1.5)	3	5.36 (0.0-12.5)	0.65 (0.5-0.8)	2.42 (0.8-3.3)	1.40 (0.0-3.2)
Reedbuck (<i>Redunca</i> spp)	9	10.59 (4.7-17.6)	1.26 (1.2-1.4)	5	8.93 (1.8-17.9)	1.08 (1.0-1.2)	2.18 (0.8-3.1)	2.33 (0.5-4.2)
Springbok (Antidorcas marsupialis)	8	9.41 (3.5-15.3)	1.12 (1.0-1.2)	2	3.57 (0.0-8.9)	0.43 (0.3-0.6)	1.94 (0.6-2.8)	0.93 (0.0-2.3)
Impala (Aepyceros melampus)	5	5.88 (1.2-10.6)	0.70 (0.6-0.8)	6	10.71 (3.6-19.6)	1.30 (1.2-1.4)	1.21 (0.2-1.8)	2.79 (0.9-5.1)
Large mammals (>50 kg)								
Sable (<i>Hippotragus nig</i> er)	3	3.53 (0.0-8.2)	0.42 (0.3-0.5)	0	-	-	0.73 (0.0-1.4)	-
Bushpig (Potamochoerus larvatus)	0	-	-	1	1.79 (0.0-5.4)	0.21 (0.1-0.3)	-	0.47 (0.0-1.4)
Black wildebeest (Connochaetes gnu)	37	43.53 (32.9-54.1)	5.21 (5.1-5.3)	13	23.21 (12.5-35.7)	2.81 (2.7-3.0)	8.96 (6.3-12.0)	6.05 (2.8-9.3)
Blesbok (Damaliscus pygargus phillipsi)	23	27.06 (18.8-36.5)	3.24 (3.1-3.4)	2	3.57 (0.0-8.9)	0.43 (0.3-0.6)	5.57 (2.8-6.3)	0.93 (0.0-2.3)
		!					J	(Table 3.1 Continues

(Table 3.1 Continued)			Contribution to diet					
		Ingeste Dry season (n = 85)		Wet seas		on (n = 56)	Dry season	Wet season
	Frequency	PO(%) (Range)	RPO(%) (Range)	Frequency	PO(%) (Range)	RPO(%) (Range)	RPO(%) (Range)	RPO(%) (Range)
		RPO (%) - Rela	ative percentage occurre	ence, PO (%) -	Percentage occurrenc	е		
Giraffe (Giraffa camelopardalis)	8	9.41 (3.5-15.3)	1.12 (1.0-1.2)	0	-	-	1.94 (0.6-2.8)	-
Nyala (<i>Tragelaphus angasii</i>)	7	8.24 (2.4-14.1)	0.98 (0.9-1.1)	7	12.50 (5.4-21.4)	1.51 (1.4-1.6)	1.69 (0.4-2.4)	3.26 (0.9-5.8)
Eland (<i>Tragelaphus oryx</i>)	5	5.88 (1.2-10.6)	0.70 (0.6-0.8)	5	8.93 (1.8-17.9)	1.08 (1.0-1.2)	1.21 (0.2-1.8)	2.33 (0.5-4.2)
Waterbuck (<i>Kobus ellipsiprymnu</i> s)	4	4.71 (1.2-9.4)	0.56 (0.5-0.8)	4	7.14 (1.8-14.3)	0.86 (0.7-1.0)	0.97 (0.2-1.9)	1.86 (0.5-3.7)
Red hartebeest (Alcelaphus buselaphus)	3	3.53 (0.0-8.2)	0.42 (0.3-0.5)	0	-		0.73 (0.0-1.4)	-
Kudu (<i>Tragelaphus strepsiceros</i>)	3	3.53 (0.0-8.2)	0.42 (0.3-0.5)	2	3.57 (0.0-8.9)	0.43 (0.3-0.6)	0.73 (0.0-1.4)	0.93 (0.0-2.3)
Gemsbok (<i>Oryx gazella</i>)	2	2.35 (0.0-5.9)	0.28 (0.2-0.4)	1	1.79 (0.0-5.4)	0.21 (0.1-0.3)	0.48 (0.0-1.0)	0.47 (0.0-1.4)
Warthog (<i>Phacochoerus aethiopicus</i>)	2	2.35 (0.0-5.9)	0.28 (0.2-0.4)	0	-	-	0.48 (0.0-1.0)	-
Plains zebra (<i>Equus quagg</i> a)	2	2.35 (0.0-5.9)	0.28 (0.2-0.4)	0	-	-	0.48 (0.0-1.0)	-
Domestic livestock								
Pig (Sus domesticus)	74	87.06 (80.0-94.1)	10.43 (10.3-10.5)	50	89.29 (80.4-96.4)	10.84 (10.7-11.0)	17.92 (14.3-21.5)	23.26 (17.4-29.2)
Cattle (<i>Bos taurus</i>)	9	10.59 (4.7-17.6)	1.26 (1.2-1.4)	5	8.93 (1.8-17.9)	1.08 (1.0-1.2)	2.18 (9.7-3.9)	2.33 (0.5-4.2)
Donkey (<i>Equus africanus asinus</i>)	4	4.71 (1.2-9.4)	0.56 (0.5-0.8)	2	3.57 (0.0-8.9)	0.43 (0.3-0.6)	0.97 (0.2-1.9)	0.93 (0.0-2.3)
Other								
Unidentified hair	63	74.12 (64.7-82.4)	8.88 (8.8-9.0)	47	83.93 (73.2-92.9)	10.19 (10.1-10.3)	15.25 (12.1-18.9)	21.86 (16.2-26.9)
Plants - seed & fruit	45	52.94 (42.4-62.4)	6.34 (6.2-6.5)	18	32.14 (19.6-44.6)	3.90 (3.8-4.0)	10.90 (7.7-13.8)	8.37 (5.1-12.3)
Bird remains	4	4.71 (1.2-9.4)	0.56 (0.5-0.8)	0	-	-	0.97 (0.2-1.9)	-
Total number of dietary items	413			215				
Non-dietary food items								
Plant matter (other)	85	100 (99.9-100.1)	11.98 (11.9-12.1)	56	100 (99.8-100.1)	12.14 (12.0-12.3)		
Bone fragments	65	76.47 (68.2-84.7)	9.16 (9.1-9.3)	42	75.00 (62.5-85.7)	9.11 (9.0-9.2)		
Brown hyaena hair	42	49.41 (37.6-60.0)	5.92 (5.8-6.0)	23	41.07 (28.6-55.4)	4.98 (4.9-5.1)		
Invertebrate remains	31	36.47 (25.9-47.1)	4.37 (4.3-4.5)	30	53.57 (41.4-67.9)	6.50 (6.4-6.6)		
Other/unidentified items	31	36.47 (25.9-47.1)	4.37 (4.3-4.5)	31	7.14 (1.8-14.3)	6.72 (6.6-6.9)		
Anthropogenic items	26	30.59 (21.2-40.6)	3.66 (3.6-3.8)	2 ¹²	21.43 (10.7-32.1)	2.60 (2.5-2.7)		
Stones	16	18.82 (10.6-27.1)	2.25 (2.2-2.4)	52	92.86 (85.7-98.2)	11.27 (11.1-11.4)		
Total number of non-dietary items	296			246				
TOTAL	709			461				

Five species from the very small (<1 kg) mammal category were identified, contributing 9% RPO (n=36) in the dry season and 6% RPO (n=13) in the wet season, to brown hyaena diet. The pouched mouse (*Saccostomus campestris*) and the multimammate mouse (*Mastomys* spp.) had the highest representation of very small mammals in the diet of the brown hyaenas. No significant differences between wet and dry season were found in the relative percentage occurrence of very small mammals (<1 kg) (χ^2 = 6.86, *p* = 0.4).

Eight small mammal (1–15 kg) species were identified in the scats and contributed significantly more to the wet season diet than to the dry season diet ($\chi^2 = 16.22$, p = 0.02). Rock hyrax (*Procavia capensis*) had the highest representation of this size category in the brown hyaena diet, while black-backed jackal, aardwolf (*Proteles cristatus*) and water mongoose (*Atilax paludinosus*) were identified in six scats in each season.

I recorded five medium sized (16-50 kg) antelope species in the brown hyaena scats, notably grey duiker (*Sylvicapra grimmia*), springbok, reedbuck (*Redunca* spp), impala (*Aepyceros melampus*), and bushbuck. These species contributed 10% to brown hyaena diet in both seasons. Of the species in this category the bushbuck contributed most to the diet during both seasons (Table 3.1).

Of the 31 non-domestic mammal species I identified, 13 were large mammal species (>50 kg). Significantly more dry season scat samples contained large mammals (RPO = 24%) than the wet season scats (RPO = 16%) (χ^2 = 23.48, *p* = 0.02). The non-provisioned species (>50 kg), sable and bushpig were found in three scats during the dry season and in one scat during the wet season. Based on relative percentage occurrence of the 11 provisioned game species in this size category (Table 3.1) black wildebeest (*Connochaetes gnou*), was the most frequently identified game species in both seasons. Blesbok (*Damaliscus pygargus phillipsi*) was the second most consumed game species in the dry season contributing 6% and nyala (*Tragelaphus angasi*) the second most consumed species in the wet season (Table 3.1).

Domestic livestock was found in all scats sampled. During the wet season, domestic livestock had the highest overall contribution to the diet of brown hyaena (RPO = 27%). The importance of domestic livestock in the diet was marginally less during the dry season (RPO = 21.1%) when large mammals contributed more to the diet (RPO = 24%) (Figure 3.7). No significant difference was found between the seasonal contributions of domestic livestock to the diet, ($\chi^2 = 0.21$, p = 0.89). Although, livestock was prevalent in the diet during both seasons, when compared to the combined contribution of other dietary items, no significant difference between the contribution of domestic species and other dietary items was found (dry season: t = 0.71, p = 0.55, df = 2.5; wet season: t = 0.43, p = 0.71, df = 2).

Plant seeds and fruits were found in 45 (53%) of the dry season samples making a relative contribution of 11% to the brown hyaena diet for this season. In the wet season plant seeds and fruits occurred in 18 (32%) of the samples contributing 8% to diet. The domestic chicken (*Gallus gallus domesticus*) was the only bird identified in the scats (feathers, beak and skin) and in four of the dry season scats.

Non-dietary plant matter (other than seeds and fruit), were found in all scats. Grass fragments were found in more scats than other plant material, especially in the dry season where 84 of the 85 scats had grass present. Overall, plant material (grass, leaves and sticks) occurred more frequently in the dry season scats. Bone fragments were found in 76% of sampled scats (dry season n=65; wet season n=42), having a relative percentage occurrence of 9% in both seasons.

Invertebrate remains were found in more than half of the wet season samples (PO = 54%). This amount was less in the dry season with a 37% occurrence. Much of the invertebrate remains included pieces of beetle carapace and pupa from the genus *Trox*. The other insect remains found in the scat could not be identified.

DISCUSSION

I was able to find 23 brown hyaena studies published since 1976, which were focused on the diet of brown hyaena or included diet as part of a study (Figure 3.8). Many of the pre-1995 studies, focused on the diets of populations in the arid and semi-arid regions of the Kahalari and Namibian deserts (Mills and Mills 1978; Owens and Owens 1978; Skinner and van Aarde 1981; Siegfried 1984). During the 2000s dietary studies of brown hyaenas investigating feeding habits on game ranches and National Parks in the North-West and Limpopo provinces of South Africa (Burgener and Gusset 2003; van der Merwe 2009) took place. Subsequently, the focus of brown hyeana dietary studies has evolved from purely dietary descriptions to include aspects such as the influence of sympatric large predators on brown hyaena diet (Yarnell et al. 2013; Comley et al. 2018; Williams 2017), the dietary overlap of brown hyaena with blackbacked jackal (van der Merwe 2009; Ramnanan et al. 2016), and investigating the diet of brown hyaenas reintroduced to the Eastern Cape (Slater and Müller 2014; Comley et al. 2018). Skinner (1976) and Skinner and van Aarde (1987) undertook the first studies of brown hyaena in the former Transvaal (now Gauteng), focusing on the general ecology and relocation of individuals into the Magaliesberg area. Since then there have been no known published studies of brown hyaena in the Gauteng province.

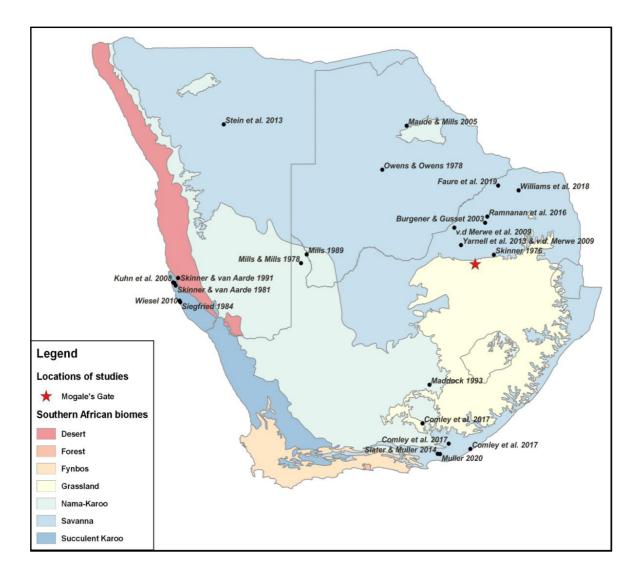


Figure 3.8. Locations of dietary studies of brown hyaena undertaken in Southern Africa (biome delineation by Mucina and Rutherford 2006).

Over a 1-year period, I collected and analysed 141 brown hyaena scats to assess the diet of the brown hyaenas on Mogale's Gate. The number of scats analysed in previous studies on brown hyaena diet ranged from 31-594 scats (Skinner 1976; Mills and Mills 1978; Owens and Owens 1978; Siegfried 1984; Skinner and van Aarde 1991; Burgener and Gusset 2003; Maude 2005; van der Merwe *et al.* 2009; Yarnell *et al.* 2013; Slater and Müller 2014; Ramnanan *et al.* 2016; Comley *et al.* 2017; Williams 2017; Faure *et al.* 2019; Müller 2020), with a mean of 119±141.8 scats analysed. While the number of scats analysed in the present study compares favourably with the number of scats analysed in other studies, species cumulative graphs are a more robust and standardised measure of sampling effort (Moreno and Halffter 2001;

Spencer *et al.* 2014). Based on the species accumulation curves generated from my study the sampling during both the dry (n=85) and wet season (n=56) on Mogale's Gate was sufficient as the seasonal species accumulation curves became asymptotic at 76 and 50 samples, respectively.

Although all attempts were made to identify all species found in the sampled scat, and species accumulation curves reached an asymptote, one shortcoming of my study was the high number of unidentified hairs. This meant that up to 20% of the potential contribution to the diet was not accounted for. Hairs from the larger mammal species are easier to set in the wax and leave clearer cuticular imprints than those from small mammals, thus making them easier and more likely to be identified. Due to their small size and fineness small mammal hairs can be "lost" in the wax solution or easily damaged when cuticular imprints are made. I recommend that future diet related studies of the brown hyaenas on Mogale's Gate, include DNA metabarcoding as this method may be more efficient at detecting small species (McInnes *et al.* 2016; Thuo *et al.* 2019).

Nevertheless, the remains of 31 of the 58-mammal species on Mogale's Gate were detected in the scat samples. This finding is not unusual for hyaena species as they are generalist feeders and scavenge opportunistically on carrion available within the landscape (Maude and Mills 2005; Alam and Khan 2015; Williams 2017; Williams *et al.* 2018). The identification of 34 mammal species (including domestic livestock) in the diet of the brown hyaenas on Mogale's Gate is comparable to that of brown hyaena in other study areas, with large predators, across South Africa. For example: 39 mammal species were identified from 288 scats analysed within 5431 km² of the Soutpansberg mountains (Williams *et al.* 2018); 25 species from 96 scats from the Mountain Zebra National Park (210 km²) (Comley *et al.* 2018) and 14 mammal species were identified from 31 scats on Shamwari Private Game Reserve (250 km²) in the Eastern Cape (Slater and Müller 2014). At 30.6 km² Mogale's Gate is substantially smaller than these areas and, except for leopard, has no large predators to provide brown hyaenas with scavenging opportunities. However due to the regular provisioning of carrion at the vulture restaurant, including ~85% of the non-domestic

large mammal species consumed, the presence of large predators as suppliers of carrion may not be essential within Mogale's Gate.

Although rarely sighted on Mogale's Gate, leopard is known to occur on both Mogale's Gate and in the surrounding Magaliesberg mountains (Carruthers 2007; Kuhn 2014). Leopards may, therefore, provide scavenging opportunities to brown hyaena, but are unlikely to be sufficient to support the population of brown hyaena on Mogale's Gate. It is impossible to establish if all mammal species were fed on within the boundary of Mogale's Gate, as brown hyaenas are likely to traverse under the Mogale's Gate boundary fence and can thus potentially source food elsewhere. Considering their home range sizes (Chapter 5) it is likely that the hyaenas do forage beyond the boundaries of Mogale's Gate.

Bushbuck, reedbuck and grey duiker were not provisioned at the vulture restaurant by management during the study period. Consequently, their occurrence in the brown hyaenas diet can be attributed to either scavenging on kills made by leopard, natural mortalities, or in the case of the grey duiker, hunting of lambs by brown hyaena. Brown hyaenas hunt springbok in the Kalahari (Mills and Mills 2013) and as grey duikers are smaller than springbok, it is possible that brown hyaena may hunt them on Mogale's Gate.

The high contribution of large mammal species and livestock to the diet of brown hyaena on Mogale's Gate was expected due to the regular carrion available at the vulture restaurant. During the dry season 19 blesbok and 24 black wildebeest were culled, and five natural mortalities of black wildebeest were recorded in the wet season (*⁴A. Tuckett pers.comm.). The innards, feet and heads of these animals were discarded at the vulture restaurant which explains the higher contribution of both blesbok and black wildebeest to the diet of brown hyaenas during the dry season. This additional source of carrion in the dry season reduced the contribution and importance of domestic livestock to the brown hyaenas diet. During the wet season when culling

⁴Mr Alistair Tuckett - Operations director, Mogale's Gate Biodiversity Centre

operations are not undertaken there is less availability of large mammal carcasses at the vulture restaurant, thus increasing the contribution of domestic livestock to the diet.

In the Makgadikgadi National Park and surrounding unprotected cattle areas, brown hyaenas have been seen to change their feeding behaviour following an increase in available carcasses (Maude 2005). Brown hyaenas in this area had different seasonal diets in response to the availability of livestock carcasses and the seasonal influx of migrating zebra and blue wildebeest (Maude 2005). At times when carcasses of these large game species were unavailable brown hyaenas scavenged on cattle carcasses either killed by lion or which had died from disease or old age (Maude 2005). More recently, in the enclosed Mountain Zebra National Park, Comley (2016) found that brown hyaenas consumed more medium sized mammal remains before the release of the lions, whereas after the release of the lions they were consuming more large mammal remains.

Small mammals accounted for 42% of the overall feeding occurrences, with their contribution to the diet being higher in the wet season. On the rare occasion when brown hyaenas have been seen hunting successfully, they have only caught small or very small mammals (Mills 1976; Maude 2005). Also, as an apex predator will seldom leave any remains of a small mammal (Ackerman et al. 1984), it would suggest that the presence of small mammal found in the diet of brown hyaenas is more likely due to hunting rather than scavenging. Maude 2005 found that brown hyaena would hunt Cape hare (*Lepus capensis*) in the lean season when the availability of carcasses was low. The relatively high proportion of rock hyrax in the hyaena's diet may be of ecological significance. In both seasons, rock hyrax occurred at least twice more in the scats than any of the other small mammals. The rock hyrax is a small (\leq 4.5 kg), compact, diurnal mammal which frequents rocky outcrops and cliff areas where there are sufficient bushes to browse from (Skinner and Chimimba 2005). Hyraxes are known to be a favoured prey species for aerial predators such as black eagles (Aquila verreauxii) (Carruthers 2007), are often hunted by leopard (Chase-Grey 2011) and have been found to occur in the diet of brown hyaena in the Soutpansberg Mountains (Williams 2017). On Mogale's Gate, the rock hyrax is a common species found on cliff faces and on rocky outcrops (pers. obs.). Despite being regarded as a diurnal prey species, using cracks and rock crevices as dens, rock hyraxes have been observed to be active at night especially during periods of full moon (Coe 1962; Brown and Downs 2005; E. Harris unpublished data). When food quantities and quality are low the rock hyrax may forage further distances away from the rock crevices increasing their predation risk (Brown and Downs 2005), thus providing a potential opportunity for brown hyaena to hunt them.

Other than brown hyaena, carnivore species were detected in 9% (n=12) of the scats in my study. This was not unexpected as several other studies have documented the occurrence of leopard, black-backed jackal, bat-eared fox (*Otocyon megalotis*), and aardwolf hairs in brown hyaena scat (Owens and Owens 1978; Burgener and Gusset 2003; Maude 2005; Stein *et al.* 2013; Slater and Müller 2014; Williams 2017). To further support my findings, camera trap images during the study period showed a brown hyaena feeding on a jackal carcass that was carried to the entrance of a maternal den (unpubl. data). Whether the brown hyaena killed the jackal or just carried the carcass found is unclear. In the Kalahari, Mills *et al.* (1978) recorded brown hyaena eating black-backed jackal and speculated that it was due to the time of year when many young jackals were around.

The high occurrence (n=38; 26%) of anthropogenic items such as irrigation piping and soft plastic found in my study compared to other dietary studies of brown hyaena, where very few scats contained these items 0.3% (n=1) to 3% (n=3) (van der Merwe *et al.* 2009; Slater and Müller 2014; Williams 2017), is concerning. Brown hyaenas have been noted to frequent farmsteads and refuse sites (Skinner and van Aarde 1987; Skinner *et al.* 1995) and chew on rubber cables and camera traps (⁵Williams pers. comm., ⁶Pitman pers. comm.) and even ingest pieces of rubber and plastic (Müller 2020). The pieces of plastic found in the scats during my study could have originated from the ear tags that are on the domestic livestock carcasses at the vulture restaurant. There are also several homesteads and a rubbish site on Mogale's gate.

⁵Dr K. Williams - Research and conservation manager, CapeLeopard Trust.

⁶Dr . R. Pitman - Managing director, Data Science, Panthera.

Bone fragments were found in most of the scats, which correspond with the findings from other studies that much of the hyaena's food consists of carrion and bone (Skinner and Chimimba 2005; Maude 2005; Yarnell *et al.* 2013; Müller 2020). The jaws of the brown hyenas are very powerful, enabling them to crush most long bones of carcasses (Suedmeyer 2015) opening the highly nutritious bone marrow (Kruuk 1972). For the hyaenas themselves, as a food, bone is also almost as good nutritionally and energetically as meat (Benson *et al.* 2009). As a food source for vultures the bone fragments resulting from the chewing and breaking of bones by hyaenas, are an essential dietary requirement, providing calcium to growing vulture chicks (Richardson and Plug 2009). When hyaenas are not present it takes months of weathering before small bones become disarticulated for vultures to consume them (Richardson and Plug 2009).

The majority of invertebrate remains found in the scats comprised of pieces of beetle carapace and pupa from the genus *Trox*. These trogids or keratin beetles, are often found in association with carcasses and carnivore scats (Scholtz and Holm 1985) as these beetles consume dry skin and other dry remains from carcasses during later stages of decay (Scholtz and Holm 1985). I assumed that the ingestion of these beetles by brown hyaenas occurred whilst the brown hyaenas were feeding on carrion (Ellis and Shemnitz 1957; Brassine 2011) or that they could have been present within the scat samples when collected (Scholtz and Holm 1985). The other insect remains found in the scat could not be identified.

Although plant material (grass, leaves and sticks) was found in more than 60% of the scats in both seasons of my study there is no confirmed reason for brown hyaenas to intentionally consume these items (Maude and Mills 2005; Mills 1990) and is therefore regarded as incidental intake whilst scavenging (Mills 1990; Burgener and Gusset 2003). Intake of fruits by brown hyaena suggests a degree of omnivorous behaviour. In arid areas brown hyaenas consume various fruits with melon-type fruits contributing >50% of brown hyaena diet in the Kalahari, even when drinking water was available (Mills and Mills 1978; Owens and Owens 1978). Seeds in scats have been identified as originating from shrub species such as *Grewia flava, Grewia occidentalis* (Mills and Mills 1978). In my study, *Diospyros lycoides* was identified in the scats, and are also

often found in jackal scats on Mogale's Gate. If not intentionally consumed, the occurrence thereof in the scat maybe a result of incidental ingestion by the brown hyaenas when feeding on the rumen of ungulates (Henschel and Skinner 1990; Müller 2020).

Overall, the predominance of provisioned large mammals in the diet of brown hyaena on Mogale's Gate suggests and in the absence of large predators, the supply of carrion at the vulture restaurant is sufficient to sustain a brown hyaena population. It is however acknowledged that some occurrences of these species in the scats could have been due to kills made by leopard, or through natural mortality. Despite this brown hyaenas on Mogale's Gate still supplement their diet with smaller species such as rock hyrax, birds and rodents as well as possibly fruits. My study however supports the ecological theory that artificial food resources can influence the feeding ecology of brown hyaenas. Furthermore, I suggest that the regularly supplied vulture restaurant mimics the supply of carrion that would be provided in areas where large apex predators such as lion and cheetah occur, providing an important source of carrion to the persistence of brown hyaenas in the Magaliesberg region.

Recently, more studies have been focused on the effects of spatiotemporal and consistent food sources such as rubbish dumps, and supplementary feeding sites, on a range of bird and mammal species (Kolowski and Holekamp 2006; Bateman and Fleming 2012; Cozzi *et al.* 2015). These studies have shown that predictable food sources significantly influence population dynamics, reproductive success, behavioural adaptations and space use of various omnivorous mammals (Fedriani *et al.* 2001; Gilchrist and Otali 2002); carnivores (Beckmann and Berger 2003; Yirga *et al.* 2012); and birds (Tortosa *et al.* 2002).

Clearly, brown hyaenas living on Mogale's Gate have derived benefits from the presence of reliable, abundant, and available carrion source provided by the livestock and game carcasses at the vulture restaurant. The study shows that brown hyaena are filling the niche of an opportunistic scavenger on this small reserve. Although vulture restaurants may be viable, positive conservation tools for vultures, there is a need for a more thorough understanding of how this predictable food source can

influence aspects of trophic dynamics, small mammal populations, and disease transmission in the broader community (Ogada *et al.* 2012; Cozzi *et al.* 2015).

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Chapter 4

Population estimates of brown hyaena on Mogale's Gate



" The soul is the same in all living creatures although the body of each is different." -Hippocrates

INTRODUCTION

With most large carnivore populations declining worldwide, practical and accurate methods of estimating populations to establish baseline parameters are of increasing importance in the development of conservation management strategies (Stander 1998; Grant 2012; Comley 2016). Collecting information on large carnivores is often challenging because many species are elusive, nocturnal, have large ranges and occur at low densities (Balme *et al.* 2009; Thorn *et al.* 2009). The abundance of animals can be assessed in two ways, either as absolute or relative abundance (Gese 2001). Using relative abundance methods are often more suitable and practical when carnivore population estimates are needed (Stander 1998). There are several cost-effective, repeatable and indirect techniques that measure density by calculating population inference indices based on data collected using the presence of animal signs. These include spoor, scat and scent markings (Long *et al.* 2007), modelling of populations based on prey biomass, and interviews (Thoisy *et al.* 2008; McCarthy *et al.* 2008; Grant 2012).

Photographic capture-recapture surveys using camera traps can obtain reliable density estimates of nocturnal, elusive carnivores that are individually distinguishable by their pelage patterns (Karanth 1995; Kelly et al. 2008; Harihar 2009). Although originally large and cumbersome to operate, camera traps have become smaller and pre-programmable making them more suitable for remote wildlife photography (Kucera and Barrett 2011; McCallum 2013). Baits attached to strings, trip wires, and treadle plates (Pearson 1959; 1960; Kucera and Barrett 2011) activated earlier versions of cameras. By the early 1990s an automatic camera system, triggered by a pulsed infrared sensor, was used in Australia to record animals moving along trails, and to identify pollinators of flowering plants (Carthew and Slater 1991). Subsequently, camera traps have become ubiquitous in wildlife research globally regardless of the taxa studied (McCallum 2013). Some examples include investigating ground-bird nest predation by raccoon dog (*Nyctereutes procyonoides*) in the archipelago of northern Sweden (Dahl and Ahlen 2019), estimating the abundance of perentie (Varanus giganteus) in north-western Australia (Moore et al. 2020), measuring the responses of small rodents and shrews to peatland restoration (Littlewood et al. 2021), estimating tiger (Panthera tigris) population dynamics in India (Karanth et al. 2006), and estimating cheetah population sizes in Kenya (Broekhuis and Gopalaswamy 2016). Remote camera trapping has been used in an increasing number and variety of studies for a range of species, playing a large part in obtaining reliable distribution data on biodiversity in general (e.g., Pardo *et al.* 2021), including rare carnivore species (Zielinski *et al.* 1995; Kucera and Barrett 2011).

There are several advantages of using camera traps: they are mostly non-invasive and can be used to survey large areas (Maffei *et al.* 2004; Parker *et al.* 2008), confirm the presence of and monitor rare species (Carbone *et al.* 2001), often at the individual level (Choo *et al.* 2020). Camera traps allow for robust sampling under different climatic conditions and in remote areas. When locations of camera traps are known they can be used to provide encounter histories of different individuals, and along with recording the date and time of captures, this information can then be used in spatial and activity pattern analysis (Ancrenaz *et al.* 2012; Comley 2016).

Camera traps in conjunction with capture-recapture techniques were first used to monitor tiger populations in India (Karanth and Nichols 1998). Subsequently, they have been used for estimating the abundance of many other carnivore species, including leopards (*Panthera pardus*; Grant 2012), striped hyaenas (*Hyaena hyaena*; Harihar *et al.* 2009), cheetahs (*Acinonyx jubatus*; Marnewick *et al.* 2008) and brown hyaenas (Thorn *et al.* 2009; Comley 2016; Williams 2017; Müller 2020).

Capture-recapture models applied to camera trap images, work on the principle of individual recognition, through unique coat patterns (Royle and Young 2008). A spatial model is fitted to the data (images) for animals that are captured and then recaptured at set locations (i.e. camera trap stations). The maximum likelihood model is recommended as being the most suitable (Efford *et al.* 2009). In combination with simulations of trap processes, the estimation of density becomes more realistic (Efford *et al.* 2009). Using the likelihood of detecting an animal during a sampling occasion is important in the converting of the sample count statistic into an abundance estimate or density. Capture-recapture sampling is the canonical estimator (Williams *et al.* 2002), where the abundance estimates rely on the count and detection of individuals. Closed capture-recapture estimators are used to estimate the population size of an

animal species in which individuals can be recognised either by unique individual markings or by artificially marking individuals that occur in a temporally closed system (O'Brien 2011).

Efford *et al.* (2004) suggested that estimators used in the model should be robust to sources of heterogeneity, which may be present in the data. These sources can include temporal variation in trappability (Mt model), learnt trap responses (Mb model) and non-spatial individual heterogeneity (Mh model). These models consider the influence of time, behavioural response, and individual heterogeneity on capture probability (O'Brien 2011). The Mo or null model assumes that the variation in capture probability is constant and does not differ amongst individuals, whereas the Mh (jack-knife) models assumes that capture probability will differ between individuals. As capture probabilities can be influenced by differences in an animal's ranging behaviour (Sunquist and Sunquist 2002), the Mh model is a more realistic choice to use in free-living populations as individual capture probability varies with sex, age and social status (Harmsen *et al.* 2001). Brown hyaenas are territorial animals that live in clans (Owens and Owens 1979; Mills 1982) and because individuals within a clan usually travel and forage alone, individuals may cover varying distances (Mills 1982), and therefore their individual capture probabilities may differ.

Capture-recapture methods estimate population abundance by sampling a proportion of the whole population (Comley 2016). The analysis relies on three assumptions (White *et al.* 1982; Grant 2012). Firstly, all individuals in the study area have an equal chance of being detected (Karanth and Nichols 1998). Secondly, all individuals are distinguishable from each other to detect recaptures (Jackson *et al.* 2006). Lastly, the population being sampled is presumed to be demographically or temporarily closed, and there are no births, deaths, immigrations, or emigrations during the survey period (White *et al.* 1982).

Due to their secretive nature and nocturnal habits, it is difficult to attain accurate estimates of brown hyaena density (Mills and Hofer 1998; Williams 2017). The first density estimates were made by Mills (1984; 1990) in the Kalahari by using indirect methods and extrapolating the data from the average territory and group sizes. More

recently, camera traps have been used to establish density estimates of brown hyaena in the Pilanesberg National Park and Mankwe Game Reserve (Yarnell *et al.* 2013). By identifying individuals from camera trap data, these authors extrapolated data to reflect a density of 2 to 6 individuals / 100 km² from an original estimate based on 1 km². In the Soutpansberg Mountains in South Africa's Limpopo province, Williams (2017) used a fixed camera trap grid and survey periods, to meet the requirements of using spatially explicit capture recapture (SECR) methodology. Brown hyaena population estimates have been calculated across several areas of its distributional range, and vary depending on habitat type, human influence, protection level, and food availability (Boast and Houser 2012; Kent and Hill 2013; Richmond-Coggan 2014; Winterbach *et al.* 2014).

Recent studies of population estimates have also focused on the reintroduction of brown hyaena into protected reserves that were formerly large areas of agricultural land or stock farms (Hayward *et al.* 2007; Welch 2014). Protected areas like Kwandwe Private Game Reserve, in the Eastern Cape are securely enclosed, have an abundance of food resources and hence optimal scavenging opportunities (Welch and Parker 2016), resulting in a high density estimate of 14 - 20 individuals / 100 km² (Welch 2014). Other than leopard, Mogale's Gate doesn't have large apex predators providing food for brown hyaenas through scavenging opportunities. However, the reserve has a long-standing vulture restaurant with regular supply of carcasses available to terrestrial scavengers. As food biomass levels have been shown to positively affect the density of carnivores and scavengers (Van Orsdol *et al.* 1985; Welch 2014; Williams 2017) I predicted that there would be a high population density of brown hyaena on Mogale's Gate.

The aim of this chapter was to provide population estimates of brown hyaena on Mogale's Gate, using camera trap surveys.

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METHODS

Sampling

Whilst driving or walking along roads searching for scats (Chapter 3), other signs of brown hyaena activity like pastings and spoor were also searched for to help me identify areas that would be suitable for the placement of camera traps. When a brown hyaena spoor was found, the GPS co-ordinates and direction of spoor were recorded. Brown hyaena pastings are strong smelling secretions produced by the anal gland and deposited on grass and bush stalks. The scent left by the pasting conveys information to other members of the clan regarding individual activity (Mills et al. 1980; Gorman and Mills 1984). Pastings normally consist of a white paste, which has a long-lasting odour, and a black paste, which has a shorter lasting odour (Wiesel 2006). When I found pastings, I took GPS co-ordinates of the location and recorded if the pasting was old or fresh. To have a reference for the approximate age of the pastings, I collected grass stalks with freshly deposited pastings and photographed the aging process at various times of the year to determine freshness under local conditions (Figure 4.1). As the white pastings showed more distinct colour changes with age than the black pastings (pers. obs.), I used them as the indicator of freshness when collecting data. I considered shiny, white pastings as being less than 24-h old, and these were therefore recorded as 'fresh'.



Figure 4.1. General change of colour of brown hyaena pastings over the first 11 days after being deposited on a grass stalk by a brown hyaena. From left to right: day1; day 3; day 7; day 11. (C. Kruger)

The GPS co-ordinates of the pastings, latrines, and spoor were plotted onto a map of the reserve. This information enabled me to identify areas within each of the 21-cell grid (Chapter 3) that had frequent brown hyaena activity. I used this to select areas within each grid cell at which to place the camera traps, thus increasing the detection probability (Karanth and Nichols 2002; Thorn et al. 2009). The 21-cell grid ensured that the reserve was well represented by the camera trap rotation (Appendix 4). The camera trap survey took place between June 2015 and September 2016, using nine cameras. One camera trap was placed permanently at the vulture restaurant (representing one cell), whilst the other eight cameras, placed in pairs, were used to survey the remaining 20 cells. In order to survey all 20 cells over the 15-month sampling period, the four pairs of cameras were moved every 12 weeks to a new cell within the grid. This equated to five camera-trapping periods: Capture period one (9 June - 6 September 2015); capture period two (16 September - 14 December 2015); capture period three (16 December 2015 - 14 March 2016); capture period four (15 March - 11 June 2016); and capture period five (16 June - 13 September 2016) (Figure 4.2).

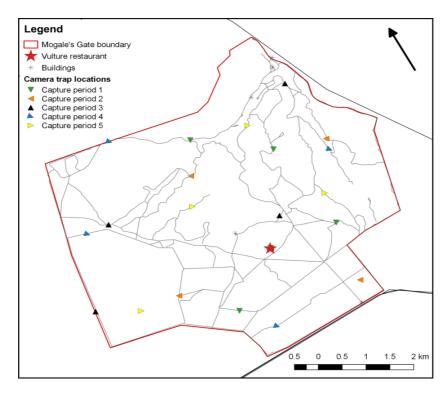


Figure 4.2. Camera trap placements on Mogale's Gate, from June 2015 to September 2016, using nine Bushnell (<u>http://bushnell.com/all-products/trail-cameras</u>) infra-red cameras. One permanent camera was placed at the vulture restaurant for the duration of the surveys.

The nine camera traps used for this aspect of the study were all Bushnell infra-red cameras: Four Bushnell Trophy Cam Essential (model 119636, Bushnell Outdoor Products, Kansas City, Missouri), two Bushnell Trophy Cam HD Aggressor (model 119676), and three Bushnell Trophy Cam HD (model 119537). Camera traps were paired at each camera location (referred to as a 'station') to photograph both sides of brown hyaenas and maximise chances of identification (Rovero et al. 2013; Comley 2016) (Figure 4.3). To minimize the chances of overexposure of images by the opposite camera's infrared flash, cameras were not placed exactly opposite to each other (Rovero et al. 2013). Cameras had an average distance of 3.6 m from the centre of the detection zone and were attached to either a tree or pole at a height ranging between 40 cm and 1 m above the ground depending on the slope of the ground. All cameras recorded images over a 24-h period with eight of the nine cameras set to take three images per trigger, with the sensitivity setting on 'auto'. The camera trap at the vulture restaurant was set to take only one image per trigger, sensitivity was set on 'auto', with a 30-second interval between images. This was to save battery and SD card space due to the high activity levels of vultures and jackals occurring at the vulture restaurant.

In line with the guidelines set out by Meek *et al.* (2014) the details of camera trap settings were recorded along with information for each station. This information included GPS location, altitude, vegetation type, direction camera was facing, reason for specific station placement e.g., active latrine, and any alterations made to the area around the cameras e.g., long grass cut in front of camera (Appendix 5).



Figure 4.3. Examples of the opposing camera trap placement at two of the camera trap sites used to estimate brown hyaena density on Mogale's Gate.

Data analysis

The number of independent photographs per trap day for each of the 12-week sampling periods were pooled and calculated to determine encounter rates of the hyaenas (Thorn et al. 2009). Photographs of brown hyaenas were considered independent if the individual could be recognised or for unidentified individuals were taken 30 min. apart (O'Brien et al. 2003). Only images using clear features that allowed individual recognition were used for analysis; any poor-guality images were discarded as per Karanth et al. (2011). Individual brown hyaenas were identified from the images using distinct features, which included the stripe patterns on the legs, distinctive pelage patterns, and notches or tears in the inner and outer edges of the ears (Figure 4.4). Identified individuals were assigned a unique identification number and images were used to compile "ID-kits" for referencing. As brown hyaena markings are bilaterally asymmetrical (Thorn *et al.* 2009) I separated the left and right-side images for each of the five capture periods. Although the camera trap grid was set up with two paired cameras per station, in many cases only one flank of the hyaena was photographed clearly. I therefore only used the side of brown hyaena with the most clear images for analysis, to avoid artificially elevating the population estimates by counting the same animal twice at a station (Singh *et al.* 2010; Kent and Hill 2013; Williams 2017).



Figure 4.4. Simultaneous left and right-side images of a brown hyaena taken with camera traps on Mogale's Gate. Some key features used to identify individuals are marked in red.

A brown hyaena detection history at each camera location was created with value '1' indicating presence and '0' indicating absence (Otis *et al.* 1978). A sampling occasion was defined as a 24-h period running from 18:00 to 18:00 to avoid the 'midnight problem' associated with nocturnal species that are active through the night, especially around midnight (Foster and Harmsen 2012). In other words, if an individual is captured before midnight and then recaptured again shortly after, it would result in two

separate occasions being recorded instead of only a single occasion (Jordan *et al.* 2011; Comley 2016). Through capture–recapture analysis an estimate of population size was generated (Karanth and Nichols 1998; Rowcliffe and Carbone 2008; Chapman and Balme 2010).

The program CAPTURE (Rexstad and Burnham 1991) was used to test for demographic closure and to select a model appropriate for the individual capture probability. In CAPTURE a series of between-model and goodness-of-fit hypothesis tests are performed to determine the various models which best suit the observed capture histories (Otis *et al.* 1978; White *et al.* 1982). Each model assumes different sources of variation in capture probability due to potential behavioural responses to camera trapping (e.g., trap avoidance), time-specific variation (e.g., weekly weather changes), and heterogeneity among individual animals (e.g., trap access or territorial status) (Karanth *et al.* 2011). Suitable models as per the CAPTURE analysis were subsequently used for capture-recapture analysis using the program DENSITY 5.0 (Efford 2012).

There are two approaches to spatial capture - recapture analysis: Bayesian methods and Maximum Likelihood models. For the purposes of this study, I used the Maximum Likelihood model due to it having more flexibility about model selection and averaging (Kalle *et al.* 2011; Comley 2016). The DENSITY program uses methods for estimating the density of animal populations using different traps, (referred to in the program as detectors), such as passive hair sampling, live - capture traps, sticky traps or camera traps (Efford *et al.* 2004).

Two types of input files were prepared in accordance with the stipulated format required by the DENSITY program. The first file specifies the trap number and location, and the second file the individual brown hyaena capture events. These input files were prepared for each of the five 90-day capture periods (12 weeks), which were analysed independently to constitute a closed population survey and to minimise demographic changes within the population (Silver *et al.* 2004; Ancrenaz *et al.* 2012; Tobler and Powell 2013).

As Mogale's Gate is not geographically closed and brown hyaenas could move in and out of the reserve, a buffer strip is required in the non-spatial capture - recapture analyses. Using data from the three brown hyaenas collared during my study (Chapter 5) I calculated the MaxDM and used this as the buffer strip for each model (Soisalo and Cavalcanti 2006). The detector type (or trapping process) was set as 'Proximity detector', as per the recommendations of Efford *et al.* (2009), because camera traps capture or detect presence of animals passively without limiting their movements.

In accordance with the results produced by the program CAPTURE the following two models were run to account for various sources of capture probability: Model M_0 assumes that the capture probability is the same for all brown hyaenas and is not influenced by behavioural response, time or individual heterogeneity (Otis *et al.* 1978; Karanth *et al.* 2011). Model M_h jackknife assumes that the capture probability will vary amongst individual animals. This robust estimator uses the linear combinations of capture frequencies to estimate population size (Grimm *et al.* 2014) and produces acceptable estimates if many individuals are captured many times (Chao 1987).

RESULTS

A total effort of 2250 trap nights produced 173531 images, of which 2220 images were of brown hyaenas. Of these 2220 images, 371 were usable, independent images (i.e. images separated by 30 min intervals or clearly different individuals from previous image) (Table 4.1). The remaining unusable images which were of poor quality were not included in the density estimation analysis. Of the 371 brown hyaena images, 221 were of the left side of the hyaenas and, these images were used for analysis purposes.

Table 4.1. Summary of the camera trap survey conducted on Mogale's Gate between 9 June2015 and 13 September 2016.

Capture period	Actual number of trap days	Number of brown hyaena images	Usable brown hyaena images	Number of independent, left side images	Number of brown hyaena identified
Capture period 1 (9 June-6 Sept 2015)	295	556	95	66	4
Capture period 2 (16 Sept-14 Dec 2015)	406	496	62	34	4
Capture period 3 (16 Dec-14 Mar 2016)	439	132	50	27	6
Capture period 4 (14 Mar-11 June 2016)	442	455	89	52	4
Capture period 5 (16 June-13 Sept 2016)	449	581	75	42	4

CAPTURE program results showed that demographic closure for each of the five capture periods was inconclusive and indicated insufficient data for the test. Despite the possible lack of closure, closed population models were used to determine population density, as closed models are more robust than open models (Karanth and Nichols 2002). Results obtained using CAPTURE for the five capture periods showed that in all cases the most appropriate models were either the heterogeneity model (M_h), which scored a criterion of 1.0, and the null model (M_o) (criterion score of 0.96). These models were therefore used for the capture data inputted into DENSITY 5.0, to estimate the abundance of brown hyaenas on Mogale's Gate.

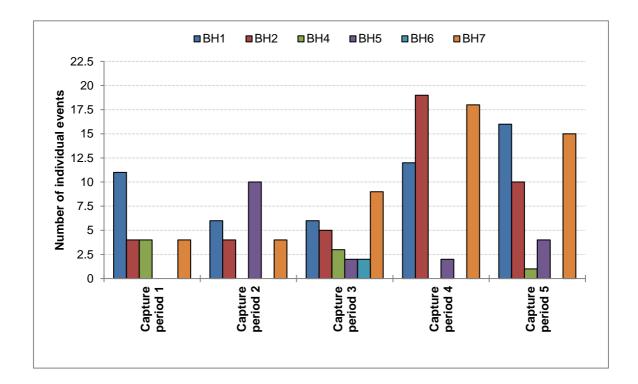


Figure 4.5. Occurrence of individually recognised brown hyaena in each capture period, based on left-side images. BH1 is the collared adult female, BH2 the collared adult male. BH3 (collared sub-adult female) was not positively identified in camera trap images and therefore not included.

For capture periods one, two and four the estimated population size using the M_0 model was four individuals. Results for the M_0 model for capture period three estimated six individuals, whilst capture period five had an estimate of five individuals. Capture probabilities for all five capture periods was above 0.9. The results produced with the M_h jackknife model for each capture period were very similar to that of the M_0 model. The M_h model estimated a population size of between four and six individuals for each capture period (Table 4.2). The mean abundance estimates calculated across the five capture periods suggest a population estimate of 4.6 ± 0.14 individuals, with a capture probability of 0.077 per sampling occasion. Based on the size of Mogale's gate (30.6 km²), density estimates of between 13 and 20 brown hyaenas / 100 km² were generated (Table 4.2).

Table 4.2. Abundance and density estimates for left-sided images from five capture periods, using DENSITY 5.0. Range (95% confidence interval) expressed in brackets. Brown hyaena density is expressed as the number of individuals per 100 km².

	Mo			M _h		
Capture period	Abundance estimates (95% CI)	Capture probability per occasion	Density estimate	Abundance estimates (95% CI)	Capture probability per occasion	Density estimate
Capture period 1	4.0 ± 0.2 (4.0 - 4.6)	0.056	13	4.0 ± 0.02 (4.0 - 4.9)	0.056	13
Capture period 2	4.0 ± 0.1 (4.0 - 4.5)	0.066	13	4.0 ± 0.01 (4.0 - 4.5)	0.066	13
Capture period 3	6.0 ± 0.3 (6.0 - 7.6)	0.046	20	6.0 ± 0.02 (6.0 - 7.0)	0.046	20
Capture period 4	4.0 ± 0.01 (4.0 - 4.2)	0.135	13	4.0 ± 0.01 (4.0 - 7.6)	0.135	13
Capture period 5	5.0 ± 0.1 (5.0 - 5.4)	0.082	16	5.0 ± 0.0 (5.0 - 9.1)	0.082	16

DISCUSSION

Camera traps have proven to be efficient tools when investigating ecological systems and making decisions regarding conservation management (Nichols *et al.* 2011). The use of capture-recapture analyses using camera trap images has become increasingly popular as a method in carnivore monitoring (Balme *et al.* 2009; Williams 2017).

At the risk of violating any of the closed population assumptions in free ranging populations, various methods have produced broad density estimates (Karanth *et al.* 2010, Grant 2012). All these methods have their own advantages and drawbacks, and it is realised that collecting perfect data for elusive, enigmatic carnivore species, is often impractical (Efford *et al.* 2009; Welch 2014). Closure was tested for in this study and the results were inconclusive due to insufficient data. When studying natural populations, the assumption of closure, required by capture-recapture methods, is often violated (White *et al.* 1982; Soisalo and Cavalcanti 2006). Indeed, closure was probably violated in my study as hyaenas can move beyond the boundaries of Mogale's Gate.

In comparison to other studies, the density estimates obtained from Mogale's Gate of 13 – 20 individuals per 100 km² falls within the higher densities recorded for brown hyaena on Kwandwe Private Game Reserve (Table 4.3). Variation in the estimated density from different study areas could be related to factors including land use type, vegetation, food availability, water availability, and the presence or absence of other large predators (Balme *et al.* 2007; Welch 2014; Williams 2017). Unlike other large carnivores such as tiger and leopard who have high occupancy in areas with high prey availability, the brown hyaena are not strongly influenced by the availability of prey but rather the availability of carrion in the environment (Thorn *et al.* 2009; Steinmetz *et al.* 2013; Williams 2017). Areas with the highest recorded brown hyaena densities have high densities of apex predators (Yarnell *et al.* 2014; Welch 2014), offering sufficient scavenging opportunities (Williams 2017).

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Table 4.3. Density estimates of brown hyaena across Southern Africa.

Study	Method used	Location	Density estimate /100 km²
a) Spoor sampling; b) SE	CR analysis using SPAC	ECAP; c) Extrapolated from home	range sizes using GPS
collar data; d) Mean terri	tory and home range dat	a extrapolation; e) CAPTURE anal	lysis; f) SECR analysis

using DENSITY; g) Data extrapolated from abundance estimates and GPS collar data; h) Identified from camera trap data; i) Questionnaires; j) Call-ups; k) SECR analysis using R language.

Müller (2020)	b, f	Shamwari Game Reserve, Eastern Cape, South Africa	7 – 10
Welch and Parker (2016)	e, f	Kwandwe Private Game Reserve, Eastern Cape, South Africa	14 – 20
Comley (2016)	k	Mountain Zebra National Park, Eastern Cape, South Africa	6 - 10'
Yarnell <i>et al.</i> (2013)	h	Pilanesberg National Park, North West province, South Africa	6*
Yarnell <i>et al.</i> (2013)	h	Mankwe Wildlife Reserve, North West province, South Africa	2 - 4*
Winterbach <i>et al.</i> (2017)	a, h, i	Central Kalahari Game Reserve, Botswana	2.94
Williams (2017)	b	Soutpansberg mountain range, Limpopo province, South Africa	3.63
Mudongo and Dipotso (2010)	a, j	Wildlife Management Areas, Botswana	2.36 - 3.9
Wiesel (2006)	g	Baker's Bay, Namibia	2.4 - 2.9
Kent and Hill (2013)	b	Ghanzi, Botswana	2.3 - 2.88
Thorn <i>et al</i> . (2009)	е	Pilanesberg National Park, North West province, South Africa	2.8
Boast and Houser (2012)	а	Ghanzi, Botswana	2.18
Maude (2005)	с	Makgadikgadi National Park, Botswana	<2
Mills (1990)	d	Kgalagadi Transfrontier Park, South Africa and Botswana	1.8
Wiesel (2006)	g	van Reenen Bay, Namibia	1 - 1.6
Funston <i>et al</i> . (2010)	а	Kgalagadi Transfrontier Park, South Africa and Botswana	1.13 - 2.17

*Data extrapolated to reflect a density of 100 km² from original estimate based on 1 km²

Possible reasons for the high density in the Kwandwe Private Game Reserve include the high prey and predator numbers on the reserve for tourism purposes, which creates enhanced scavenging opportunities for the brown hyaenas (Welch and Parker 2016). Unlike the Kwandwe Private Game Reserve and Mountain Zebra National Park where the boundary fences are impenetrable, the brown hyaena on the Shamwari Game Reserve can make use of warthog holes burrowed under the electrified boundary fence (Müller 2020), and the high densities of brown hyaenas on the property are a result of high scavenging opportunities available. The fences of Mogale's Gate do not restrict the movement of brown hyaena in or out of the reserve. Although two of the three-collared brown hyaena in this study did not move beyond the boundaries of the reserve during the study period, there are others which maybe transient.

Due to the removal of free ranging large predators (other than leopard) from Mogale's Gate and the greater Magaliesberg region, brown hyaena are taking advantage of regular carcasses available at the vulture restaurant on Mogale's Gate. The Mogale's Gate vulture restaurant is one of the three original, official vulture restaurants established to provide supplementary food for the Cape vultures breeding in the Magaliesberg mountains and has been active for more than 30 years (⁷K. Wolter pers. comm.). The long-standing nature of this site has most likely contributed to the persistence of the brown hyaena population on Mogale's Gate and surrounding regions. Due to the amount of food available at the vulture restaurant, one may expect hyaena density to be higher on Mogale's Gate compared to other sites with apex predators. Benefits from the vulture restaurant are perhaps manifested in other ways, such as through increased survival and increased reproduction. The decrease in foraging times due to the predictable nature of the food supply, consequently improves these fitness components and physiological aspects such as body mass and condition (Oro *et al.* 2013). The adult female (BH1) was in very good condition when captured and weighed ca. 7 kg more than the largest recorded female brown hyaena in Gauteng

⁷Kerri Wolter - CEO and founder of VulPro (Vulture Programme for the Conservation of Vulture Species in southern Africa)

and Limpopo (Skinner and Ilani 1979). Moreover, the adult male (BH2) although often found in poor condition, was estimated to be over 10 years of age, therefore suggesting improved survival prospects as a result of the vulture restaurant. Along with a dependable food source, the protection offered by protected areas such as Mogale's Gate in the Magaliesberg region can collectively benefit the conservation of the brown hyaena.

Numbers of individuals identified from the camera trap images, can be considered to be an indication of the minimum number of brown hyaena on Mogale's Gate. With many of the brown hyaena images not being clear enough for identification, the potential for a higher number of brown hyaenas on Mogale's Gate is possible. In order to continue monitoring future changes in population numbers, increased precision is needed to identifying brown hyaenas on camera trap images. One suggestion made by Comley (2016) is the use of scent lures placed infront of the cameras which increases that chances that the animals will stop in front of the camera, so better images can be taken.

Based on the ecological theory that abundant food sources facilitate higher population densities (Welch and Parker 2016; Müller 2020) it is not surprising that, given the regular and predictable carrion available on Mogale's Gate that the brown hyaena population density is higher than in areas where availability of carrion is unpredictable.

One of the objectives of this study was to produce a population estimate for the brown hyaena on Mogale's Gate, in the presence of a reliable anthropogenic food resource. As Mogale's Gate is small (<100 km²) presenting results as number of individuals per square kilometre (0.13 - 0.2 individuals) is a more accurate representation for the density estimates (Rinehart *et al.* 2014). Therefore, Mogale's Gate has a minimum population estimate of 4 to 6 brown hyaena. However, for comparative reasons to other density studies the results were reported as 13 to 20 individuals per 100 km². Extrapolating density results from this small trapping area to a density per 100 km², as is commonly done in other studies, may result in inaccurate, inflated results (Welch and Parker 2016), assuming that the landscape features, prey abundance and space use of the hyaena population are uniform (Rinehart *et al.* 2014; Welch and Parker

2016). Extrapolating density estimates to 100 km² is usually done when the effective trapping areas are larger than 100 km², and density is more likely to be more uniform across the landscape (Rinehart *et al.* 2014). Smaller areas may include disproportionately high levels of good-quality habitat, and increased prey abundance, and are thus able to support higher densities (Rinehart *et al.* 2014). Mogale's Gate is surrounded by a mosaic of different land use types - agricultural lands, conservation areas, and housing developments with increased infrastructure development. These areas vary in their availability of food and protection offered to the brown hyaenas, so numbers may be lower than that of Mogale's Gate, which provides a predictable source of carrion in quality habitat.

However, brown hyaenas are resilient and survive in many unprotected, and human altered areas (Richmond-Coggan 2014) across southern Africa. In the Magaliesberg, there are currently three other vulture restaurants along with Mogale's Gate that are accessible to terrestrial scavengers (Nooitgedacht -25.85054S; 27.53287E, Nyoka Ridge -25.80797S; 27.71541E, and Rhino & Lion Park -25.96280S; 27.77776E, 17 km, 19 km, and 14 km from Mogale's Gate, respectively) (⁸K. Wolter pers. comm.) which could be contributing significantly to the persistence of the brown hyaena population in the region. However, threats such as vehicle collisions, persecution by farmers and snaring associated with them traversing areas surrounding Mogale's Gate needs be investigated and mitigated, to gain a better understanding of the status of the brown hyaena population at a larger scale.

⁸Kerri Wolter - CEO and founder of VulPro (Vulture Programme for the Conservation of Vulture Species in southern Africa)

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Chapter 5

Home range and habitat utilisation of brown hyaena on Mogale's Gate



" They are intelligent, powerful, and yes, even beautiful"

- G. Mills

INTRODUCTION

The home range of an animal is defined as the area traversed by an individual during its day-to-day activities to meet necessary resource requirements, such as sustenance, mating and caring of young (Burt 1943). The larger the animal the larger the home range will need to be to meet the metabolic needs of the animal (Gittleman and Harvey 1982). Animals demonstrate a familiarity with areas in which they occur, knowing locations of regular food resources, den sites and potential mates (Powell 2012) and will therefore utilise some areas more than others (Spencer 2012). In terms of understanding and conserving a species, investigating movements and spatial utilisation in relation to resource availability gives us insight into a species' selection for or avoidance of food resources, habitat, topography, and potential interactions with other species and conspecifics (Fieberg and Kochanny 2005).

Information on factors such as prey distribution, abundance and human influence can provide an indication of the importance and contribution of resources towards overall behaviour patterns (Henschel 1986; Grant 2012). For example, the quantity of resources (food, water, shelter) in different land use and habitat types influences the territorial behaviour and spatial organisation of scavengers, such as black-backed jackal (Canis mesomelas) (James et al. 2016). In both Namibia and South Africa, significantly more black-backed jackals are recorded in areas where there are plentiful, and clustered carrion available (Hiscocks and Perrin 1988; Yarnell et al. 2014; James et al. 2016). From November to Januaruy each year the number of brown hyaena occurrences increases on the Namibian coastline when the female Cape fur seals are pupping (Wiesel 2006). The mortality rate of new born pups is highest during this period, when they are left alone and are relatively inactive (De Villiers & Roux 1992), this provides the brown hyaenas with large amounts of fresh carcasses washed up along the beaches (Skinner et al. 1995). From January onwards, seal pups are older and more mobile, spending more time at sea. The resultant reduction in seal availability to brown hyaenas forces them to search for food further inland, moving greater distances and bigger home ranges (Wiesel 2006).

The results of collected movement data and other aspects of an individual's behaviour provide information as to how an animal uses its home range in making decisions that affect its fitness and survival (Powell 2012). Once ranging areas of individuals have been determined, software generated polygons can be overlaid onto vegetation and/or habitat maps and finer scale habitat utilisation information can be investigated. For example, in Makgadikgadi National Park, Botswana, results from GPS collars on brown hyaenas, indicated that the home range sizes of these animals were influenced by resource dispersion hypothesis (Maude 2005). Where, the brown hyaena's home range size is largely influenced by how food is distributed, while aspects of social organisation, such as clan (family group) size are determined by the quantity and amount of food resources available (Mills and Mills 1982). A plentiful food supply potentially reduces the mean distance between food 'patches', resulting in an increased density of brown hyaenas in that area and a decrease in home range sizes of individuals (Maude 2005). In Botswana, Houser et al. (2008) used GPS collars to investigate the use of farms and conservation land by free-ranging cheetah. Stratford and Stratford (2011) and Welch (2014) used GPS collars to determine fine-scale movements and space use by spotted hyaena (Crocuta crocuta) in Namibia, and the home range and space use of individual brown hyaenas in Kwandwe Private Game Reserve, South Africa, respectively.

The development of radio telemetry has enhanced the study of animal movements especially those of elusive and/or nocturnal mammals (Powell 2012; Kie *et al.* 2010), monitoring of which was often limited to opportunistic observations or sightings at specific locations (Karanth *et al.* 2010). A GPS collar fitted to an animal has become one of the most accurate methods to determine movement patterns and home range size (Pebsworth *et al.* 2012; Williams 2017). Although GPS collars fitted on animals can provide information for 24-hs per day if required (Kie *et al.* 2010), caution should however be used when interpreting data from small sample sizes, i.e., only a few collared animals, as these may not adequately represent an entire population's behaviour (McCarthy *et al.* 2005). The simplest way to estimate home range size using GPS data is by creating a Minimum Convex Polygon (MCP) (Mohr 1947). Although a good method for comparative purposes with older studies MCPs tend to over-estimate home range sizes by including areas not frequented or by including features in the

landscape that an animal would not make use of, e.g., buildings or large water bodies (Kenward 2001). To overcome these concerns, methods such as Kernel Density Estimation methods (KDE) (Worton 1989) are recommended in conjunction with MCPs (Kie *et. al.* 2010). In contrast to the MCP, KDE methods do not rely on the outer most fixes, but instead produce a probability surface to determine the area's most likely to be frequented by an individual (Quinton 2016). The KDE considers areas of high and low utilisation in the construction of convex hulls (Getz *et al.* 2007; Williams 2017) and combined with the element of time, adds a temporal aspect to the calculations of the greatest distance an animal could have travelled during the study period. (Rodgers and Kie 2011).

Various studies on the home ranges of brown hyaena have taken place (Maude 2005; Welch 2014; Williams 2017; Müller 2020) and have found considerable variation in the home range sizes of individual brown hyaenas (Richmond-Coggan 2014). As with other species, variation in home range size is influenced by food dispersion, sex of the individual, seasonality, and levels of human persecution (Mills 1990; Owens and Owens 1996; Williams 2017). Brown hyaenas utilise a wide variety of habitat types including desert, semi-desert, open scrubland, grasslands, and open woodland savanna (Mills and Hofer 1998; Williams 2017). Their home ranges typically vary in size from 100 km² to 500 km² (Mills 1983; Owens and Owens 1996; Skinner *et al.* 1995; Maude 2005; Thorn *et al.* 2009; Williams 2017), although extremes of ~43 km² and 1250 km² have been reported in the Kwandwe Private Game Reserve, South Africa (Welch *et al.* 2016) and along the Namibian coastline (Wiesel 2006).

Protected areas potentially offer more frequent sources of carrion than unprotected areas, as they tend to be stocked with higher numbers of game, and may host large predators such as leopards (*Panthera pardus*), lions (*Panthera leo*), and cheetah (*Acinonyx jubatus*) from which brown hyaena scavenge (Swanepoel 2008; Richmond-Coggan 2014; Williams 2017). However, across their distribution range, brown hyaenas are sufficiently adaptable to survive outside of formal, protected areas (Maude 2010; Thorn *et al.* 2011). As South Africa has many small and fragmented protected areas (Richmond-Coggan 2014), the unprotected areas in between become more important for the long-term conservation of brown hyaena populations. Despite

their fragmented nature these protected areas maintain genetic connectivity between populations, not only within South Africa, but also with Botswana, Zimbabwe and Namibia (Winterbach *et al.* 2017). Although a large proportion of brown hyaenas in southern Africa occur in unprotected areas (Winterbach *et al.* 2017), protected areas provide greater protection against human-predator conflict and provide more feeding opportunities (Williams 2017).

Mogale's Gate is in an area where leopards are the only remaining large, free-roaming predator, with brown hyaena, black-backed jackal and caracal being considered meso-predators (Carruthers 2007). The long-standing vulture restaurant, which is regularly supplied with carcasses, provides a plentiful, regular and clumped food resource. Based on resource dispersion hypothesis and optimal foraging concepts, which states that the distribution and abundance of food resources can influence the ranging behaviour of a species, I predict that brown hyaenas on Mogale's Gate would have smaller home ranges than reported in other protected areas.

The aim of this chapter was to investigate the spatial and habitat utilisation of brown hyaenas on Mogale's Gate.

OBJECTIVES

The objectives of this chapter were to:

- Determine the home range size and distribution of brown hyaena in the presence of a regular, clumped food source (vulture restaurant)
- Determine the utilisation of available habitat and land use types by collared brown hyaena

Research questions

- What are the seasonal home range sizes of brown hyaenas on Mogale's Gate?
- What are the movement patterns of the collared brown hyaenas?

- Was there seasonal variation in the utilisation of the vulture restaurant?
- Is there proportional utilisation of all the habitat types within the home ranges of the collared brown hyaenas?

METHODS

Capture and immobilisation

Suitable sites for placing cage traps were identified using signs of frequent brown hyaena activity (Chapter 4) using spoor, paste markings and scat. Drop door, box traps (dimensions: 2430 x 850 x 750 mm; mesh size: 50 x 25mm) were used to catch the brown hyaenas and were hidden in a clump of bushes to make them less obvious (Figure 5.1). When trapped, brown hyaena tend to scratch at the floor of cage traps and bite the cage in their attempts to escape, which can cause injuries to feet and teeth (Swanepoel 2011). Consequently, the base of the cage was covered with a thick layer of soil; the interior of the cage was also regularly inspected for sharp edges or breaks in the mesh.

Before attempting brown hyaena capture on Mogale's Gate, the animals were habituated to the presence of the cage traps. During this cage habituation phase, nontriggered cage traps were baited using piglet carcasses from the vulture restaurant (Figure 5.1). A camera trap (Stealthcam STC-Z31RTL 2012, GSM outdoors, Texas, USA) was placed near the entrance of the trap to record the visitation frequency and the behaviour of the hyaenas at and around the open, unset cage trap. Initially the piglet carcasses were placed outside the entrance of the cage trap and when camera trap images showed that brown hyaenas were removing the carcasses, the piglet carcasses were progressively moved deeper into the cage. Once the camera trap images indicated that one or more hyaenas were entering the cage traps to retrieve the bait, the cage trap was baited and set, by attaching the release pin wire of the door to the bait at the back of the cage. Cages were set each evening at dusk and checked each morning before sunrise. If a hyaena had been caught, the cage was covered with a tarpaulin to keep the cage dark and cool as well as to reduce stress on the hyaena in the cage. A pole syringe was used by the veterinarian to anaesthetise the hyaena (Figure 5.1). A mixture of 40 mg Zoletil (Zolazepam 500 mg, Virbac (Pty) Ltd., RSA) and 4 mg Medetomidine, (Zalopine 20mg/ml, Wildlife Pharmaceuticals, Karino, RSA), was used to anaesthetise the hyaenas. One of the captured hyaenas (adult female BH1) required one additional dose of 2 mg Medetomidine and 50 mg Ketamine (Kyron laboratories (Pty) Ltd., RSA) possibly due to her large mass (52 kg). One brown hyaena (adult male BH2) was caught by free darting from a vehicle. A CO₂ dart pistol (DAN-INJECT Aps, Denmark) with a dart containing 50 mg Zoletil and 3 mg Medetomidine was used. All details of the processing from the time the hyaenas were darted until they woke up was recorded using a capture details form (Appendix 6).



Figure 5.4. Baited and set cage trap (left); release pin holding up the door (centre); and immobilisation of a brown hyaena in cage trap covered with a tarpaulin (right) on Mogale's Gate.

Once immobilised, the general health of the hyaenas were assessed by the veterinarian, where after they were weighed using a hanging scale and canvas sling, sexed, and aged using teeth eruption patterns and wear. Morphometric measurements as per Skinner and Chimimba (2005) were made and included: total body length, tail length, head length and width, shoulder height, length of the ears, feet length and width. Blood, hair, tissue and parasite samples were also collected for future analyses. To assist in future identification, each immobilised brown hyaena was micro-chipped (Identipet, Identipet (Pty) Ltd., RSA) and ear-notched. The microchip was inserted subcutaneously in the right tail base fossa to prevent migration of the chip in the body and to allow for ease of scanning (Figure 5.2).



Figure 5.5. Collecting morphological data from the brown hyaenas. From top left to right: Inserting the microchip; taking body measurements; drawing blood samples; measuring canine teeth; weighing the brown hyaena; and fitting of the GPS collar.

Ear notches served for both identification and tissue sampling. Ear notching was conducted by the veterinarian who first sterilised the area with a Chlorhexidine - alcohol solution. Using a sterile scalpel blade and mosquito haemostat a piece of tissue was removed from the ear. The ear was then washed and a topical antibiotic spray (Engemycin spray, Intervet South Africa (Pty) Ltd., RSA) was administered to prevent infection (Figure 5.3).



Figure 5.6. Ear notches of the three brown hyaenas collared on Mogale's Gate. From left to right: adult female (BH1), adult male (BH2) (natural tear used for identification, no notching required), and sub-adult female (BH3).

Whilst immobilised each hyaena was fitted with a satellite collar (Africa Wildlife Tracking, Pretoria, RSA). Each collar weighed 700 g, which was within the acceptable ethical limits of less than 2% of the mean body mass of a brown hyaena (40.9 kg, Skinner and Chimimba 2005; Sikes *et al.* 2011; Welch 2014). All three brown hyaenas were anaesthetised for less than an hour and the effects of the Zoletil - Medetomidine were reversed with 20 mg Atipamezole (Antisedan 5mg/ml, Orion Pharma, Finland).

Once the antagonist was administered the hyaenas were left to recover in a shaded area. Each animal was observed from a distance until ambulatory. All procedures for, and during, capture was carried out in accordance with the protocol as determined by the veterinarian.

As brown hyaenas are predominantly nocturnal (Mills 1978) the collars of two of the captured hyaena (adult female BH1 and sub-adult female BH3) were set to record a GPS location every hour between 16:00 and 07:00, and once during the day at 12:00, allowing for a maximum of 18 months battery life of the collar. The adult male (BH2) was known to be active during both the day and night and therefore the collar was set to record the GPS location every three hours (starting at 12:00 on the day of capture).

Data from the collars fitted to each brown hyaena could be viewed and downloaded by accessing Africa Wildlife Tracking's website (<u>www.awt.co.za</u>). As part of the

information generated by the collar for each GPS 'fix' there is a measure recorded of the maximum horizontal accuracy of the GPS location in the horizontal plane based on the geometric location of the satellites it used to calculate the location (HDOP) (⁹S. Haupt pers. comm.). This measure is used as an indicator of the accuracy of each GPS point recorded, with lower numbers (<20) indicating a higher accuracy than higher numbers (>20). All HDOP readings ≥20 were thus removed from the data set as these have a high probability of being inaccurate (Dussault *et al.* 2001). Furthermore, all duplicate entries having the same date and time of readings were removed. Data were sorted for seasonal analyses (dry season: May to October and wet season: November to April) in Microsoft Excel (2007) and imported into QGIS V2.18 and program R 3.5.0 for further analyses.

Range estimation

The home range sizes of the three collared brown hyaena were determined using the Minimum Convex Polygon (MCP) method (Mohr 1947) and the Kernel Density Estimate Method (KDE) (Worton 1989). The core area (50%) and home range (95%) probabilities were chosen for both the MCP and KDE methods, as they are generally considered the most robust estimators of the core and total range areas which an animal utilises (Mizutani and Jewell 1998; Broomhall *et al.* 2003).

I used QGIS V2.18 in combination with the *adehabitatHR* package (version 0.4.19) (Calenge 2006) in program R 3.5.0 (R Core Team 2018) to construct the 95% (home range) and 50% (core area) MCPs and KDEs for each of the collared hyaenas. The function 'kernelUD' of the package *adehabitatHR* uses a default bivariate normal kernel placed over each relocation, and values of these functions are averaged together (Calenge 2019). The smoothing parameter *h* controls the "width" of the kernel functions placed over each point, and for purposes of this study I used the default *h*-*ref* or reference bandwidth option in 'kernelUD'.

⁹Sophie Haupt, African Wildlife Tracking, Pretoria, South Africa.

Autocorrelation (statistically dependent data) occurs when the assumption of independence between successive observations is violated, and the data produces a biased home range estimate (Swihart and Slade 1985). As animal movements are frequently non-random, large GPS data sets are normally autocorrelated (De Solla *et al.* 1999; Welch 2014). To avoid autocorrelation among sequential GPS data points from collars many studies use only one fix per day (Broomhall *et al.* 2003; Welch 2014; Müller 2020). However, this topic has long been debated in the literature and the loss of critical biological information and fine-scale details of movement through the removal of autocorrelated data is fraught with contention (De Solla *et al.* 1999; Kie *et al.* 2010; Williams 2017). Moreover, if the time between consecutive locations remains relatively constant, autocorrelation should not decrease the strength of home range estimates (Rooney *et al.* 1998; De Solla *et al.* 1999).

Due to the large variation in the number of GPS fixes between the three collared hyaena in this study (ranging from 248 - 2419 GPS fixes), I chose to compare home range size based on three sampling scenarios. Firstly, for comparative purposes with other brown hyaena studies, one fix per day, taken at 21:00, was used (Boydston *et al.* 2003; Welch 2014; Müller 2020); secondly, random fixes throughout the 24-h period up to a maximum not exceeding the number of 21:00 fixes used for each individual; and thirdly, all GPS fixes were used to calculate range estimates for each individual.

To estimate home range adequate sample sizes are required, typically a minimum of 30 but preferably >50 locations per individual (Seaman *et al.* 1999; Laver 2005). For the adult male (BH2) and the sub-adult female (BH3) using only one 21:00 GPS fix per day or the equivalent number of random fixes resulted in sample sizes ranging between 14 and 45 GPS points, which are below the recommended minimum number of points. Although, for comparative purposes I ran the same three sampling scenarios for all three of the brown hyaenas, it is acknowledged that the sample sizes using the 21:00 and random fixes, for the adult male (BH2) and the sub-adult female (BH3) are potentially too small to give accurate home range estimates.

Movement patterns

To determine the distances travelled by the three collared brown hyaenas, I calculated the straight-line distances moved between successive GPS positions (Wiesel 2006), using an excel plug-in formula (Müller 2020).

Distance between two points = Acos(Cos(Radians(90-Lat1))*Cos(Radians(90-Lat2))+Sin(Radians(90-Lat1))*Sin(Radians(90-Lat2))*Cos(Radians(Long1-Long2)))*6371⁽¹⁾

(1) Where 6371 is the earth's radius in kilometres

From which, the mean, minimum, maximum and total distances moved by each hyaena were calculated using Microsoft Excel (2007). I used a t-test (independent samples) to compare the seasonal distances moved by each hyaena. A one-sample t-test was used to compare the distances each hyaena moved between time intervals. These analyses were done using Real Statistics Resource Pack software (Zaiontz 2015).

Seasonal movement data for the adult female (BH1) and sub-adult female (BH3) were based on 1-h GPS fixes between 18:00 and 06:00 and were used for comparison with each other as well as to determine when these two individuals were most active. The adult male (BH2) movements were based on 3-h GPS fixes taken over a 24-h period, 15:00; 18:00; 21:00; 00:00; 03:00; 06:00; 09:00; 12:00.

As the distances moved between each GPS fix are based on a straight-line calculation the results thereof represent the minimum distance the animal moved between GPS fixes. Furthermore, considering that the adult male's (BH3) movements are based on 3-h GPS fixes, the distances recorded for this individual are potentially highly underrepresented.

For a 39-day period between June 2016 and October 2016 both the adult female (BH1) and the adult male (BH2) were collared and therefore their movement data was compared in terms of the total and mean distances moved. Only days on which both collars recorded GPS fixes was used in the calculations. In addition to the 3-h night

time intervals mentioned above, the day time intervals (06:00; 09:00; 12:00; 15:00) were included for the adult male (BH2) as he was known to be active in the day.

Habitat utilisation

A vegetation map of Mogale's Gate (Tuckett 2013) was used to determine habitat utilisation by the three collared brown hyaena. Nine broad plant communities, including two wetlands, two woodlands and five grassland plant communities are represented on Mogale's Gate (Tuckett 2013). For the purposes of my study, these nine broad communities were grouped into three broad habitat types: grassland (2451.2 ha), wetland (42.9 ha) and woodland (569.7 ha).

For areas outside of Mogale's Gate, aerial maps, terrain feature tools and 'OpenStreetMaps' in QGIS V2.18 were used to divide the land use types into two broad categories: natural areas (tourism and/or conservation) and agricultural land (crop and livestock production). Areas covered by infrastructure (e.g., factories), which a hyaena is not likely to access were excluded from the range area. The Vector Intercept Tool in QGIS V2.18 was used to determine how many GPS fixes were found within each of the three broad habitat types on Mogale's Gate and the two land use types outside of Mogale's Gate.

The utilisation of each of the above habitats or land-use types in relation to their availability within the home ranges of each brown hyaena was determined using the method described by Neu *et al.* (1974). The Chi-square Goodness-of-Fit test was used to determine if there was a significant disproportionate utilisation of the available habitat or land use types in relation to the availability of each habitat or land-use type within each brown hyaena's range. Bonferroni confidence intervals were then generated to determine which habitat or land use types were utilised more or less than expected based on the habitat/land use type availability. To determine habitat utilisation by the adult female (BH1) and sub-adult female (BH3) during their nightly activities, their GPS points recorded between 18:00 and 6:00 were used. As the adult male (BH2) was active both during the day and night, habitat utilisation was determined using 24-h periods.

Vulture Restaurant utilisation

To determine the seasonal utilisation of food resources at the vulture restaurant of each collared brown hyaena, a 250 m buffer was created around the vulture restaurant using QGIS V2.18 Vector Tools. The Vector Intercept Tool was used to determine the number of GPS location fixes from each brown hyaena that fell within this 250 m buffer area.

The times at which brown hyaena were present at the vulture restaurant were determined. For comparative purposes, the times at which brown hyaena were recorded at the vulture restaurant were grouped into 3-h intervals to coincide with the GPS fixes of the adult male (BH2): 18:00-20:59; 21:00-23:59; 00:00-02:59; 03:00-05:59, in this way the frequency of occurrence of each brown hyaena at the vulture restaurant within each time interval could be determined. For the adult female (BH1) I used a Student's t-test to determine if there was a significant difference in her occurrence at the vulture restaurant between seasons. As the data for the adult male (BH2) was not normally distributed, a Mann-Whitney U Test was used to determine if there was a significant difference in his occurrence at the vulture restaurant between seasons.

RESULTS

Capture and immobilisation

During the study period three brown hyaenas were captured, two using cage traps and one by free darting. Initially one cage trap was baited for 45 nights (one week a month for nine months between January 2015 and September 2015) which resulted in the capture of one brown hyaena (adult female BH1). Subsequently, from November 2015 to December 2016 two cage traps were baited for 70 nights (140 trap nights), resulting in the capture of one brown hyaena (sub-adult female BH3). The adult male (BH2) never went near or entered a cage trap although one was set in close proximity to the vulture restaurant where he was frequently seen. He was ultimately free darted in May 2016 from a vehicle, in the vicinity of one of his dens. During the baiting of the cage traps, four individual brown hyaenas were identified from the camera trap images used to monitor the activity around the cage traps. Two of these brown hyaenas were caught and collared (BH1 and BH3). Morphological measurements and data collected whilst the brown hyaenas were immobilised are presented in Table 5.1.

	BH1	BH2	BH3	
Mass (kg)	52 48		35	
Age estimate (years)	6-7	6-7 >10		
Sex	Female	Male	2-3 Female	
Method of capture	Cage trap	Free dart	Cage trap	
Collaring date	28 October 2015	16 May 2016	16 December 2016	
Collar end date	13 October 2016	18 December 2016	15 March 2017	
Collar end date reason	Collar found in veld	Collar failure	Animal dead in snare	
Body measurements (cm)				
Total length	145	131	108	
Tail length	20	23	24	
Head length	32	34	27	
Head width	20	20	23	
Shoulder height	74	70	70	
Left ear length	15	16	15	
Right ear length	15	15	14	
Canine measurements (mr	n)			
Tooth: Length (diameter)				
Left upper	28 (13)	33 (20)	17 (12)	
Left lower	25 (13)	20 (20)*	18 (9)	
Right upper	27 (13)	21 (19)* 18 (11)		
Right lower	24 (12)	30 (20) 17 (11)		

Table 5.1. Morphological and capture details of three brown hyaenas on Mogale's Gate.

*broken canines

Movement data

The movement data collected varied considerably between the three study animals, with the GPS collar data extracted ranging from 49 to 351 days (Table 5.2). After cleaning up the data points, 4726 (90%) of BH1 points; 835 (80%) of BH2; and 248 (82%) of BH3 points were used for analyses (Table 5.2).

Table 5.2. The number of GPS points recorded, cleaned and used for analysis, for each of the collared brown hyaena.

Hyaena ID	Period of data collection	Number of days of data collected	Total GPS points	Number of duplicate & inaccurate points removed	Number of points analysed
BH1	28/10/2015 - 13/10/2016	351	5250	524	4726
BH2	01/05/2016 - 18/12/2016	231	1050	215	835
BH3	02/02/2017 - 15/03/2017	44	304	56	248

Range estimation

Home range estimates for the dry and wet seasons were calculated for the adult female (BH1) and the adult male (BH2), whilst for the sub-adult female (BH3) only a wet season estimate was calculated.

During this study, neither the adult female (BH1), nor adult male (BH2) were located outside of the Mogale's Gate boundary (Fig. 5.4 to Fig. 5.7). However, the sub-adult female (BH3) roamed over a much larger area than either the adult female (BH1) or the adult male (BH2), during the wet season. The 95% KDE home range of the sub-adult female (BH3) was more than fifteen times larger than either of the adult brown hyaenas (Table 5.3, Fig 5.8).

Both the home and core range of the adult females (BH1) doubled in size in the dry season when compared to the wet season. Whereas the adult male's (BH2) home and core range remained similar in both seasons (Table 5.3, Fig 5.4 to Fig 5.7).

Using the three sampling scenarios (fixes at 21h00, random fixes, and all fixes) produced different home range size estimates for two of the brown hyaenas. For the adult female (BH1) home and core range sizes were similar when the three sampling scenarios were used in the MCP and KDE calculations. However, the ranges of the adult male (BH2) and the sub-adult female (BH3) varied depending on the sampling approach (Table 5.3).

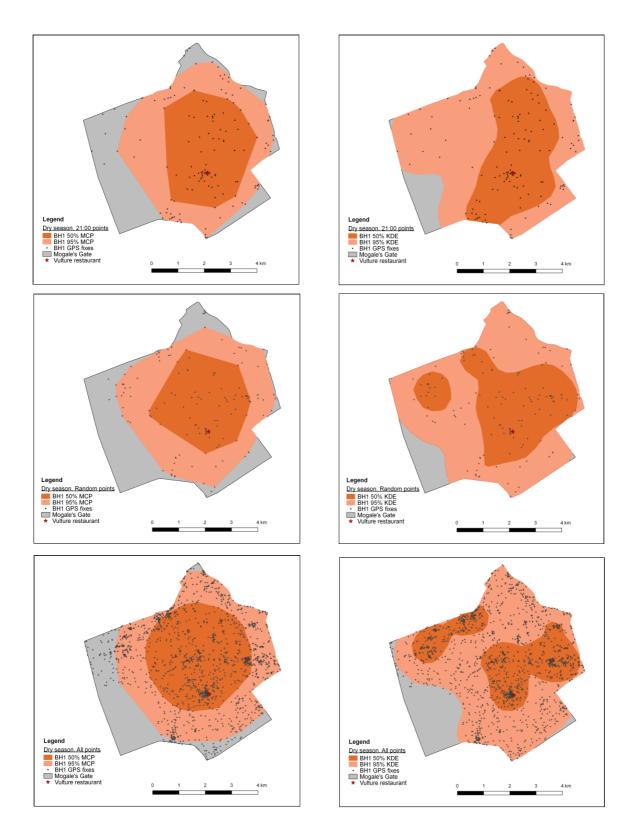


Figure 5.4. The dry season home range (95%) and core range (50%) estimates for the brown hyaena (BH1), calculated using minimum convex polygons (MCP) and kernel density estimates (KDE). Plots are based on GPS fixes at 21:00 (top panel), randomly selected GPS fixes (middle panel), and all GPS fixes (bottom panel).

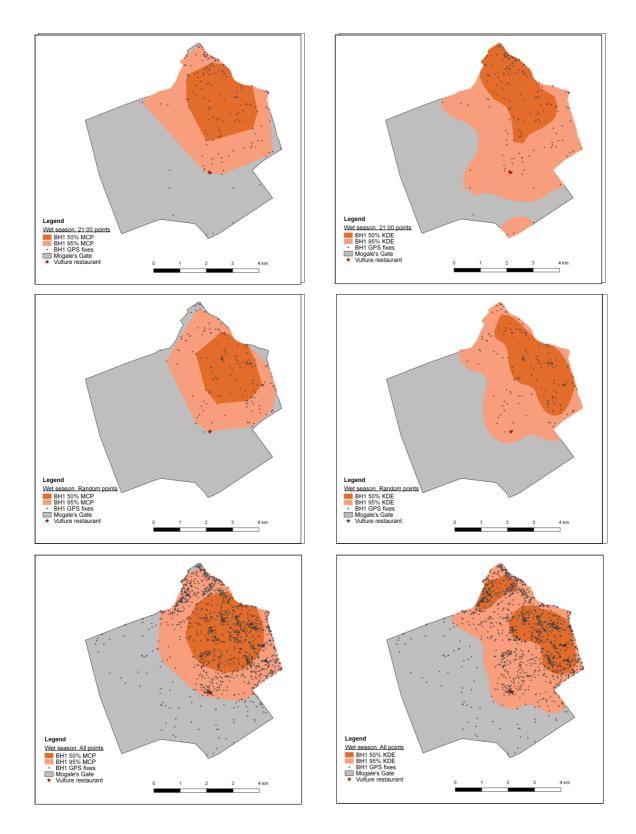


Figure 5.5. The wet season home range (95%) and core range (50%) estimates for brown hyaena BH1, calculated using minimum convex polygons (MCP) and kernel density estimate (KDE). Plots are based on GPS fixes at 21:00 (top panel), randomly selected GPS fixes (middle panel), and all GPS fixes (bottom panel).

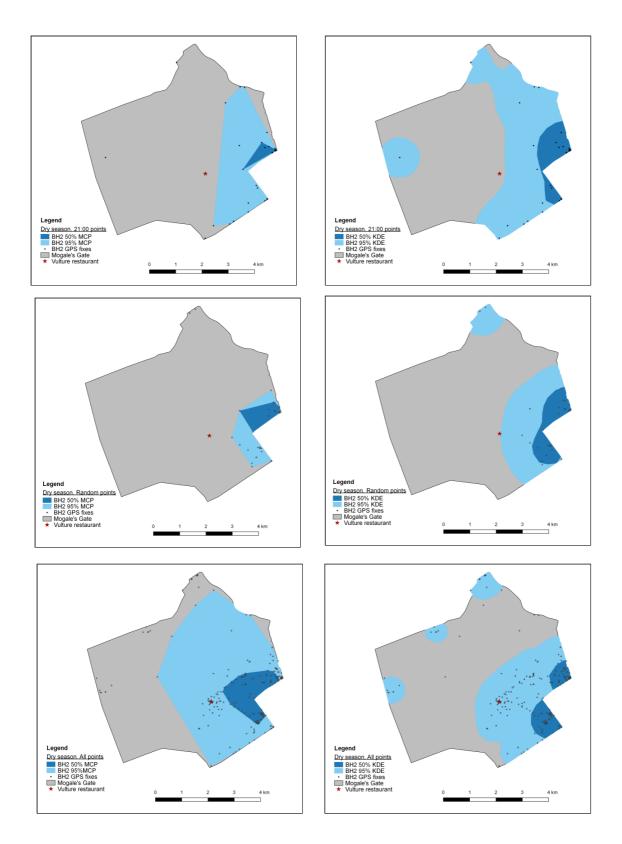


Figure 5.6. The dry season home range (95%) and core range (50%) estimates for brown hyaena BH2, calculated using minimum convex polygons (MCP) and kernel density estimate (KDE). Plots are based on GPS fixes at 21:00 (top panel), randomly selected GPS fixes (middle panel), and all GPS fixes (bottom panel).

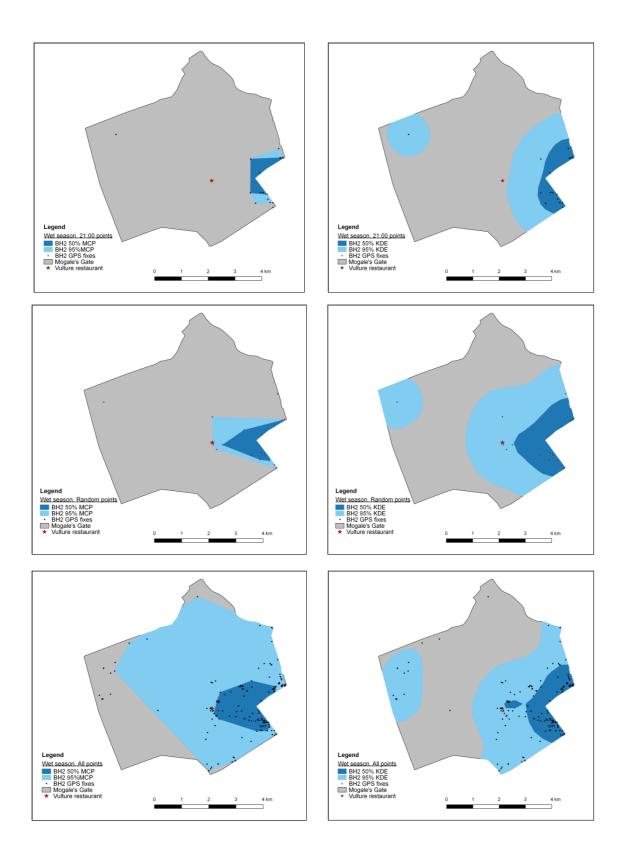


Figure 5.7. The wet season home range (95%) and core range (50%) estimates for brown hyaena BH2, calculated using minimum convex polygons (MCP) and kernel density estimate (KDE). Plots are based on GPS fixes at 21:00 (top panel), randomly selected GPS fixes (middle panel), and all GPS fixes (bottom panel).

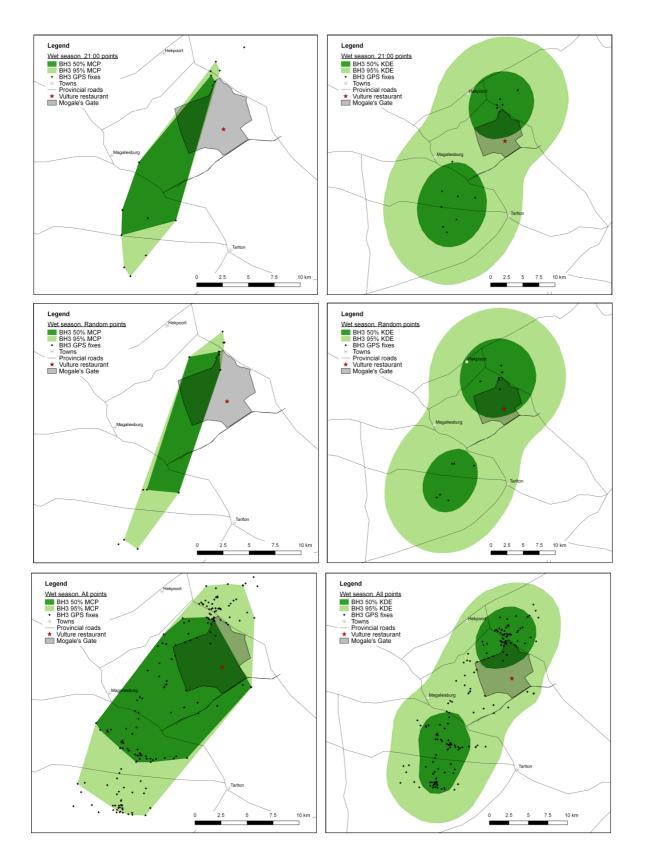


Figure 5.8. The wet season home range (95%) and core range (50%) estimates for brown hyaena BH3, calculated using minimum convex polygons (MCP) and kernel density estimate (KDE). Plots are based on GPS fixes at 21:00 (top panel), randomly selected GPS fixes (middle panel), and all GPS fixes (bottom panel).

Table 5.3. Home range estimates for the three collared brown hyaena using minimum convex polygon (MCP) and kernel densities estimates (KDE) at 95% (home range) and 50% (core areas) based on three different sampling scenarios. N = number of GPS fixes used for analyses.

Hyaena ID & season		MCP (km²)			KDE (km²)	
	Point selection	95%	50%	Ν	95%	50%
BH1. Dry season	21:00	25.5	10.6	146	31.7	11.4
	Random	22.1	8.8	146	38.5	13.1
	All	26.0	11.3	2374	31.4	8.8
BH1. Wet season	21:00	14.0	5.7	171	19.3	5.6
	Random	11.1	4.2	171	17.9	5.2
	All	14.7	6.1	2419	18.6	4.6
BH2. Dry season	21:00	7.3	0.3	45	28.8	4.3
	Random	3.1	0.8	45	15.8	3.3
	All	17.9	2.4	571	17.2	2.4
BH2. Wet season	21:00	1.7	1.1	22	15.5	3.3
	Random	3.4	1.3	22	23.2	4.9
	All	23.5	2.8	277	22.9	4.0
BH3. Wet season	21:00	64.9	50.4	14	631.1	169.4
	Random	54.4	38.1	14	602.8	155.2
	All	179.9	110.1	248	352.0	89.1

Movement patterns

Distances for 153 days (dry season) and 162 days (wet season) were calculated for adult female (BH1). Distances for the adult male (BH2) were calculated based on 53 dry season and 21 wet season days whereas only 18 days of distance data within the wet season were available for the sub-adult female (BH3).

The mean daily distance that the adult female (BH1) brown hyaena moved did not differ seasonally (t = 1.74, p = 0.09, SE = 0.11). Although only 18 days of movement data were available for sub-adult female (BH3) in the wet season, she moved, significantly further per night than the adult female (BH1); t = 4.56, p < 0.00046, SE = 0.23 (Table 5.4).

Table 5.4. The mean, minimum and maximum straight-line distances moved between GPSfixes per night for adult female (BH1) and sub-adult female (BH3).

Hyaena ID	Season	Distance	e moved per ni	Total	Days		
Tiyaena ib	ocason	Mean±SE	Minimum	Maximum	distance	monitored	
BH1	wet	8.8 ± 0.8	0.1	12.4	1379.8	162	
BH1	dry	11.1 ± 0.8	0.1	4.3	1647.6	153	
BH3	wet	21.2 ± 4.7	0.1	11.0	327.4	18	

In both seasons the adult female (BH1) was most active between 18:00 and midnight, covering a mean distance of 5.5 ± 0.5 km (wet) and 6.5 ± 0.4 km (dry season), versus 3.3 ± 0.3 km (wet season) and 4.6 ± 0.4 km (dry season) between midnight and 06:00. She moved the greatest distance between 19:00 - 19:59 in the wet season (1.3 ± 0.1 km), but similar distances between 18:00 - 18:59 (1.4 ± 0.9 km) and 19:00 - 19:59 (1.3 ± 0.9 km) in the dry season. As night-time progressed so her distances travelled decreased with the shortest distances being in the hour before sunrise (05:00 - 05:59) in both seasons (Fig. 5.9).

The sub-adult female's (BH3) shortest distances moved were between 18:00 - 18:59 (0.7 \pm 0.3 km). She was more active than BH1 from 23:00 onwards, covering a mean distance of 15 km (SE = 3.2) before 06:00. She was found to be most active between 23:00 and 23:59 (3.3 \pm 0.7 km), after which the distances she travelled decreased (Fig. 5.9).

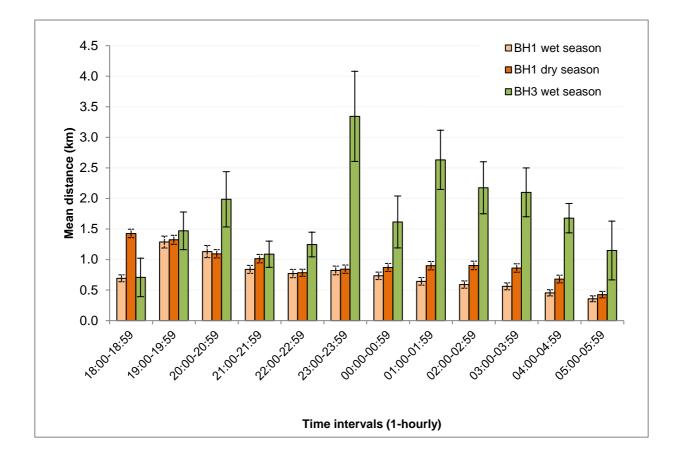


Figure 5.9. Mean distances (km) moved in hourly intervals at night, for adult female (BH1) and sub-adult female (BH3). Bars represent standard error.

Based on 3-h time intervals for a 24-h period, the adult male (BH2) moved a total distance of 528 km in 53 days of monitoring (dry season), with a mean of 10.0 ± 2.0 km (range 0.05 - 6.0 km); and 240 km in 21 days of the wet season, with a mean of 11.4 ± 2.9 km (range 0.05 - 6.2 km) (Table 5.5). There was no significant difference between the seasonal distances moved by adult male (BH2), t = 0.57, *p* = 0.58, SE = 0.13.

		Dry season (n=	=53)	Wet season (n=21)			
	Time interval	Total distance (km) Mean±SE		Total distance (km)	Mean±SE		
	18:00-20:59	54.6	1.4±0.2	36.9	1.8±0.3		
Night	21:00-23:59	56.5	1.6±0.3	24.5	1.4±0.4		
	00:00-02:59	60.4	1.5±0.3	26.0	1.2±0.3		
	03:00-05:59	57.9	1.6±0.3	25.0	1.6±0.5		
	-	229.3		112.4	_		
	06:00-08:59	56.2	1.6±0.3	31.3	1.4±0.4		
	09:00-11:59	82.0	1.6±0.2	30.9	1.6±0.3		
Day	12:00-14:59	80.1	1.6±0.2	32.2	1.7±0.3		
	15:00-17:59	79.9	1.6±0.2	33.2	2.4±0.4		
	-	298.2		127.6	_		

Table 5.5. Distances (km) moved by adult male (BH2) during the dry and wet seasons, basedon 3-h intervals over a 24-h period.

For 39 days (6 June to 3 October 2016), BH1 and BH2 had overlapping collar days, which were used to compare movement distances between the two individuals. The adult female (BH1) moved a significantly greater total distance (314.8 km, mean distance - 8.1 ± 0.8) over the 39-day period, compared to the adult male (BH2) (120.7 km, mean distance - 3.9 ± 0.9) (t = 4.96, *p* = 0.009, SE = 13.4). At night, both individuals moved the greatest distances between 18:00 and 20:59, moving mean distances of 2.9 ± 0.2 (BH1) and 0.8 ± 0.2 km (BH2) respectively. With decreasing mean distances moved as the night progressed, both individuals were least active in the time interval between 03:00 - 05:59 (Fig. 5.10).

Over the 39-day period, the majority (60%; 72.4 km) of BH2's movements were during the day, predominantly from midday to 17:59. Of this total, 24.9 km was moved between 12:00-14:59 and 40.6 km was moved between 15:00-17:59 (Fig. 5.10).

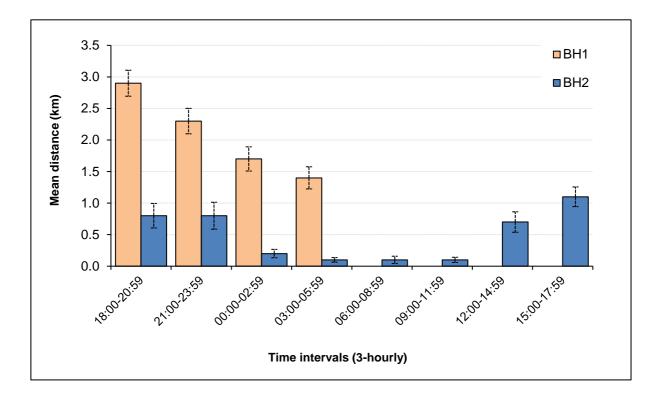


Figure 5.10. Mean straight-line distances (km) moved in 3-h time intervals for the adult female (BH1) and the adult male (BH2), based on 39 days of overlapping GPS collar data. No daytime data was recorded for the adult female (BH1). Bars represent standard error.

Habitat utilisation

During the study period neither BH1 nor BH2 were recorded outside of Mogale's Gate (Fig. 5.5 to Fig. 5.7). Chi square Goodness-of-fit tests showed that the expected utilisation of each habitat, based on each respective habitat availability within each brown hyaena's calculated range, differed significantly from the observed usage of habitat types by the adult female (BH1) and adult male (BH2) during both the dry (BH1 $\chi^2 = 95.29$, *p* < 0.00001; BH2 - : $\chi^2 = 37.87$, *p* < 0.00001) and wet season (BH1 - $\chi^2 = 296.63$, *p* < 0.00001; BH2 - : $\chi^2 = 78.98$, *p* < 0.00001). Both hyaenas used wetland habitat in proportion to availability in both seasons (Table 5.6). BH1 used woodland habitat significantly more but the grassland habitat significantly less than expected in both seasons, whereas BH2 used the grassland habitat type significantly more and the woodland habitat significantly less than expected. (Table 5.6).

The sub-adult female (BH3) largely ranged outside of Mogale's Gate (Fig. 5.8) and, in doing so, did not utilise the three land use types in proportion to their availability within her range ($\chi^2 = 33.76$, p < 0.00001). Mogale's Gate was used less than expected, surrounding tourism / conservation areas were used as expected and the agricultural land use type was used significantly more than expected (Table 5.6). Fifteen (of the 282) GPS fixes over a period of four nights were collected within the boundaries of Mogale's Gate, and all were in the higher lying (1535 - 1648 m.a.s.l) grassland habitat of the Witwatersberg mountain range, in the northern part of the reserve.

	Habitat type	Total hectares	Proportion ^a of total hectares (p _{io})	Number of hyaena GPS locations	Expected ^b number of hyaena locations	Proportion observed in each habitat (p _i)	Confidence interval on proportion of occurrence $(p_i)^c$ (95%)	Utilisation more / less than expected
	Woodland	570	0.186	517	407	0.236	$0.215 \le p \le 0.257$	More
BH1 Dry season	Wetland	43	0.014	71	31	0.032	$0.011 \le p \le 0.053$	As expected
Dry Season	Grassland	2451	0.800	1603	1753	0.732	0.711≤ <i>p</i> ≤ 0.753	Less
	Woodland	570	0.186	746	431	0.322	$0.301 \le p \le 0.342$	More
BH1 Wet season	Wetland	43	0.014	6	32	0.003	$0.000 \le p \le 0.023$	As expected
Wel Season	Grassland	2451	0.800	1566	1855	0.676	$0.655 \le p \le 0.696$	Less
	Woodland	570	0.186	12	84	0.027	$0.000 \le p \le 0.073$	Less
BH2 Dry season	Wetland	43	0.014	3	6	0.007	$0.000 \le p \le 0.053$	As expected
Dry Season	Grassland	2451	0.800	436	361	0.967	$0.921 \le p \le 1.013$	More
	Woodland	570	0.186	8	45	0.033	$0.000 \le p \le 0.096$	Less
BH2 Wet season	Wetland	43	0.014	5	3	0.021	$0.000 \le p \le 0.083$	As expected
Wel Season	Grassland	2451	0.800	230	194	0.947	$0.884 \le p \le 1.009$	More
BH3	Mogale's Gate	3064	0.172	15	48	0.053	$0.000 \le p \le 0.112$	Less
	Tourism / conservation	3468	0.194	55	55	0.195	$0.137 \le p \le 0.253$	As expected
	Agricultural land	11362	0.635	212	179	0.752	$0.693 \le p \le 0.810$	More

Table 5.6. Seasonal habitat utilisation of brown hyaena, on Mogale's Gate and surrounds, Gauteng province, South Africa.

^a Proportions of total hectares represent expected hyaena location proportions, as if hyaena occurred in each habitat in exact proportion to availability.

^b Calculated by multiplying proportion $p_{io} \times n$; e.g., 0.800 x 1603 = 1753.

^c p_i represents theoretical proportion of occurrence and is compared to corresponding p_{io} to determine if hypothesis of proportional use is accepted or rejected, i.e., $p_i = p_{io}$.

Vulture restaurant utilisation

Only BH1 and BH2 were recorded in the vicinity of the vulture restaurant during the study period. A total of 186 GPS points was recorded within the 250 m buffer area around the vulture restaurant for the adult female (BH1), of which 139 points (86 days) were in the dry season and 47 points (35 days) in the wet season. The adult male (BH2) recorded 37 GPS points at the vulture restaurant, 25 points (22 days) in the dry season and 12 GPS points (12 days) in the wet season.

To compare the occurrence data between BH1 and BH2, at the vulture restaurant, the GPS point data for the adult female BH1 was grouped into 3-h intervals. BH1 occurred most frequently at the vulture restaurant between 18:00 and 20:59, in both seasons, dry - 31% (n=44) wet - 43% (n=20), t = 5.39, p < 0.002, SE = 4.45 (Fig. 5.11a). When GPS data were grouped into hourly time intervals, BH1 had the highest number of occurrences (n=24, 17%) at the vulture restaurant between 20:00 - 20:59 in the dry season, and between 19:00 - 19:59 (n=11, 24%) in the wet season (Fig. 5.11b).

There were no seasonal differences in the occurrences of the adult male (BH2) at the vulture restaurant, U = 31, p = 0.91, z = -0.10). In both seasons, most GPS fixes of BH2 at the vulture restaurant were between 15:00 - 17:59 (dry: 64%, n=23; wet: 67%, n=8) (Fig. 5.11a). During the dry season he was only recorded at the vulture restaurant during the day, whilst during the wet season he was recorded at the vulture restaurant twice: once between 18:00 - 20:59 and another between 00:00 - 02:59.

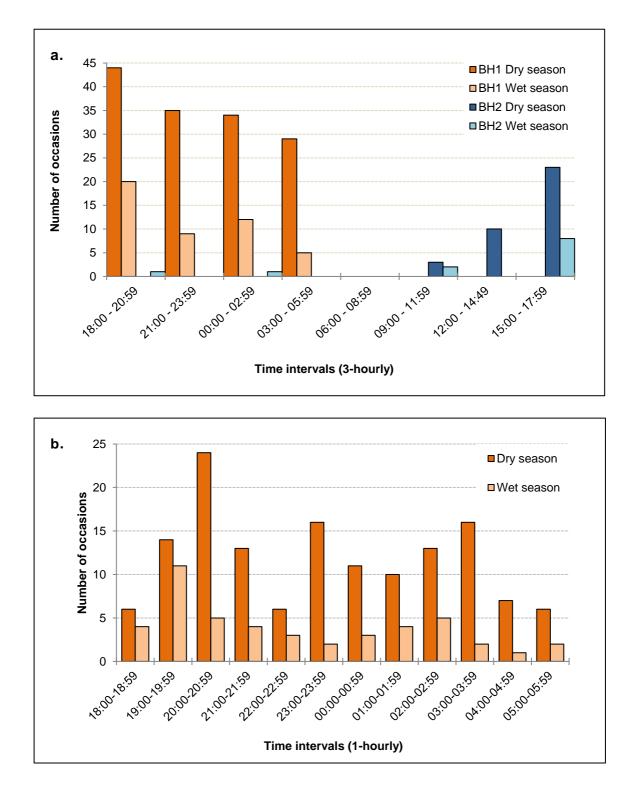


Figure 5.11. Number of occasions that the adult female (BH1) and the adult male (BH2) were at the vulture restaurant during (a) the dry and wet seasons, based on 3-h time intervals. (b) Occasions of the adult female (BH1) at the vulture restaurant based on 1-h time intervals.

Both hyaenas displayed a similar trend in visitation to the vulture restaurant seasonally, with more than two thirds of their occurrences at the site being between June and September (Fig. 5.12). The adult female (BH1) occurrences within the 250 m buffer around the vulture restaurant peaked in August and then decreased going into the wet season, remaining below 10% occurrence throughout the wet season, until April when occurrences increased again. Similarly, the adult male (BH2) occurrence at the vulture restaurant peaked in July, after which it dropped to below 10% occurrence at the beginning of the wet season. Unlike, the adult female (BH1) the adult male's occurrence at the vulture restaurant increased to 21% in November.

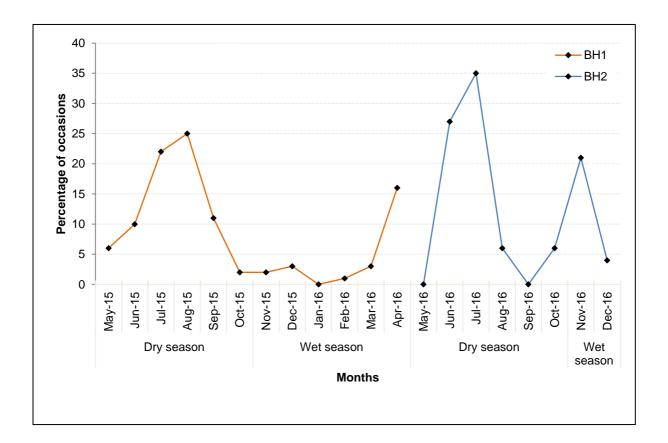


Figure 5.12. The percentage number of occasions, based on collar GPS points, that adult female (BH1) (n = 186) and adult male (BH2) (n = 48) occurred at the vulture restaurant.

DISCUSSION

Cage traps have often been used for the capture of brown hyaenas (Mills 1990; Maude 2005; Wiesel 2006; Grant 2012) but are often criticised for causing large amounts of stress and injury to the captured animal as it tries to escape (Grant 2012; Welch 2014). Other than the opportunistic capture of the adult male (BH2), due to logistical constraints, using cage traps to catch brown hyaena was the only feasible option for my study. The two brown hyaena that were caught using cage traps during my study only sustained minimal, superficial injuries to their noses and paws which were treated with topical wound spray whilst they were anaesthetised. However, as the adult female (BH1) kept re-entering the cage trap in the months after her initial capture and fitting of the tracking collar, the trauma associated with being caught in the trap was obviously not sufficient to prevent her from further entries. Adult male (BH2) was not identified in any of the camera images as one of the brown hyaena approaching or entering the cage traps and was hence opportunistically darted from a vehicle. Although the premature failure of the adult male (BH2) collar shortened the proposed tracking period, overall, the satellite collars performed well in this mountainous environment where physically following brown hyaena would have been impractical.

A wide range of home range sizes have been reported for brown hyaena across their range, from large estimates of 4370 km² recorded in the desert areas of Namibia (Wiesel 2006) where resources are few and greatly dispersed, too much smaller home ranges of between 26.3 km² and 205 km² in small, enclosed conservation areas of the Eastern Cape (Welch 2014; Welch *et al.* 2016; Müller 2020). The varying sizes in home ranges and the adaptable nature of brown hyaena suggests an ability to persist in a mixture of protected and unprotected areas, thus their movements may cover several properties and land use types (Welch *et al.* 2016; Williams 2017).

In my study the three collared brown hyaena home range sizes ranged from 1.7 km² to 179.9 km² using the MCP method, and 15.5 km² to 631.1 km² using the kernel density estimate method. The varying sizes being dependent on the number of GPS points used in each analysis. With auto-correlated data, conventional methods, such as MCP and KDE are likely to significantly over-estimate the size of an individual's home range (Fleming *et al.* 2015). In this study, this was not always true in the case

of KDE range sizes, with the adult female's (BH1) home range not varying greatly when the three GPS point sampling scenarios were used. With her dry season range estimation ranging between 31.4 km² and 38.5 km² (146 and 2374 GPS fixes), and wet season range size varying between 17.9 km² and 19.3 km² (171 and 2419 GPS fixes. When a suitable sampling period is used, kernel density estimation is more lenient towards the influence of underestimation of the home range sizes, when using auto correlated data (Swihart and Slade 1997; De Solla *et al.* 1999; Laver 2005). A suitable sampling period is one which surpasses the time needed for an animal to cover each temporal range (Lair 1987; Otis and White 1999; Laver 2005), this gives the animal the chance to visit all areas it would normally visit in the sampled time period. Considering that the adult female (BH1) was never recorded leaving the boundary of Mogale's Gate, and in the time, she was collared traversed the extent of the property, the home range estimates for her would be expected to remain fairly constant regardless of sampling size.

The largest home range recorded was that of the sub-adult female (BH3) at 631.1 km², when using the KDE method (21:00 points; n=14). As kernel density estimators use intensity of use algorithms to determine home range size an adequate sample size is required, typically a minimum of 30 locations, but preferably 50 locations (Seaman et al. 1999; Laver 2005). In this case, the use of only 14 GPS points gives a highly unrealistic, and inflated estimate of the sub-adult female (BH3) home range, as points are too few and dispersed. Using all the GPS points available for this individual (n=248) may give a more realistic kernel density home range estimate of 352 km². Although, the range size generated for BH3 should be viewed with caution due to the limited number of GPS fixes collected, the points could perhaps rather be used as an indication as to how she moved across the landscape in such a short period of time. The unfortunate death of BH3 a few weeks after collaring has resulted in a gap in our understanding of home range sizes and habitat utilisation of a young, non-breeding female moving outside the boundaries of Mogale's Gate. Despite the risk of persecution by farmers, potential vehicle collision and dispersed and variable food resources in large agricultural areas surrounding Mogale's Gate, she spent little time moving in the reserve. This sub-adult female was possibly not part of the "Mogale's Gate clan" (Owens and Owens 1979).

Unlike the sub-adult female (BH3) in this study and brown hyaenas found in other small, protected areas such as Kwandwe private game reserve (Welch 2014), Mountain Zebra National Park (Welch et al. 2016) and Shamwari game reserve (Müller 2020), the two brown hyaena remaining on Mogale's Gate had smaller home ranges (BH1 - dry season 31.7 km², wet season 19.3 km²; BH2 - dry season 28.8 km², wet season 15.5 km²) by comparison (based on one point at 21:00). Home range sizes have been associated with food availability (Mills 1982; 1990; Maude and Mills 2005) and the dispersion of food resources. Where food resources are localised, home ranges are smaller than in those where food resources are widely distributed (Skinner et al. 1995; Wiesel 2006). Based on this the comparatively small home range sizes of the two brown hyaena on Mogale's Gate are not surprising given the regular provision of carcasses at the vulture restaurant. The fences of Mogale's Gate are not impenetrable and the brown hyaena could potentially utilise holes underneath the fences to move through as they do in other areas (Kesch et al. 2013; Richmond-Coggan 2014). Nevertheless, these two hyaenas were not recorded having left the reserve during the study period. Although the small sample size of my study is not robust enough to make reliable or certain assumptions regarding the home range sizes of other brown hyaenas on the reserve or in the surrounding areas of the Magaliesberg, it does highlight that a regular, predictable and concentrated food source can influence the home range size of individual brown hyaenas. These findings support my prediction that home range sizes and movements of brown hyaena on Mogale's Gate would be smaller in the presence of the vulture restaurant. This is not surprising considering globally that in other studies involving anthropogenic activities such as rubbish dumps, hunting leftovers and supplementary feeding, many species have been found to alter movement patterns and reduce home ranges (Craighead et al. 1995; Wilmers et al. 2003; Kolowski et al. 2008; Oro et al. 2008; Jones 2011; Bicknell *et al.* 2013).

Variations in home range sizes can also be attributed to an individual's behaviour in context of the landscape in which it occurs (Borger *et al.* 2006; Grant 2012). Habitats with abundant prey, good water sources, and suitable denning sites are important resources, around which carnivores such as leopard will arrange their home ranges (Bailey 1993; Swanepoel 2008). Boydston *et al.* (2003) found that impact of human

disturbance could also influence aspects of preferred habitat usage. In a wildlife area in Kenya, female spotted hyaena who were often harassed or killed by livestock herders, had a disproportionately high preference for dense vegetation cover, although most of their territory was made up of open grassland (Kolowski *et al.* 2007). Welch (2014) on the other hand found that in the Kwandwe private game reserve, where brown hyaenas are not persecuted by people, hyaena space use was not predictable, and individuals varied greatly with different combination of variables.

The adult female (BH1) hyaena home range was concentrated in the northern portion of Mogale's Gate, which is dominated by woodland habitat, whereas the adult male (BH2) preferred the grassland habitats in the southern portion of the reserve. Skinner and van Aarde (1987) found that brown hyaenas in the Magaliesberg preferred to move along kloofs and valleys, which lead from their shelters on the mountain ridges to farmsteads where they scavenged for food. In Namibia, mountains provide safe refuge from competitors and other threats. (Wiesel 2006; Williams 2017). The woodland habitats and steep slopes of the mountains in the northern portion of Mogale's Gate potentially offer protected locations for maternal dens, one of which was found during the course of my study in a wooded area in a valley. In the central Kalahari, communal dens were surrounded by bushes and tall grasses, where the residents were alerted to the approach of another animal by the noise created moving through the vegetation (Owens and Owens 1979). In Namibia, most of the brown hyaena den sites are hidden in mountainous areas (Wiesel 2006). Likewise, on Shamwari Game Reserve in the Eastern Cape brown hyaena maternal dens are found in dense thickets and are well camouflaged (Müller 2020).

The adult male (BH2) preferred the grassland habitat, in the south-eastern portion of Mogale's Gate; this area being predominantly flat, open grassland with minimal tree cover. This adult male made use of two main den sites within this area and was seen to sleep in the proximity thereof on a number of occasions. A quarter of all his GPS points fell within the vicinity of these dens and much of this time spent there was during the day, especially in the dry season. The den sites were in proximity (1.7 km) to the vulture restaurant and tall grass veld suggests that this would be a potentially good area for him to rest. His core range encompassed these den sites and the vulture

restaurant. This male was an old hyaena, estimated to be well over 10 years old. I often encountered him on route or at the vulture restaurant during the day. I suggest that this old male (BH2) was using the daytime availability of carcasses at the vulture restaurant to obtain food and avoid competition with other hyaenas, which was a strategy that outweighed the effects of high daytime temperatures and the potential dangers of being out in the open. An old adult female previously occurring on Mogale's Gate displayed similar diurnal behaviour and also had a den located approximately 1 km from the vulture restaurant in the open grassland with no cover (¹⁰A. Tuckett pers. comm.).

The sub-adult female (BH3) showed no preference for the higher elevation offered by the mountainous areas, in the tourism / conservation areas. She moved in close proximity to homesteads and main tar roads at night, and on two occasions the 00:00 GPS points were located 250 m from homesteads. To maximise access to feeding opportunities, and reducing the risk of being shot by farmers, brown hyaena in the Makgadikgadi wildlife management areas in Botswana would rest away from the cattle posts during the day and only move into the cattle post areas to forage at night (Maude 2005). Likewise, Skinner and van Aarde (1987) found that brown hyaena in the Magaliesberg often scavenged from rubbish dumps near farmstead at night.

The distances travelled by the brown hyaenas in my study are lower than most other published studies, which due to the regular and abundant source of food at the vulture restaurant resulted in shorter mean distances (between 2.75 km and 9.5 km). However, my study's mean distances are comparable to a study conducted in the small and enclosed reserve of Shamwari game reserve, where the brown hyaenas' mean nightly distances travelled ranged between 5.4 and 15.4 km (Müller 2020). In arid environments where food resources are more temporally and spatially dispersed, brown hyaenas cover longer distances per night; for example, in the central Kalahari hyaenas travelled from 10 - 20 km per night (Owens and Owens 1978), whereas in the Namib and southern Kalahari brown hyaenas moved between 12.3 km - 31.1 km per night (Mills *et al.* 1978; Mills 1990). In the Makgadikgadi National Park, brown

¹⁰Mr Alistair Tuckett, Operations director, Mogale's Gate Biodiversity Centre

hyaenas moved between 37.6 km and 46.2 km per night (Maude 2005), whilst, in the bushveld area of the Soutpansberg mountains, Limpopo province, South Africa, Williams (2017) recorded the mean nightly distances moved by two individuals as 9.7 km and 17.0 km. Relocated brown hyaena in the Magaliesberg area, consisting of a mixture of grassland and mountain bushveld, moved mean nightly distances of between 8.4 km and 22.6 km (Skinner and van Aarde 1987).

Carnivores alter their daily activities to changes in their environment, access of food, the risk of predation, and reproductive needs (Aschoff 1964; Daan and Aschoff 1982; Kolowski et al. 2007). Individual characteristics such as sex and social status also may influence daily activity patterns (Daan and Aschoff 1982; Zalewski 2001). Although, brown hyaenas in the Magaliesberg were found to be predominantly nocturnal in their behaviour, only leaving their dens well after sunset (Skinner and van Aarde 1987), the Mogale's Gate adult male's diurnal behaviour seems conducive with an old or lowranking individual avoiding conflict with stronger, higher-ranking hyaenas. By moving in the daytime, he avoided conflict with other hyaenas who would only be active at night. Camera trap footage from the den site showed that this male hyaena often lay at the entrance of his den just after sunset and made short foraging trips, again returning to the den, throughout the night. At the approach of other adult hyaenas, especially the adult female (BH1) and another large unidentified adult, he would avoid conflict by dashing into the hole. On a few occasions when caught unawares the other adult hyaenas would fight with him. This antagonistic behaviour was especially prevalent in the last few months before he was found dead in August 2017.

Although BH1 and BH2 regularly made use of the food provided at the vulture restaurant, they were present in its vicinity independently. As with other hyaenas (based on camera trap images), the adult female (BH1) visited the vulture restaurant at night. Camera trap footage at the vulture restaurant showed that several hyaenas made use of the carrion available, sometimes feeding alone and at other times up to four hyaena were present at the vulture restaurant at the same time. The adult male (BH2) was however only recorded at the vulture restaurant during daylight hours and was always alone, being most active at the vulture restaurant between the hours of

12:00 – 18:00 (Figure 5.13). The proximity of the vulture restaurant from his den sites offered him a regular food source, especially in the dry season.



Figure 5.13. Adult male (BH2) at the vulture restaurant during the day (C. Kruger).

The longer distances travelled by the adult female (BH1) on Mogale's Gate during the dry season compared to the wet season are in accordance with Maude's (2005) study in the wildlife management areas of the Makgadikgadi National Park. In his study, brown hyaenas moved longer distances in the lean season versus that of the peak season due to the distances between significant food items being greater in the lean season (Maude 2005). Although there are regular livestock carcass deliveries at Mogale's Gate vulture restaurant throughout the year, the quantity varies. On 81% (n= 90) of occasions when she was within the area of the vulture restaurant during the dry season the carcasses delivered during the day were finished by the vultures and black-backed jackals by night fall.

During the dry season, particularly between June and October more vultures were present at the vulture restaurant. As Cape vultures start laying their eggs in April and

the chicks hatch 57 days later (Tarboton 2001), the hatching period would coincide with the increased numbers of birds seen at the vulture restaurant after June, when adult vultures require more food to feed growing chicks (Borello and Borello 2002). This high utilisation of carcasses by the vultures over this period may reduce the amount of food available to the brown hyaenas. This is also apparent when results of the diet of the hyaenas are considered (Chapter 3), and the percentage of small mammals in the diet almost doubles during the dry season in comparison to the wet season.

Distances moved by BH1 from early September 2016 until the collar dropped off in mid-October 2016 decreased and cannot be definitively explained. However, over this period, her mean nightly distance moved halved and, by October, she was moving a maximum of 1.2 km a night. From September 2016, she was not identified in any of the camera trap images operational through Mogale's Gate, and I speculate that she may have died from rabies as there was an outbreak on Mogale's Gate during the last three months of 2016. The outbreak resulted in over three-quarters of the jackal population on Mogale's Gate being eradicated; many black-backed jackals in the Magaliesberg succumbed over that period (¹¹Dr R. Jeffery pers. comm.). The subsequent finding of three decomposed brown hyaena carcasses shortly after the collar dropped off in mid-October, in proximity to the last GPS location recorded for the adult female (BH1), also suggests loss to disease.

The movements of the sub-adult female beyond the boundaries of Mogale's Gate maybe a reflection of the behaviour of a young, dispersing individual, or it could suggest that brown hyaenas living outside the reserve have larger home ranges. The use of GPS collars in this study provides insight into the temporal and spatial behaviour of two females and an old male brown hyaena on Mogale's Gate, two of which were indeed found to have smaller home ranges and moved shorter distances than in other studies. Based on resource dispersion hypothesis and its influence on ranging behaviour of species, as I predicted the brown hyaenas on Mogale's Gate do

¹¹Dr Ryan Jeffrey (BVSc) - African Plains Veterinary and Wildlife Consultants, Magaliesberg.

have smaller home ranges than reported in other protected areas, due to the regular food source provided at the vulture restaurant.

The small sample size of only three brown hyaena, all of different sex and age, limits the study to individuals, and may not accurately describe the home range features of the Mogale's Gate population of brown hyaenas. In order to do this more individuals would need to be collared and monitored. Further studies incorporating more than the protected environment of the reserve and one which includes more of the surrounding land use types would be necessary to establish home range estimates at a population scale. In 2018, there are three active vulture feeding sites accessible to terrestrial scavengers within a 20 km radius of each other (including Mogale's Gate) (¹²K. Wolter pers. comm.). How these other feeding sites and potential new sites influences aspects of movements and home range of the brown hyaena population in the Magaliesberg region would be a very interesting and an insightful, future study.

¹²Kerri Wolter - CEO and founder of VulPro (Vulture Programme for the Conservation of Vulture Species in southern Africa)

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Chapter 6

Conclusions



"The way in which societies portray animals, and especially carnivores, moulds attitudes and influences actions towards them..." - Brownlow (2000)

Availability of space for brown hyaena and other carnivores has been reduced by the expansion of agriculture, development and increased human populations (Swanepoel 2008). Historically, protected areas were considered to be the most important areas for the conservation of species. However, this approach to conservation is changing and the role of private land, game farms and agricultural zones are seen as important contributors to conservation targets (Woodroffe 2001; Swanepoel 2008). Coexistence between predators and people depends greatly on the availability of space, human tolerance of sharing this space, and the adaptability of the predator in the face of ongoing landscape and environmental changes. Although the collective focus on conserving large predators for a complex mix of ecological and symbolic reasons (Kellert *et al.* 1996) has not diminished, over the past three decades the world's attention has been drawn to the need to maintain biological diversity in all its forms and interrelationships (Weber and Rabinowitz 1996). Hence the importance of such protected areas such as Mogale's Gate and the Magaliesberg Biosphere Reserve.

In South Africa apex predators have almost completely been eradicated from nonprotected areas (Hayward et al. 2007). Although heavily persecuted, low densities of leopard and cheetah still occur outside of protected areas in the Southern Africa. In the last 150 years large carnivores such as lions have been extirpated from the Magaliesberg mountains (Carruthers 2007). Although there is speculation regarding population numbers (Carruthers 2007), leopard and brown hyaena do survive in the Magaliesberg region, despite human encroachment, intervention and possible persecution (Kuhn 2014). In general, to some extent brown hyaena are able to adapt and benefit from living in proximity to people (Winterbach et al. 2013) and occur in viable populations throughout Southern Africa (Maude and Mills 2005). This species is likely to be one of the few large carnivores that can co-exist with farmers (Maude 2005). Being predominantly scavengers with a variable diet (Mills and Hofer 1998) livestock carcasses form a reliable and abundant food source in agricultural areas (Maude and Mills 2005). Ecologically, the role scavengers are important (Wilson and Wolkovich 2011). They remove decomposing carcasses of animals that have died due to predation, disease, parasites and accidents (DeVault et al. 2003), and contribute to nutrient cycling (Wilson and Wolkovich 2011).

The aims of my study of brown hyaenas on Mogale's Gate were to determine their seasonal diet, provide information on their home range and movements and to produce population estimates, in the presence of a vulture restaurant. My study was conducted on a small-protected reserve surrounded by increasing residential developments, agriculture and commercial farming. Furthermore, there is only a handful by published studies on the ecology of brown hyaena in the Magaliesberg and Gauteng grasslands, none of which includes the influence of a vulture feeding site.

Habitat transformation and human population increase has changed ecosystems to the point that human activities are the main drivers of global change (Oro *et al.* 2013). Apart from other direct impacts, ecosystems are being changed by food subsidies to animals (Oro *et al.* 2013). Some species such as rats, foxes and gulls, which exploit these increased food resources, have become 'over-abundant', while others have benefitted physiologically leading to increased fitness and reproduction (Carey *et al.* 2012; Oro *et al.* 2013). Negative influences of predictable, abundant food subsidies include the increase pathogen spread, altered predator-prey dynamics, changes in the food web, changes in spatial use, dispersal and foraging behaviour (Wilson and Wolkovich 2011; Olson *et al.* 2012; Oro *et al.* 2013; Yarnell *et al.* 2014). Normally carrion is transient in nature and its availability temporally patchy, hence, vertebrate carnivores will not pass on a free meal and will consume carrion when it is found (De Vault *et al.* 2003).

The supplementation or provision of extra food is used as a conservation tool to provide species such as vultures uncontaminated food to increase survival rates (Deygout *et al.* 2010; Yarnell *et al.* 2014). In an optimal situation, this food would be provided in a way that closely resembles the spatial and temporal abundance of food in nature (Piper 2005). However, vulture restaurants are most often at fixed sites and only the temporal aspect of carcass delivery may vary (Piper 2005). Whilst this regular feeding has proven successful in the reduction of vulture mortality rates, the broader impact of regular feeding on other terrestrial species is poorly understood (Cortes-Avizanda *et al.* 2012; Yarnell *et al.* 2014).

Although there are negative implications of a fixed food source such as vulture restaurant and the effects on community dynamics is not well understood (Yarnell *et al.* 2014), for a threatened species such as the brown hyaena, this provisioning can be beneficial. Other small reserves have reported high brown hyaena densities (Welch and Parker 2016; Müller 2020) due to the presence of high prey and predator numbers. It is suggested that in an area such as the Magaliesberg Biosphere Reserve where large predators such as lion do not occur anymore, the vulture restaurant on Mogale's Gate, and other areas within the region, act as an alternative food source for brown hyaenas, maintaining potentially viable populations and thus acting as a buffer to the localised extinction this species (Welch and Parker 2016).

The findings of my study confirm that brown hyaenas on Mogale's Gate have a highly diverse diet for such a small area, in relation to other studies. Overall, the high frequency of large mammals and domestic livestock in the diet suggests that there is sufficient carrion available to the brown hyaenas on Mogale's Gate, which is supplemented with smaller prey species such as rock hyrax and rodents. Although this study only represents the diet of brown hyaena over a one-year period and may not be reflective of the larger region, it provides confirmation of the influence that a regular and predictable anthropogenically supplied food source can have on diet, individual distances travelled, home range size and population density.

The home ranges of brown hyaena on Mogale's Gate are small in the presence of a constant anthropogenic food source, although the sample size is not robust enough to make definite assumptions of all brown hyaenas living in the surrounding areas, it is possible that similar patterns exist around other vulture feeding sites.

In comparison to many other studies, the density estimates obtained from this study are comparable to the density estimates of 14 - 20 individuals/ 100 km² recorded at Kwandwe Private Game Reserve in the Eastern Cape, South Africa (Welch 2014). Although the plentiful supply of carcasses and hunting offal allows for higher densities of brown hyaena on Mogale's Gate, extrapolating density results from this small area to include the larger standard density for 100 km² would result in highly inflated

numbers for a landscape that varies considerably in terms of land use type, prey availability and richness, and risk factors.

In a landscape of continuous change and reduced potential range size, this study is a testament to the resilience and adaptability of the brown hyaena. Brown hyaenas take advantage of a long term and regular food source on a small, protected reserve, and adapt their behaviour in terms of space use and diet. Brown hyaena occurrence in non-protected areas is common (Thorn *et al.* 2011; Kent and Hill 2013) and non-protected areas may be important for the conservation of the species (Skinner and van Aarde 1981; Maude and Mills 2005; Kent and Hill 2013). Hence, the need for further studies in agricultural areas surrounding Mogale's Gate, to determine the role of and factors that are influencing the survival of brown hyaena populations in the greater Magaliesberg area.

Small, protected areas are more frequently exposed to anthropogenic pressures, random processes, and strong edge effects, which results in extermination of small populations (Linnell *et al.* 2000; Kafley *et al.* 2016). Therefore, these small areas are often deemed unsuitable for the conservation of large carnivores (Williams 2017). Furthermore, these small areas are becoming increasingly isolated and natural habitat buffers surrounding them are dwindling (Kafley *et al.* 2016). However, small, protected areas remain critical in the conservation of global biodiversity, watershed protection, and cultural & educational services (De Fries *et al.* 2007). The long-term survival of populations of brown hyaenas is best achieved by protecting existing populations, such as those on Mogale's Gate, but also providing dispersal corridors and opportunities to link with other populations (Müller 2020). The expansive movements of the sub-adult female hyaena outside the boundary of Mogale's Gate in the surrounding agricultural farms and other natural areas, shows that there is some dispersal of individuals in the area. Her death due to snaring does however highlight the threats faced by brown hyaenas in the surrounding agricultural areas.

Within the Magaliesberg Biosphere Reserve, there are six long-term vulture-feeding sites other than Mogale's Gate, of which two are currently accessible to terrestrial carnivores, such as brown hyaena. Large-scale area conservation initiatives such as the Magaliesberg Biosphere Reserve therefore play an important part in the conserving of core natural areas and controlling increased infrastructure development. This increases the frequency of good quality habitat patches in potentially environmentally stressed landscapes (Thorn *et al.* 2011). Although habitat alteration and fragmentation have the potential to change spatio-temporal structures of species, carnivores with a wide niche breadth can survive in fragmented landscapes (Atwood *et al.* 2004). The agricultural zones surrounding small-protected areas such as Mogale's Gate can also play an important role in the connectivity between other wildlife farms, in that they can act as corridors for carnivore populations (Winterbach *et al.* 2013). These wildlife farms can act as refuges from anthropogenic threats (Thorn *et al.* 2011). As brown hyaenas are secretive and adaptable scavengers who pose little threat to people, they seem to benefit to some extent from living in close proximity to people (Maude and Mills 2005; Winterbach *et al.* 2013).

In terms of limitations of this study, these varied, depending on the aspect of study. For the dietary and population density aspects large amounts of raw data were collected through scat samples and camera trap images, respectively. Some species could potentially have been excluded from the diet due to many unidentified, small hair samples found in the scats. Also, no provisioning rates were recorded at the vulture restaurant during the study period, and with vulture and jackals utilising the carrion during the day, it was not possible to quantify the amount of food available to the brown hyaenas. Although a large number of camera trap images were collected, many of the brown hyaena images were not clear enough for positive identification, which potentially led to the underestimation of the population. Increased precision of the population estimates would be important for monitoring density changes in the future. Range use estimates were hampered by a small sample size and exacerbated further by the three study animals, one of which died shortly after collaring, being of different age and sex classes. Despite these shortcomings this study has provided important insights into brown hyaena feeding and spatial ecology in the presence of a vulture restaurant.

Large carnivore conservation can be successful if the approach is a coordinated effort on an international, regional and local level, and ecological and human aspects are addressed (Balme *et al.* 2009; Winterbach *et al.* 2013). Lindsey *et al.* (2013) suggested that a coexistence of tolerance between people and carnivores needs to be achieved if carnivores are to be conserved. In the case of brown hyaenas, landowners and farmers need to be educated about their foraging behaviour to change the perception of farmers that brown hyaenas pose a threat to livestock, and to reduce conflict (Winterbach *et al.* 2013). In doing so the natural scavenging behaviour and the beneficial 'cleaning up' actions, including keeping diseases to a minimum, have to be highlighted (Kent and Hill 2013).

To further enhance our understanding on conserving this species within the broader extent of the Magaliesberg, further research should be undertaken on how the other vulture restaurants within the Magaliesberg Biosphere Reserve are linked to brown hyaena movements, population and genetic structure.

The vulture restaurant on Mogale's Gate has been operational for over 30 years, in which time brown hyaena numbers could have varied due to the changing spatial and temporal predictability of their food supply. Likewise, foraging time for the opportunistic brown hyaena would have been decreased and potentially increased fitness and reproductive success. Concurrently, the number of other scavengers such as blackbacked jackal increased, thus potentially increasing competitive interactions with brown hyaenas for food. The aggregation of large numbers of these scavengers at the vulture restaurant can increase the risk of the spread of diseases such as rabies (Ogada et al. 2012; Yarnell et al. 2014). There are only a few studies, where the reduction or closure of artificial feeding sites has recorded the effects on target and non-target species. In these studies, it was shown that the closure of longterm sites, for example the closure of dumps in Yellowstone National Park, had an impact of the population of grizzly bears (Ursus arctos) who fed almost exclusively at these sites (Craighead et al. 1995). Results suggested that bear mortality increased rapidly and there was a more than fivefold increase in annual home ranges (Craighead et al. 1995; Oro et al. 2013). Although, the diet of the brown hyaena on Mogale's Gate is varied and does not only includes the remains of animals found at the vulture restaurant, one would expect that a similar population decline would occur if supplementation at the vulture restaurant was suddenly ended.

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Appendices

Appendix 1. UNISA Ethics clearance for the project.

UNISA university
2014-02-25
Ref. Nr.: 2013/CAES/132
Te:
Applicant: Dr K Slater Department of Environmental Sciences
College of Agriculture and Environmental Sciences
Dear Dr Slater
Request for Ethical approval for the following research project:
Behavioural ecology of Brawn Hyaenas in two semi-arid areas of South Africa
The application for ethical clearance in respect of the above mentioned research has been reviewed by the Research Ethics Review Committee of the College of Agriculture and Environmental Sciences, Unisa. Ethics clearance for the above mentioned project (Ref. Nr.: 2013/CAES/132) approved after careful consideration of all documentation submitted to the CAES Ethics committee. Approval is given for the duration of the research project.
Please be advised that should any part of the research methodology change in any way as outlined in the Ethics application (Ref. Nr.: 2013/CAES/132), it is the responsibility of the researcher to inform the CAES Ethics committee. In this instance a memo should be submitted to the Ethics Committee in which the changes are identified and fully explained.
The Ethics Committee wishes you all the best with this research undertaking.
Kind regards,
Jup
Prof E Kempen, CAES Ethics Review Committee Chair
CAES Ethics Review Committee Chair
MUT Prof MJ Linington Executive Dean: College of Agriculture and Environmental Sciences
University of South Africa Preiler Street, Muckleneuk Ridge, Chy of Tshwane PO Box 392 UNISA 0003 South Africa Telephone: +27 12 429 3111 Facemie: +27 428 12 429 4150 www.unisa.ac.za

Appendix 2. List of mammal species found in Mogale's Gate.

Chiroptera	Mauritian Tomb bat	Taphozous mauritianus
	Yellow house bat	Scotophilus dinganii
	Common slit-faced bat	Nycteris thebaica
	Geoffroy's horseshoe bat	Rhinolophus clivosus
Insectivora	Greater dwarf shrew	Suncus lixus
	Lesser red musk shrew	Crocidura hirta
	South African hedgehog	Atelerix frontalis
Macroscelidea	Rock elephant shrew	Elephantulus myurus
Rodentia	Singe-striped mouse	Lemniscomys rosalia
	Pygmy mouse	Mus minutoides
	Woodland dormouse	Graphiurus murinus
	House rat	Rattus rattus
	Common molerat	Cryptomys hottentotus
	Porcupine	Hystrix africaeustralis
Lagomorpha	Scrub hare	Lepus saxatilis
	Jameson's red rock rabbit	Pronolagus randensis
Hydracoidea	Rock hyrax	Procavia capensis
Perissodactyla	Plain's zebra	Equus quagga
Suiformes	Warthog	Phacochoerus aethiopicus
	Bushpig	Potamochoerus larvatus
Ruminantia	Giraffe	Giraffa camelopardalis
	Black wildebeest	Connochaetes gnou
	Red hartebeest	Alcelaphus buselaphus
	Blesbok	Damaliscus pygargus phillipsi
	Common duiker	Sylvicapra grimmia
	Springbok	Antidorcas marsupialis
	Oribi	Ourebia ourebi
	Steenbok	Raphicerus campestris
	Impala	Aepyceros melampus

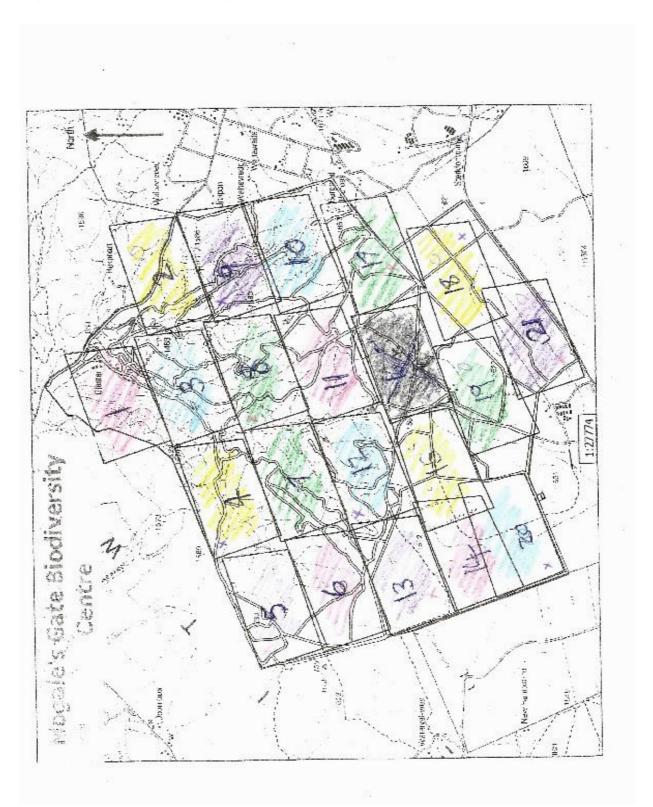
MAMMAL SPECIES OF MOGALE'S GATE

	Gemsbok	Oryx gazella
	Greater kudu	Tragelaphus strepsiceros
	Nyala	Tragelaphus angasii
	Bushbuck	Tragalaphus scriptus
	Eland	Tragelaphus oryx
	Common reedbuck	Redunca arundium
	Mountain reedbuck	Redunca fulvorufula
	Waterbuck	Kobus ellipsiprymnus
	Klipspringer	Oreotragus oreotragus
Carnivora	Aardwolf	Proteles cristatus
	Brown hyaena	Hyaena brunnea
	Leopard	Panthera pardus
	Small-spotted cat	Felis nigripes
	Caracal	Felis caracal
	Serval	Leptailurus serval
	Black-backed jackal	Canis mesomelas
	Cape fox	Vulpes chama
	Honey badger	Mellivora capensis
	Large-spotted genet	Genetta tigrina
	Small-spotted genet	Genetta genetta
	Water mongoose	Atilax paludinosus
	Yellow mongoose	Cynictis penicillata
	Slender mongoose	Galerella sanguinea
Primate	Lesser bushbaby	Galago moholi
	Chacma baboon	Papio ursinus
	Vervet monkey	Cercopithecus aethiops
Tubilidentata	Antbear	Orycteropus afer

Appendix 3. Estimated annual game counts on Mogale's Gate Biodiversity Centre, for 2014 and 2015 (Source: Mogale's Gate internal information).

Estimated game numbers for Mogale's Gate Biodiversity Centre							
	Species	2014	2015				
1	Blesbok	410	295				
2	Blesbok, White	42	22				
3	Eland	71	53				
4	Gemsbok	60	40				
5	Giraffe	11	12				
6	Hartebeest, Red	77	68				
7	Impala	55	57				
8	Kudu	47	35				
9	Nyala	30	27				
10	Oribi	12	4				
11	Ostrich	12	12				
12	Reedbuck, Common	12	12				
13	Sable Antelope - Matetsi	12	13				
14	Springbok	225	215				
15	Waterbuck	62	43				
16	Wildebeest, Black	253	238				
17	Zebra, Burchell's	208	177				
18	Warthog	57	43				
19	Reedbuck, Mountain	21	21				

Appendix 4. Mogale's Gate, 21 cell (143 ha each) grid used for the placement of camera traps and collection of scat samples.



Appendix 5. Example of form completed for the placement of each camera trap.

	Station 1		Station 2		Station 3	Station 4		Vulture hide		
Survey period	June to Septe	mber 2015								
Installation date	· · · ·	9 Jun 15		9 Jun 15		9 Jun 15		9 Jun 15	9 Jun 15	
Removal date	1									
Grid cell location	8			17		19) 4		16	
Gps x co-ordinate	-25.94967		-25.96490		-25.98328		-25.94779		-25.97023	
Gps y co-ordinate	27.64283		27.65464		27.63643		27.62718		27.64232	
Descriptive location	Eastern main	road junction	Intersection s	outh of old	Eucalyptus pl	antation south		d junction with	A.tortillis at VH	
	with firebreak		film khayas		of guards can		cement bridge			
Altitude		1497		1613		1586		1446	1591	
Vegetation type	saddle, open		upper slope, o wood/grass	·	Upper slope, plantation, gra	assland	Valley, bushve		Midslope ,Grassland, open wood	
Camera trap ID	1		2	5					9	
SD card ID	San 1 (4gb)	San 4 (4gb)	San 2 (4gb)	San 5 (4gb)	San 3 (4gb)	San 7 (4gb)	San 6 (4gb)	Lex 8 (16gb)	San 9 (32gb)	
Battery set ID's	1 & 1b	4 & 4b	2 & 2b	5 & 5b	3 & 3b	7 & 7b	6 & 6b	8 & 8b	9 & 9b	
Direction ct facing	135deg SE	315deg NW	180deg S	290deg NW	180deg S	45deg E	300deg W	200deg S	135deg SE	
Distance to centre of	4.7m	3.2m	4.5m	3.7m	4.1m	4.7m	4.3m	3.6m	7m	
detection zone Height above ground (from bottom of box)	0.7m	0.45m	0.45m	0.45m	0.45m	0.5m	0.55m	0.55m	1m	
Post used to secure ct	pole	pole	tree	pole	tree	tree	pole	pole	tree	
Reasoning of placement	Well used latr	•	Away from fer	•	Away from fe		This position	1	Camera placed in	
Area alterations	and main road from both		centre point in road. Lure of stinky mix to judge initial Grass cut short between		through gum plantation. tracks, pastings and scat detected here. Trees available for ct.'s. Low fire risk. Highest risk is trees being felled. Inform mgt to Grass cut short between two cameras, logs removed from one side		changed it so that at least one cell is representative of a valley area. Well used latrine on an intersection of 2 main roads, one has bridge crossing point, Not much grass to cut or remove, relatively clear to begin with. Some branches		position, but facing new restaurant closer to the hide. Camera 1m from ground on tree. Permanent placement for No clearing needed	
	firebreak. Immediate area		presentation against fire.		(ct3) and saplings and branches cut out/ removed in immediate vicinity of both cameras. Ground cleared around tree bases		cut of tree above ct 6. Ct 8 next to road on firebreak side, hence cleared.			
Date of first check		11 June 2015		11 June 2015		11 June 2015		11 June 2015	11 June 2015	
Days not functional	0	0	0	0	1	0	0	0		
Total no. images per camera	1644 downloaded	80 downloaded	388 downloaded	108 downloaded	3684 downloaded	632 downloaded	238 downloaded	110 downloaded	900 downloaded	
Battery level		full	1/4. Take batteries to recharge	full		full		full	3/4	
Positioning Alterations	Camera height decreased to 0.6m. Angled more downwards	Angled more downwards	Camera height increased to .65m. Angled more downwards	Angled more downwards	Camera height increased to 0.7m. Angled more downwards		Pole moved forward so new distance is 3.3m. Height increased to .55m. Angled more down.	Angled more downwards	None	
Camera adjustments	Take at night only	None	Take at night only. Sensor level : high. LED to high.	None	level to high.	Take only at night. Sensor level to high. LED to high.	None	None	None	

Appendix 6. Capture details form used during the capturing and collaring of the brown hyaenas on Mogale's Gate.

MOGA	LES BROWN HYA	ENA CAPTURE	SHEET							
DATE:							Captu	ured		
GPS LOC	ATION:				S		Darted			
DESCRIP	TIVE LOC:				JE		Processir	ng begin		
CAPTURE	E METHOD:				TIMES		Processi	ng end		
	PRESENT:					•	Awa			
VETERIN	ARIAN:						Vet arrive	& depart		
	Est. Age				1		(mm)	Length	Diameter	PHOTOS
	Sex				1		Left Upper			
LS	Overall condition				S	2	Left Lower			
A	Existing injuries						Right Upper			
	WEIGHT		Natural	ear markings & NOTCH	CANINES		Right Lower			
0	Total length (cm)		1		A		Notes of dentition	on:		
ANIMAL DETAILS	Tail length		1		0	,				
Σ	Head length		4							
Z	Head width		4	Dunie S						
◄	Shoulder height		4	YXX			(Tatal law ath		Mainislah
	Left ear length	_	4	00			(mm) Left front	Total length	Main length	Main width
	Right ear length				FEET	i	Right front			
	Collar No. & name						Left back			
	Magnet removed	Yes / No					Right back			
	indgriet remoted	1057110			1					
	Microchip number							Left	Right	
S	Microchip location	-			- 1		Overall side			
5	Temperature logger	Yes / No			1.		Head & ears			Include pics of
ž	Temp. logger postion				SO		Dentition			process: darting,
SAMPLES	Blood sample				PHOTOS		Front leg-side			measuring, temp logger insertion, microchip, ear
S	Hair sample	Yes / No Yes / No			2		Front leg-side			
	Parasites sampled	Yes / No			- -		Hind leg- side			notching, collaring, release
	Ear notching	Left	B	ight	- 1		Hind leg - front			
	Lai notening	2010		-B-rc			Face - front			t l
	ļ									I
	Immobilization drugs	& dosages:					Gloves			
							Dictaphone			
							Phone			
	How administered:				1		Sample bags			
	Other drugs used:						Sample tubes			
					1		Hanging scale			
					1		Measure tape			
	Injuries sustained & t	reated:					Veniers			
S	1 -				ut I		Camera			
DRUGS	Development ware to a set of				Equipment					
R	Reversal post proced	ure, drug & dosag	ge:		din din		Tarp			
					8	F	Rope			
					4		Water			
	How administered:						Leatherman			
					4		Data sheets			
	Notes on release:	Notes on release:					Pens			
e										
THER										