Human-wildlife conflict issues on commercial farms bordering the Sperrgebiet and Namib-Naukluft National Parks borders, southern Namibia

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PhD Thesis

Declaration of authorship

I, Sarah Edwards, declare that this thesis and the work contained within it in is entirely my own. Where I have consulted the work of others, this is always clearly stated.

Signed:

Date: 8th September 2015

Abstract

Human-wildlife conflict is a global and growing problem, threatening carnivore conservation as well as the viability of farming practices in many areas. This study represents the first human-wildlife conflict study on commercial farmlands in southern Namibia, an arid environment with difficult farming conditions and low density carnivore populations which are highly susceptible to lethal control. Through novel combinations of ecological and questionnaire techniques to link the human perspective of the problem to the ecological data collected, the study aimed to identify areas in which to focus mitigation measures. It addressed two key research questions; which are the key farmland features carnivores are attracted to, and are these features identified by farmers as associated with higher levels of livestock losses? Additionally, as arid environments present a challenging environment for researchers, the study aimed to examine which methods are effective for surveying carnivores in such conditions. Using camera trapping, non-invasive hair collection devices and stable isotope analysis of diet, the study identified water sources, habitats with cover, and anthropogenic food sources as attractive to carnivores. Both water sources and mountain habitat were positively associated with carnivore risk scores and livestock losses respectively, and represent areas to avoid when kraaling smallstock. However, perceived risk of carnivore species was not associated with levels of livestock losses. The study revealed that whilst camera trapping is an effective method of surveying carnivores in an arid environment, the most efficient positioning of traps is dependent on the aim of the survey, with non-invasive hair collection devices being unsuitable for this environment. Being one of the first human-wildlife conflict studies to use both ecological and human perspective data simultaneously, it has demonstrated the need for this approach, suggesting the use of just one method is unlikely to provide a thorough understanding of this complex problem.

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1.0 Introduction

1.1 Human-wildlife conflict

An expanding human population, along with its associated effects of habitat fragmentation and destruction, all too often means wildlife is increasingly forced to live in close proximity to humans. It is in these circumstances, where competition for resources occurs, that human-wildlife conflict is most likely to occur (Inskip and Zimmerman 2009). Human-wildlife conflict has been defined by the World Wide Fund for Nature (WWF) as "any interaction between humans and wildlife that results in a negative impact on the human, social or cultural life, on the conservation of wildlife populations, or on the environment." (Anonymous, 2005). Jones and Barnes (2006) defined conflict as occurring when an animal damages or destroys human property or injures or ends human life and that animal is killed, injured or harmed as a result. General trends have shown human-wildlife conflict to be increasing in both frequency and severity in recent decades (Madden 2004), which is believed to be a result of global human population increases and subsequent expansion of human activities (Woodroffe, 2000).

There are a number of ways in which human-wildlife conflict can occur. One example is livestock depredation, such as snow leopards *Uncia uncia* predating domestic livestock in the Spiti region of the Indian Trans-Himalaya (Bagchi and Mishra 2006). Carnivores may also predate species raised for sport hunting such as when hen harriers *Circus cyaneus* predate on red grouse *Lagopus lagopus scottius* in Europe and are sometimes illegally killed as result (Hanley et al. 2010). Crop raiding by a range of species across the globe has been recorded, for example both Indian elephant *Elephas maximus* (Gubbi 2012) and Asiatic black bear *Ursus thibetanus* raid crops in Asia (Liu et al. 2011). Direct human fatalities are often a major cause of conflict such as those caused by lions in Tanzania's Ruaha landscape (Dickman et al. 2014). Less severe and uncommon forms of conflict include stone martens *Martes foina* climbing into car engine components in continental Europe (Herr et al. 2009) and attacks on humans by Australian magpies *Gymnorhina tibichen* (Jones and Thomas 2012). Human-wildlife conflict centred around the depredation of domestic livestock and wild game species are the two most well known carnivore issues across the globe (Graham et al. 2005), and are the focus of this study.

Although the reasons and causes of conflict situations vary, the main cause seems to be the expansion of human activities and increased use of natural resources and habitats which often result in wildlife being forced to live in close proximity to humans (Inskip and Zimmerman 2009). Such proximity inevitably causes conflict when humans and wildlife compete for the same, limited resources (Graham et al. 2005; Dar et al. 2009; Takahata et al. 2014). As carnivores, like humans, require a protein-rich diet and usually have large home ranges, they often come into recurrent competition with humans (Treves and Karanth 2003). Additionally, many carnivores have evolved to specialise in predating ungulates (Meriggi and Lovari 1996), and therefore are, or are commonly perceived to be, engaged in domestic livestock predation (Fonturbel and Simonetti 2011). Such conflict is especially common in areas where the natural prey base has been depleted through human activities (Agarwal and Mumtaz 2009). It is believed livestock depredation by large carnivores occurs in all areas where they coexist (Karlsson and Johansson 2010).

The effect of human-wildlife conflict on wildlife can have vast and far reaching consequences for the conservation of the wildlife populations involved. It is believed that most large carnivore species are experiencing global declines, due almost entirely to involvement in conflict situations (Michalski et al. 2006). Furthermore, it is believed that 75 % of the world's 37 extant cat species, 43 % of which are of conservation concern, and are affected by human-wildlife conflict (Inskip and Zimmerman 2009). African wild dogs *Lycaon pictus* are a clear example of a species which has suffered as a result of human-wildlife conflict. A minimum of 3,404 individuals were killed between 1956 and 1975 in Zimbabwe alone, and the species has now been extirpated from 20 of 39 former range countries, having been killed as vermin in government programmes as late as 1979. It is now one of the rarest carnivores in Africa (Fanshawe et al. 1991). Similarly Amur tiger *Panthera tigris altaica* still come into conflict with people in the Russian Far East, mainly through depredation of domestic livestock and attacks on humans, resulting in a total of 32 tigers being killed or removed from the wild between 2000 and 2009 (Goodrich et al. 2011). This species dropped to just 30 - 40 animals in the 1930's and is currently listed by the International Union for the Conservation of Nature (IUCN) Red List as Endangered with a global population estimate of 360 individuals (Miquelle et al. 2011).

Apex predators are known to stabilise food webs through both their consumptive and non-consumptive use of smaller carnivores and prey (Allen et al. 2013). Therefore, the removal of problem animals from an environment might have trophic cascade effects, for example the removal of large carnivores from an ecosystem might result in increases in the local population size of smaller carnivores, termed ‘mesopredator release’ (Prugh et al. 2009; Watts and Holekamp 2009). Such a release may not be desirable in habitats managed for agriculture, for example Rust and Marker (2013) found within Namibia, black-backed jackal *Canis mesomelas* were the most frequently perceived predator to account for 69 % and 68 % of goat *Capra aegagrus hircus* and sheep *Ovis aries* kills, respectively. However, not all subordinate carnivores react the same to large carnivore removal, for example a study by Yarnell et al. (2013) found the density of apex predators (lion *Panthera leo* and African wild dog) positively influenced brown hyena *Hyaena brunnea* density, yet negatively affected black-backed jackal density. It was believed the predatory behaviour of the apex predators produced more ungulate carcasses benefitting the brown hyena, a specialist scavenger (Yarnell et al. 2013). Such increases in subordinate carnivore populations can, in turn, be associated with declines in smaller prey items such as song birds, reptiles and small mammals (Berger et al. 2008).

It is important to also consider the effects of human-wildlife conflict on the human populations involved, which can be equally as vast. For example over the entire country of South Africa, the estimated costs of livestock depredation in 2010 was US$ 171 million (Cruise 2014). Subsistence farmers and low income households are often the most vulnerable to the costs of human-wildlife conflict as they often have little else to fall back on when crops or livestock are destroyed (Dickman 2005; Jones and Barnes 2006). A study of 80 agro-pastoral households bordering the Kibber Wildlife Sanctuary in the Indian trans-Himalaya showed the average loss of livestock by snow leopard and wolves *Canis lupus* equated to 50 % of the average annual per capita income (Mishra 1997). In a survey of 147 communal and resettled farmers in Namibia, Rust and Marker (2013) calculated the average cost per year due to livestock depredation to be US$ 3,461 per farm, with approximately one third of smallstock (sheep and goats) farmers making no profit, or losing more livestock to predators annually than replaced by births.

The economic impact of livestock depredation for humans can be defined in terms of direct and indirect costs. Direct costs such as loss of market value, veterinary costs for injured animals, replacement of breeding stock, and decrease in profits may be experienced. Indirect costs can include the measures to protect stock from carnivores, for example kraaling (enclosing livestock in a small fenced in area, often to a house) at night which may have the associated costs of increased disease spread through close contact of animals, and where lethal control is used, the costs of ammunition for firearms and poison (Mosert-Davies et al. 2007). In South Africa, the estimated cost of lethal control, such as traps, poisons and bullets, was US$ 3.30 per head of livestock, whilst non-lethal control methods such as guardian animals was estimated at US$ 3.08 per head (Cruise 2014).

Human-wildlife conflict near protected area boundaries, such as National Parks or conservation areas, can have larger consequences than the loss of livestock, income and carnivore life. It is often associated with negative attitudes towards the protected area, which in turn may foster anti-conservation sentiments in the local communities (Anthony 2007). Wang et al. (2006) found 52.2 % of local farmers disliked the Jigme Wangchuck National Park in central Bhutan, giving livestock depredation by carnivores as the primary reason for such an attitude. Such situations are especially problematic, as the establishment or expansion of protected areas is often considered to be the preferred method of carnivore conservation and a direct way to halt the loss of biodiversity in an area (Liu et al. 2010). Indeed, the ultimate success of protected areas is often significantly influenced by the attitudes of local communities (Dimitrakopoulos et al. 2010). Therefore, the lack of local support for protected areas may halt the conservation of the species within them.

Conflict situations often escalate when the people experiencing the conflict believe that the needs of wildlife causing the conflict are put over their own by either governments, international conservation bodies, or local authorities (Madden 2004). The establishment of protected areas often involves the exclusion of local communities which may further promote negative attitudes before any conflict situations arise, for example the creation of the Selous Game Reserve in Tanzania in 1922 saw the resettlement of 40,000 local people (Nelson et al. 2007). Meanwhile, between 100,000 - 600,000 people were displaced in India for the creation of protected areas for tiger *Panthera tigris* conservation (Lasgorceix and Kothari 2009). However, in a questionnaire by Harihar et al. (2014) of 158 households in the Terai Arc Landscape in the Indian-Nepalese trans-border, where 25.1 % of farmers experienced livestock depredation by both tiger and leopard, there was overwhelming support for resettlement, with 99 % of respondents supporting the measure as a means of improving their own well being.

1.2 Conflict resolution methods

A myriad of methods have been and are currently used to stop or reduce livestock losses to predators. For livestock farming to be successful, stock must be well-managed so that the number of livestock lost to predators is reduced to an acceptable level, through implementation of cost-effective mitigation methods (Mitchell 2004; Marker et al. 2005a). The lethal removal of wildlife has been a traditionally used method for a number of species, for example wolves *Canis lupus* and cougars *Puma concolor* were nearly eradicated in government predator control programmes in the western US in the 20th century (Riley et al. 2004). Terrestrial carnivores, with their relatively low density and slow reproductive rates are relatively easy to eliminate, although it is thought that well managed removal has the potential to decrease threats to livestock production without serious risk of extinction to wildlife populations (Treves and Naughton-Treves 2005). However, such an approach may be met with criticism from the general public, for example a survey regarding coyote *Canis latrans* in the US, Arthur (1981) found public opposition to lethal control, with a preference for non-lethal, experimental methods.

Within the category of lethal control, several different strategies are used; eradication, public hunts, culling and selective removal. Eradication aims to remove every single individual from a particular area, whilst other lethal control methods such as public or recreational hunting aim to reduce the overall population size in an area (Treves and Naughton-Treves 2005). Eradication can have unpredictable consequences on community structure, with the removal of one species having secondary effects on the abundance of another species. For example Palomares et al. (1995) found the removal of Iberian lynx *Lynx pardinus* in southern Spain to increase the predation of rabbits *Orytolagus cuniculus* by mongoose (Herpestidae) species. Similarly, coyotes play a keystone role in their environments, and Henke and Bryant (1999) found rodent species diversity and richness decreased significantly within the first nine months following coyote removal.

Public hunts have been used for species such as the red fox *Vulpes vulpes* in the UK and the Eurasian lynx *Lynx lynx* in Norway, however in the case of the Eurasian lynx the size of benefit from removal was so small that Herfindal et al. (2012) found it to be of little practical use. Such a strategy may gain more public support if local communities can derive benefit from the hunt such as in the form of hunting revenue (Treves and Naughton-Treves 2005). Culling is different to public hunts in that it is conducted by government bodies by hiring trained professionals, although by private citizens on private land (Treves and Naughton-Treves 2005). An example of culling is the removal of over 20,000 badgers *Meles meles* in the UK as part of the British TB control policy, due to the suggested transfer of bovine tuberculosis between badgers and domestic cattle (Donnelly et al. 2002).

Lethal control of specific problem causing individuals as opposed to indiscriminate removal (Smuts 2008) has been cited as the only option for those individuals repeatedly removing livestock (Jones and Elliot 2007), being more effective than non-selective removal (Jaeger et al. 2001). The main justification behind selective control is that conflict declines once the problem animal is removed, however once a territory becomes vacant following the removal of a problem animal, it is open for new individuals, which may potentially cause conflict, to move in (Treves and Naughton-Treves 2005; Davies-Mostert 2007). For example Blejwas et al. (2014) found in California removing breeding coyotes only temporarily reduced predation, and for territories with access to lambing pastures, predation of lambs resumed within an average of 43 days. Marker et al. (1996) also found on northcentral Namibian farmland the number of cheetahs in an area to actually increase following the removal of the resident cheetah, before a new individual became resident.

The actual methods of killing carnivores include shooting, poisoning and snaring (Ogada et al. 2003), with shooting done either when seeing the animal on sight or trapping first, often using the kill of the carnivore as bait in the trap (J. Bosman, pers. comm.). In more recent years, livestock guarding collars have been developed, consisting of a small rubber bladder containing a toxin such as sodium monofluoroacetate (Compound 1080) attached to the neck of the sheep or goat. Such a device is aimed at predators such as coyotes, which attack the neck of the ungulate. When the bladder bursts during attack, the toxin is ingested causing death of the predator (Walton 1991). Although this may alleviate conflict by targeting the specific problem causing individual, Connolly and Burns (1990) found the mean time of death from initial ingestion of Compound 1080 to be 217 minutes (range 115 to 436 minutes), which may raise concerns about the ethics of such a device.

Non-lethal control and conflict mitigation methods, which aim to reduce or stop predation without killing the carnivore species involved, are increasingly used and largely favoured by conservationists. Traditionally, non-lethal control was mainly a cost-benefit consideration, however in today's society it is also favoured due to conservation and ethical reasons (Breitenmoser et al. 2005). Translocation, the live capture of a specific problem animal in one area and movement and subsequent release of that animal to a new area, has been a standard management tool for conflict resolution for a number of decades (Linnell et al. 1997). However the process has been extensively debated due to high costs (Miller et al. 2011; Weise et al. 2014) and low success rates (Fonturbel et al. 2011). Atherya et al. (2011) reviewed 29 leopard translocations in India used to mitigate conflict, where the average translocation distance was 39.5 km from site of capture. It was found most leopards did not stay in the release area, and translocation actually increased the number of leopard attacks on humans. It was suggested that increased aggression due to the stress of the translocation process, movement through unfamiliar human-dominated landscapes, and fear of and aggression towards humans as a result of the translocation process were to blame (Atherya et al. 2011). However, in a recent study of six leopard translocations in Namibia, Weise et al. (2015) found the selective removal of six opportunistic stock raiders, stopped conflict for at least 16 months, and that only one translocated individual resumed livestock predation - however this involved livestock being illegally herded into a protected area.

Translocation, as a mitigiation method is widely accepted; as a costly endevour, in a review of translocations of carnivores in southern Africa and North America, Fonturbel et al. (2011) found the mean cost per individual was US$ 3,756 (± 357), which equated to up to 30 head of livestock in financial compensation. A study of large carnivore translocations in Namibia by Weise et al. (2014a) introduced the 'Individual Conservation Cost' (ICC) concept, which is defined as the cost of one successfully translocated individual, adjusted by the costs of unsuccessful events of the same species. Within Namibia the ICC for cheetah was US$ 6,898 and US$ 3,140 for leopard. The success of translocations often differs with species, with a number of biological and non-biological factors influencing success (Miller et al. 1999). Fonturbel et al. (2011) found 83 % of translocated carnivores were killed by humans and suggested that challenges associated with establishing new territories coupled with homing behaviour in carnivores can often mean translocated individuals have little chance of success.

Compensation schemes for wildlife damage are now widely used as a strategy to mitigate conflict (Schwerdner and Gruber 2007). It is believed that by spreading the economic burden and moderating the financial risks of wildlife damage, there will be a decrease in the negative consequences associated with conflict (Nyhus et al. 2003a). Such approaches to solving conflict are not new, with the approach being historically used by governments (Nyhus et al 2003a). Several countries including Kenya, Botswana, Malawi and Zimbabwe have used compensation schemes as a conflict mitigation tool (Maclennan et al. 2009), and it has gained popularity in recent years with governments and conservationists alike (Bulte and Rondeau 2007).

Challenges associated with compensation schemes may include lack of funds, fraud and more practical barriers such as farmers in remote locations having to travel long distances to report predation events (Bulte and Rondeau 2007). Additionally, when compensation becomes an option, farmers may become less risk-averse and are less likely to adopt conflict prevention methods or improve existing husbandry techniques (Nyhus et al. 2003b). Livestock losses to carnivores may also be exaggerated by farmers, for example in a study of cheetahs trapped on Namibian farmland that were perceived by farmers to be problem animals, Marker et al. (2003a) found just 3 % were actually likely to be killing livestock. The success of such schemes varies between projects, the Mbirikani Predator Compensation Scheme in Kenya is heralded as hugely successful, having all but stopped illegal lion killing in the area. The scheme pays a flat rate, close to the market value of the livestock, after a predator kill is verified, and imposes penalties for poor livestock husbandry methods (Maclennan et al. 2009). In contrast, in northern Portugal where compensation is paid to farmers for wolf predation on livestock, illegal killing of wolves still frequently continues in the area, with respondents expressing concerns with late payments and no compensation for lost livestock (Milheiras and Hodge 2011).

Livestock husbandry techniques may be crucial in reducing levels of conflict and depredation (Jones and Elliot 2007), and fencing is one example which has long been favoured as a mitigation method for physically stopping predators gaining access to livestock. Predator or wildlife-proof fencing is used extensively throughout southern Africa, for example within Namibia Lindsey et al. (2013), recorded 87 % of 250 farmers using it. In Kenya wildlife fencing was found to effectively control conflict with most problematic species (Kassily et al. 2008). A number of fencing types from basic thorn bush to electrified fencing are currently used globally (Breitenmoser et al. 2005). Additionally, visual barrier fencing, which consists of the bottom metre of fencing covered with a material such as shade cloth, is believed to halt the trigger of hunting behaviour as the carnivore does not actually see the livestock (Good et al. 2008).

Whilst fencing has been used to exclude carnivores from the livestock production areas, the effectiveness of this approach is influenced by how well a fence is maintained (Kesch et al. 2013). An alternative to electrifying pre-existing fencing has been the invention of the swing gate, a small gate fitted in fencelines which when pushed allows the passage of certain wildlife species through (Schumann et al. 2006). As the activity of digging animals such as porcupine *Hystrix africaeaustralis* and aardvark *Orycteropus afer*, often compromises the effectiveness of fences at excluding predators, swing gates aim to reduce the number of holes created in fence lines by such animals (Rust et al. 2014). Schumann et al. (2006) found swing gates to be effective, with no carnivores being recorded passing through, and to be more cost effective than electric fencing. However this also raises concerns regarding the demographic effects of hindering the movement of wildlife populations through an area (Weise et al. 2014b).

Kraals or bomas, fenced enclosures made to contain livestock in a small area, often overnight, are believed to be an essential part of livestock husbandry practices where carnivores are present (Good et al. 2008). In a study of the efficiency of livestock husbandry practices in limiting depredation by large carnivores in Kenya, Ogada et al. (2005) found when herds were closely attended by herdsmen whilst out grazing in the day and enclosed in traditional bomas at night, they experienced the lowest levels of predation. Maternity kraals for smallstock and cattle, when either pregnant or after birth, are thought to be especially effective when combined with synchronised breeding. Matching the breeding of livestock with that of wild ungulate populations means predators are more likely to target the young of natural prey rather than livestock (Good et al. 2008).

An increasingly popular non-lethal mitigation method has been the use of livestock guarding animals. Within southern Africa the use of Anatolian livestock guarding dogs is becoming common. Livestock guarding dogs differ from traditional herding dogs in that they protect the livestock rather than herd it (Rigg 2001). The Anatolian is a large breed, originating from Turkey, and has been used for over 6,000 years to protect livestock, using its threatening bark used to scare intruders and predators away. Anatolians show naturally attentive and protective behaviour towards the livestock they were raised with (Marker et al. 2005a; Marker et al. 2005b). In a study by Marker et al. (2005a) on the perceived efficiency of Anatolian livestock guarding dogs placed on Namibian farms, 73 % of farmers reported large declines in depredation levels, with a high level of satisfaction reflected by 96

% of farmers willing to recommend the scheme. However, in a recent review of performance of Anatolian livestock guarding dogs, Potgieter et al. (2015), challenged the categorisation of dogs as a non-lethal mitigation method, after recording killing of non-target carnivores by dogs. Additionally, it was seen between them, farmers and dogs killed more black-backed jackals in the survey year than the farmer killed alone in the year before acquiring a dog (Potgieter et al. 2015). Donkeys, with their natural aggression towards carnivores and social nature which bonds them to the livestock they live with, also make good livestock guarding animals. Llamas are the most recent animal to be used as livestock guarding animals (Braithwait 1996), and were found to result in fewer lamb losses to coyotes in Utah (Meadows and Knowlton 2009).

1.3 Agriculture in Namibia

Agriculture is an important industry in Namibia, contributing 5 % of the GDP in 2005, and earning N$ 1,258 million (approximately £ 96 million) in 2004 (Directorate of Planning 2005). Agriculture is the largest employer, supporting directly or indirectly 70 % of the population, and is the largest source of wage employment in Namibia, employing around 36,000 people (IFAD 1997). Land tenure is classified into three broad categories, the largest being commercial or “free hold” land which accounts for 44 % of the country, occurring mainly in the central and southern regions, followed by communal at 41 %, with the remaining 15 % being state land (Sweet 1998). The commercial sub-sector consists of 36.2 million ha, owned by 4,200 farmers, with an average farm size of 86.2 km^2 (Ministry of Agriculture, Water and Rural Development 1995). In 2005, the commercial livestock sector contributed 62.8 % of the national agricultural output (Directorate of Planning, 2005).

Reliable crop production under rain fed conditions can only occur in areas receiving an area of 400 mm rain annually, comprising just 34 % of the country (Ministry of Agriculture, Water and Rural Development 1995); therefore livestock is the main farming activity. Commercial farms primarily produce red meat, mainly based on cattle (Burke 2004a) for international markets, and secondarily supply domestic consumers (Kroll and Kruger 1998). Livestock is usually raised under extensive range conditions with reliance on natural pasture occasionally supplemented by salt licks (Sweet 1998). Commercial livestock farming involves the rearing and selling of cattle, small stock (namely sheep and goats), and ostrich for meat production. Latest census (2004) results show around 2.3 million cattle, 2.6 million sheep, 1.9

million goats, 30,000 ostrich and smaller numbers of pigs and poultry for Namibia, with beef production cited as the most important activity (Directorate of Planning 2005).

Agriculture in Namibia is not limited to commercial ventures, and most Namibians are believed to depend on the land for their subsistence (MET 2005). Whilst the commercial sector is characterised by being well-developed, capital intensive and export orientated, subsistence farming tends to be labour intensive with a limited use of technology and external inputs (Sweet 1998). Approximately 85 % of consumption poor households in Namibia are found in rural areas, with people making their living from subsistence farming. With subsistence farmers being the poorest members of the agricultural sector, they are considered the most vulnerable to the effects of human-wildlife conflict (MET 2005).

1.4 Community based natural resource management (CBNRM) within Namibia

Nature tourism as a means of promoting rural economic development and conservation in remote areas has gained widespread popularity across southern Africa (Silva and Mosimane 2012). Such an approach usually means community-based natural resource management (CBNRM). Within Namibia, this involves the establishment of communal conservancies which are legally recognised and geographically defined areas, demarcated by the communities themselves (Silva and Khatiwada 2012), which are cooperatively managed with livestock using ecosystem sensitive management plans (Marker and Boast 2015). Membership of conservancies is voluntary and free, requiring registration with the community management committee, and complete compliance with national conservation policies that promote sustainable environmental practices, protect biodiversity and increase wildlife stocks (Silva and Mosiname 2012). Through the establishment of conservancies, CBNRM aims to provide additional income to traditional farming for its residents whilst increasing wildlife populations for productive gain and halting the loss of biodiversity outside of protected areas (Denker 2011). It is believed conservancy members have a vested interest in the welfare of local wildlife populations through the economic benefits they derive from them following conservancy management guidelines (Marker and Boast 2015).

The conservancy movement within Namibia rapidly gained momentum its initiation in 1996; by the end of 2007 there were 50 registered conservancies covering a total of 118,700 km^2, housing 220,000 residents, having generated income and benefits totalling N$

39 million (NASCO 2015). The fact that Namibia is one of the few countries in Africa with an increasing herbivore population, and increasing or stable populations of large carnivores, has largely been attributed to CBRNM (Jones and Elliot 2007). A testimony to the conservation value of conservancies is the fact that now critically endangered black rhino *Diceros bicornis* are being translocated from National Parks into conservancies (Denker 2011).

Conservancies may generate income from photographic tourism and trophy hunting by joint ventures with outside companies, for example the Doro Nawas Lodge on the Doro !Nawas Conservancy is a joint venture between the conservancy and Wilderness Safaris. The lodge is the largest source of income for the conservancy and also provides essential employment (Denker 2012a). Conservancies may zone their land in relation to different land use strategies used. For example, the Ehi Rovipuka Conservancy in the Kunene region uses different areas for tourism, farming and hunting (Denker 2012b).

1.5 Human-wildlife conflict within Namibia

Namibia's Ministry of Environment and Tourism (MET) has cited human-wildlife conflict as one of the most difficult problems it faces and one which is only intensifying (MET 2005). It is believed the country's flourishing wildlife populations are giving rise to an increase in human-wildlife conflict, with a total of 3,194 problem incidents reported country wide from conservancies in 2005 (Jones and Elliot 2007). Within conservancies, economic analysis has shown the income generated through wildlife utilisation and photographic tourism is higher than the losses suffered by human-wildlife conflict (Jones and Elliot 2007). However, for commercial or subsistence agriculture, where alternative sources of revenue from wildlife are limited, losses of livestock to predators may cause a more significant impact.

In its national policy on human-wildlife conflict management (MET 2009), MET recognised that addressing human-wildlife conflict requires reaching a balance between conservation and the needs of rural communities living with wildlife. MET's policy on dealing with conflict promotes both biological diversity and self reliance, with the government delegating decision making to the lowest level (MET 2009). MET developed the 'Human-wildlife conflict Self-Reliance Scheme', which is not a compensation scheme, rather a means of directly offsetting the losses caused by conflict on State land, i.e. conservancies (MET 2010a). The scheme pays out set amounts to conservancy members having experienced damage as a result of conflict. Members must report the incident within 24 hours and the event must be verified by an MET staff member or a conservancy game guard. The amounts paid do not compensate the full market value of the crops or livestock lost, but are rather meant to offset the loss (MET 2010a), for example in January 2014 cattle were being sold in auctions at an average price of N$ 4,430 (Namibian Economist 2014), compared to an offset price of N$ 2,000 (see Table 1.1). A total of N$ 60,000 from the Game Products Trust Fund, which uses revenue from trophy hunting activities to support wildlife conservation, was given to each conservancy to start the self-reliance scheme with conservancies expected subsequently to add their own funding (MET 2010a).

Livestock	**Amount (N$)**
Cattle (cow or bull)	1,500.00
Goat	200.00
Sheep	250.00
Horse	500.00
Donkey	250.00
Pig	250.00

Table 1.1: Approved amounts paid for livestock loss in the Human-wildlife Self-Reliance Scheme, where payments are used to offset livestock losses, rather than as a source of compensation. Source: MET (2010a)

No self-reliance or compensation schemes exist for the commercial sector and commercial farmers therefore often remove carnivores as part of routine pre-emptive control or as a first response to conflict. Current legislation allows the owner or lessee of land to lethally remove a 'problem animal', i.e. one that is causing damage to or threatening livestock, life or property, on that land (Cirelli & Morgera 2010). Although farmers have the potential to allow trophy hunting of problem animals in order to gain revenue which could be used to compensate losses, Stein et al. (2010) found most Namibian farmers felt it easier to simply remove the animal themselves, due to the logistical issues in gaining a trophy hunting permit. Such relatively uncontrolled removal has previously resulted in large numbers of wildlife removal, for example Marker et al. (2003b) estimated 9,588 cheetah were removed from farmland nationwide from 1974 to 1994.

Most conservancies are located in the central and northern areas of Namibia, as shown in Figure 1.1, with the southern area consisting of the Tsau//Khaeb (Sperrgebiet) and Namib-Naukluft National Parks and mainly commercial livestock farms. Where protected areas directly border areas where species removal takes place, there is the potential for a species to be lethally removed on one side of the fence line, whilst enjoying full protection on the other, and this has the potential to affect sink-source dynamics (Andreasen et al. 2012). Pulliam (1988) defined a sink population as one where the death rate exceeds to birth rate and is generally in risk of extinction unless 'rescued' by immigrants other outside populations. In contract, in a source population, the birth rate exceeds the death rate leading to excess individuals which may emigrate to other populations (Pulliam 1988). Andreasen et al. (2012) found hunting pressure on mountain lions *Puma concolor* to create sink-source affects on population dynamics, causing populations experiencing removal by hunting to become sink populations. Therefore southern Namibia provides an excellent area to study human-wildlife conflict, especially on those farms bordering protected areas. Here lethal removal, which may often be a first choice of conflict resolution given the lack of compensation or self-reliance scheme, has the potential to create sink and source populations, which could ultimately hinder the conservation efforts of the National Parks.

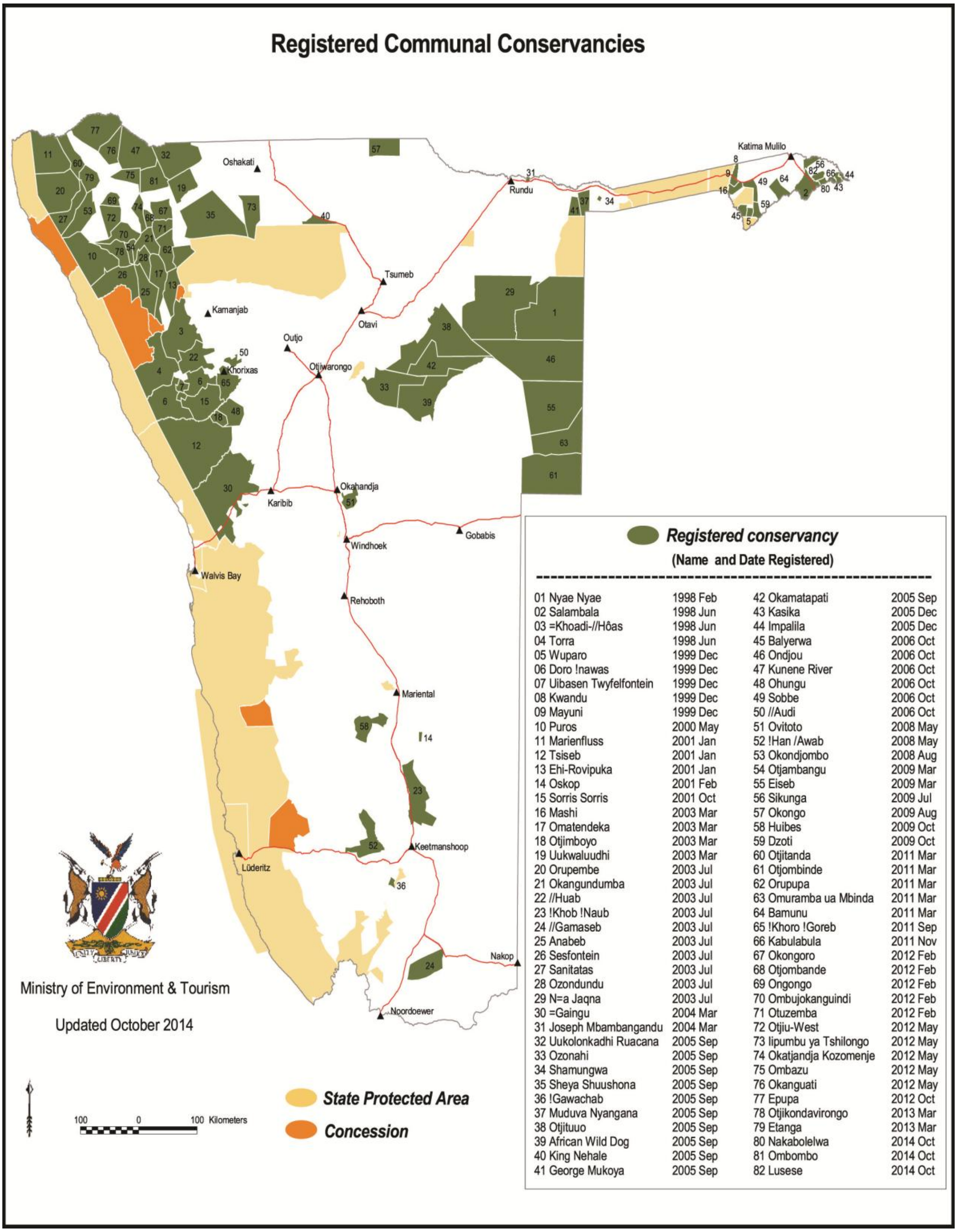


Figure 1.1: 2014 map of registered Namibian conservancies. Source: www.nasco.org.na

1.6 Aims and objectives

Overall, this project aims to investigate the real degree, i.e. rather than that simply perceived by farmers, of human-wildlife conflict occurring on commercial farmlands bordering either the Tsau//Khaeb (Sperrgebiet) National Park or Namib-Naukluft National Park, southern Namibia. As this area has not been studied previously and represents contours of 'no known occurrence' in the current Namibian Large Carnivore Atlas (Stein et al. 2012), confirming which carnivore species are present and in which densities or relative abundances will be crucial. Carnivores inhabiting arid and desert environments are usually understudied due to the challenges of associated low sample sizes, therefore determining most efficient methodologies for carnivores in such conditions will also be of future use.

Many previous studies of human-wildlife conflict fail to accurately confirm if domestic livestock is present in the diet of perceived problem animals, making it difficult to know which species are truly problematic and which are merely perceived to be so. Therefore, this project aims to use the relatively new technology of stable isotope analysis to examine the relative contribution of domestic livestock to carnivore diets. Additionally farmer questionnaires were be carried out to allow comparison of the ecological data collected to the farmers' perception of the conflict situation.

The study attempted to link ecological data to the human perception of the local conflict situation. Many published studies of human-wildlife conflict focus on the human perspective of the problem only, through the use of the questionnaire (e.g. Gusset et al. 2009), or through analysing a combination of questionnaire data and conflict event book records (e.g. Dickman 2008), without collecting ecological data pertaining to the conflict causing species themselves. This divide between human sciences and ecology was noted by Hemson (2008), who attempted to use novel techniques to span this divide and create a more holistic view of the conflict situation between cattle farmers and lions in Botswana. As this is the first ecological study of human-wildlife conflict in southern Namibia, it is important to collect data on both carnivore ecology and human attitudes towards conflict, in order that a comprehensive picture of the conflict situation is gathered. In turn, this should lead to the study being able to produce more informed recommendation regarding potential mitigation methods.

This thesis aimed to examine human-wildlife conflict on commercial farmlands bordering the Sperrgebiet and Namib-Naukluft National Parks, southern Namibia, by investigating both the ecology of carnivores and the human perspective of the problem. Additionally, given the fact that arid environments receive little attention from researchers, the thesis aimed to compare and develop methodologies for surveying a guild of carnivores in an arid environment.

The thesis will consist of the following experimental chapters, each with their own aims, specific objectives and hypotheses.

1. Modelling conflict-causing carnivore occupancy on arid commercial farmlands in southern Namibia. The aim of this chapter is to use an occupancy model approach to investigate the microhabitat features preferred by black-backed jackal, spotted and brown hyena and leopard, with the following objectives:

a) To produce a list of environmental variables/microhabitat features, as identified by the best fitting models as increasing occupancy and probability of detection for each focal carnivore species.

b) To compare these aforementioned lists between species, sites and seasons

c) To use information regarding the preferences of focal carnivore species to make informed recommendations regarding conflict resolution, by identifying areas preferred by carnivores, which should be avoided for grazing and kraaling

The specific hypotheses linked to this chapter are:

a) As water is a rare and essential resource across all study sites, it will be a microhabitat feature preferred by all species

b) Due to their known preferences for denning in mountainous areas, sites within mountain habitat will be preferred by brown and spotted hyena

c) Due to their preference for hunting in areas with cover, leopard will prefer sites with cover, specifically mountain and open plains/mountain transition habitat

d) Being a more opportunistic species, no microhabitat preferences will be seen for black-backed jackal

2. Spatio-temporal resource partitioning within a carnivore guild and between carnivores and prey, at waters on commercial farmlands, southern Namibia. This chapter aimed to examine the degree of temporal and spatial partitioning both within the carnivore guild and between focal carnivore species and domestic livestock and wild game, given the potential for such sites to be centres for activity for all wildlife species. The specific objectives for the chapter are;

a) To use camera traps at water points to identify the temporal and spatial patterns of activity at water points by carnivores, wild game (specifically oryx and springbok) and domestic livestock (specifically cattle and horses)

b) To compare and identify differences in temporal activity patterns at water points between each species pair, with significant differences in activity patterns being indicative of temporal partitioning

c) To compare and test for associations between the proportion of visits between species pairs at water points, with a significant, negative association taken as suggesting spatial partitioning as occurring

d) To test for an association between difference in body mass and degree of both temporal and spatial partitioning between species pairs, both within the carnivore guild and between carnivores and herbivores

The specific hypotheses for this chapter are:

a) Based on previous studies, it is hypothesised the carnivore guild will show mainly nocturnal activity, with the exception of cheetah, which will show mainly nocturnal activity, and honey badger and black-backed jackal which are hypothesised to show crepuscular activity patterns.

b) Due to the hypothesis of carnivores mainly showing nocturnal activity at water points, it is hypothesised herbivores, both wild game and domestic livestock would show diurnal activity.

c) As water points are rare and occur at a low density, it is hypothesised temporal, rather than spatial, would be the main mechanism used, both within the carnivore guild and between carnivores and herbivores, to avoid direct encounters at water points

d) As body mass has been cited as a predictor of predation, it is hypothesised associations between difference in body mass between species pairs and the degree of temporal partitioning will be seen. Species pairs with larger differences in body mass, will show a greater degree of temporal partitioning

3. Leopard density estimates from commercial farmlands in southern Namibia; a comparison to farmer estimates. This chapter aims to estimate leopard density across the two study sites and compare farmer estimations of leopard numbers on their land, to the number estimated to be present by camera traps, with the specific objectives:

a) To use the program CAPTURE with camera trap data to estimate leopard abundance on both the northern and southern study sites

b) To then use the half mean maximum distance used by individual leopards between camera traps to estimate the total area covered by the camera traps, and convert the abundance estimate into a density estimate

c) To gain estimates from study farm owners concerning the number of leopards present on their land, and to make comparisons between these estimates and the number of leopards recorded on camera trap on each property.

The following hypotheses apply to this chapter:

a) Due to the arid conditions, that leopard density will be low, as defined by the National Leopard Survey

b) Due to the secretive nature of leopards, farmers will be unable to accurately determine the number of leopards on their property

4. Examination of diet of carnivores on commercial farmlands, using stable isotopes and camera trapping. This chapter aims to use stable isotope analysis of hair samples, to examine and compare the diet of scavenging species, specifically brown hyena and black-

backed jackal, at the northern site, where an offal pit is not used, and the southern sites where an offal pit is active. It also aims to document the species utilising cattle carcasses, which were opportunistically found on NBR.

The chapter has the following specific objectives:

a) To analyse carnivore hair samples, and prey tissue samples, to obtain a carbon and nitrogen value for each species, using stable isotope analysis.

b) To make statistical comparisons between the carbon and nitrogen values, as well as the isotopic niche space occupied by black-backed jackal and brown hyena from the northern and southern study sites

c) To produce a species inventory of species visiting the offal pit, as well as calculating relative abundance indices, as a measure of activity, for each species, using camera traps

d) To use camera traps to compile an inventory of those species utilising two cattle carcasses on NBR

The specific hypotheses for this chapter are:

a) Due to the presence of an offal pit on Tsirub, black-backed jackal and brown hyena, will have similar isotopic signatures in the southern sites, and show a greater overlap of isotopic niche space between the two species, than in the north

b) In the north, due to the lack of an active offal pit, it is hypothesised that black-backed jackal will occupy the largest isotopic niche space and have the highest carbon value, indicative of a width of dietary items within the diet, due to its opportunistic nature

c) As aardwolf are known to specialise in termites which have a lower nitrogen value than herbivores, it is hypothesised aardwolf will have the lowest nitrogen value of all carnivores

d) Due to their known behaviours as scavengers, it is hypothesised brown hyena and black-backed jackal will be the only species visiting the offal pit at Tsirub.

e) As spotted hyena and black-backed jackal are the resident scavenging species in the north, it is hypothesised they will be the only species utilising the cattle carcasses on NBR

5. Assessing the human perspective of human-wildlife conflict on commercial farmlands in southern Namibia. This chapter aims to use a questionnaire approach to examine the human perspective of the human-wildlife conflict situation in southern Namibia.

The chapter has the following specific objectives:

a) To use a questionnaire to collect data regarding various physical aspects of each respondents farm, as well as data regarding the livestock management and current conflict mitigation methods used by each respondent

b) For each respondent to gain a perceived risk score for each focal carnivore species, incorporating a measure of perceived risk towards each livestock type on the farm, and the farmers attitude towards the carnivore, i.e. if they tolerate the species, or should shoot on site.

c) To produce a list of significant associations between those variables described in the first objective and carnivore risk scores

d) To calculate the number of respondents experiencing conflict with baboons, a problem noted by study farm owners, and to produce a list of the problems caused by baboons

e) To produce an inventory of those species identified by respondents as causing water pipe damage, a problem also noted by study farm owners.

The chapter has the following hypotheses:

a) Given the complex nature of conflict and the variety of respondents, there will be no significant associations between farm physical characteristics or management practices and the perceived risk scores of carnivores

b) Baboon conflict will be a common problem across respondents, affecting the majority of respondents who have baboons present on their property

c) Water pipe damage will be mainly caused by porcupine, a species known to cause damage with their teeth

6. Comparison of methods for surveying a guild of carnivores in an arid environment. This chapter aims to examine and develop effective and efficient methods of surveying a guild of carnivores in an arid environment.

The specific objectives for this chapter are:

a) Produce relative abundance estimates, latency until first detection and naive occupancy estimates for each carnivore species, for two camera trap survey designs, one with traps set up at water and another where traps are set up along roads

b) Where possible, use statistical analysis to compare the metrics listed in the first objective, as a measure of efficiency of each survey design

c) To compile a list of species detected by non-invasive hair collection devices, namely hair snares and rub stations, to compare to the species inventory as detected by camera traps, with hair samples analysed genetically to species level

d) To calculate the proportion of photographs obtained from each camera trap survey design, which could be used for individual identification, for African wild cat, brown hyena and leopard.

The chapter has the following hypotheses:

a) Due to the low density of and relative importance of water sources, the water point camera trap survey design will produce higher relative abundance indices, lower latency until first detection and higher naive occupancies, for all carnivore species

b) As carnivores are more likely to stop and drink at water points, it is hypothesised the proportion of photographs obtained which are suitable for individual identification, will be higher for the water point survey design.

c) Carnivores with a social system will be detected more frequently by rub stations than solitary species, due to the advantages of receiving more attention in the form of allogrooming from conspecifics, which has previously been documented for spotted hyena

The final discussion chapter then aims to link the microhabitat features identified by the ecological data as being preferred by carnivores, to those associated with higher levels of carnivore perceived risk in the questionnaire chapter.

2.0 Methods

2.1 Study Site Descriptions

The study site (Fig. 2.1), lies in south west Namibia, near the settlement of Aus (-26.6667/ 16 .2667), in the Karas region and consists both Namib Desert and Succulent Karoo biomes (Giess 1971). Average annual temperature is 17.5 ^{o}C (22.8 ^{o}C summer, 15.2 ^{o}C winter), ranging from -5 ^{o}C to 42 ^{o}C (Namibia Weather Network, 2014). Altitude lies between 1,000 - 1,500 metres, with an average annual rainfall of 80 mm. The area is positioned within a winter-summer rainfall transitional zone (Burke 2004), although most rain during the study period occurred during summer months (November to March).

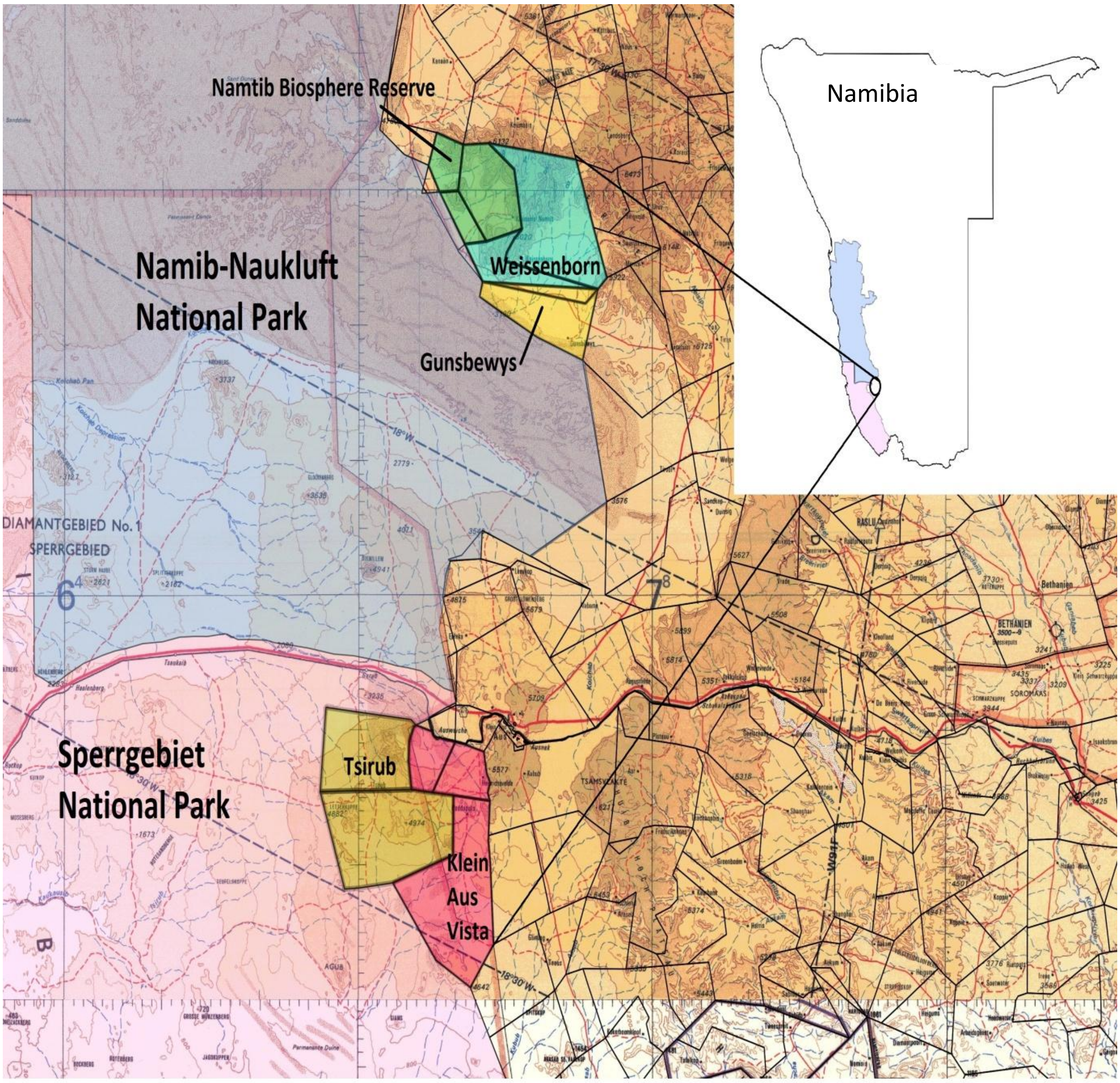


Figure 2.1: Map showing location of study area, with the five study farm borders outlined, along with the two National Parks in southern Namibia, in relation to the study farm's position within Namibia.

The area is characterised by mountains and large, flat, open grassy plains, dominated by *Stipagrostis* grass species with relatively few trees and shrubs (Fig. 2.2). Both the Tiras Mountains (Fig. 2.3) in the north and Aus Mountains are formed from granite and are part of the Namaqua Metamorphic Complex (Bertram 2003). No free-flowing water exists in the area in the form of permanent rivers; rather natural water is restricted to permanent springs (Fig. 2.4) and ephemeral pools forming after heavy rains in mountainous habitats. As a consequence, farmers are forced to provide water for domestic livestock and game via artificial water troughs (Fig. 2.5), with kilometres of plastic piping being used to transport water from boreholes to such troughs. Oryx *Oryx gazella*, springbok *Antidorcas marsupalis*, and ostrich *Struthio camelus* are the predominant game species within the area, with smaller numbers of greater kudu *Tragelaphus strepsiceros*, steenbok *Raphicerus campestris* and klipspringer *Oreotragus oreotragus* occurring.

Figure 2.2: Open plains habitat with ostrich

Figure 2.3: Mountain on NBR

Figure 2.4: Natural spring in mountain habitat

Figure 2.5: Leopard using artificial water trough

All study farms directly border either the Namib-Naukluft or Tsau//Khaeb (Sperrgebiet) National Park. The two national parks border each other along the tar road from Luderitz to Aus at the Sperrgebiet's northern border. The Namib-Naukluft National Park (NNNP) is Namibia's oldest and largest conservation area, covering 49,768 km^2 (MET 2008a). The National Park was first proclaimed in 1907 and was later expanded to provide a protected area for Hartmann's mountain zebra *Equs zebra hartmannae*, a species endemic to Namibia and southern Angola. In 1986, the protected area was again expanded to incorporate two former diamond mining areas (MET 2008a). Namibia's only population of wild horses *Equus ferus caballus* resides within the park, and are provided with an artificial water trough at Garub, close to Aus.

The Tsau//Khaeb (Sperrgebiet) National Park, at 26,000 km^2 was proclaimed in 2008, having been restricted from public access since 1908 following the discovery of diamonds near the coastal town of Luderitz (MET 2008b). Despite national park designation, access is still restricted to the general public and diamond mining concessions are operating within the area. The Sperrgebiet is one of the world's top 25 biodiversity hotspots largely due to the high abundance of succulents; 234 endemic species and 284 species are Red Data listed. The Orange River at the southern border is a designated Ramsar site and the Sperrgebiet coastline is Namibia's first Marine Protected Area (MET 2008b).

The study took place across five commercial farmlands; Namtib Biosphere Reserve (NBR), Weissenborn, Gunsbewys, located in the Tiras Mountain area north of Aus, and Klein Aus Vista (KAV) and Tsirub close to Aus. Each farm practiced a different combination of farming activities, and not all farms were carnivore friendly, i.e. lethal control methods are used to regulate problem animals and as a first response to conflict. Weissenborn and Gunsbewys were part of the Tirasberge Nature Conservancy. Conservancies, legally protected areas where landowners cooperatively manage and share resources amongst members, are an emerging movement in Namibia. Management policies are based on the principles of sustainable use and conservation of natural resources, and the reinstatement of natural biodiversity (CANAM 2011).

Base camp for the study was located at Namtib Biosphere Reserve (-26.002/16.234), a commercial farm and tourist accommodation approximately 70 km north of Aus, bordering the Namib-Naukluft National Park. The farm covers 164 km^2, with approximately 56 % consisting of mountain habitat, the remainder being open plains habitat. The farm has just three artificial water points provided for domestic livestock and game, one of these being in a kraal where carnivores and game cannot gain access, with a water point density of 1.83 water sources/100 km^2. The farm has few internal fences; a kraal for sheep *Ovis aries* at night and a smaller grazing camp for horses *Equus ferus caballus*, the rest being open. Five natural springs are known to exist on the farm, two of them being permanent and all being located within mountain habitats.

The main farming activity is small stock; damara sheep, a breed traditionally used for meat production, with a few goats *Capra aegagrus hircus*. At the start of the study, in

Jue 2012, the farm had close to 1000 sheep in two flocks (Fig. 2.6), but through sales and culling for meat, only 300 remained at the end of field work. The farm rented grazing to another local farmer and at the start of the study approximately 200 cattle *Bos taurus* were present, this number being reduced to 30 individuals by the end of the study. In November 2013, fifteen horses were bought onto the farm to be used for commercial horse safaris. The farm classes itself as predator friendly with non-lethal conflict mitigation methods being used; sheep are accompanied by a shepherd and Anatolian livestock guarding dog in the day and kraaled at night using jackal-proof fencing. Cattle and horses are free-roaming, with bulls running with the cows all year round. Horses and cattle are checked on every other day.

Farm Weissenborn (-26.153/16.441), was used primarily as an additional site for the National Leopard Survey (NLS)*, and was surveyed from March 2013 to May 2014. Weissenborn is primarily a cattle farm with approximately 350 cattle and at the start of the study, in June 2013 also had karakul sheep, a breed used for its pelt, which were all sold in December 2013. Sheep were kraaled close to the house at night, but were sent out to graze without a shepherd in the day. The farm borders the Namib-Naukluft National Park, and covers 330 km^2, 35 % being mountain habitat and 65 % being open plains. Seven artificial water troughs are located throughout the farm at a density of 2.12 water sources/100 km^2, and livestock is checked on once in five days. Weissenborn is divided up into smaller grazing camps, which cattle are rotated through to prevent over-grazing. Bulls and cows are kept separately until the breeding season. The farmer is carnivore intolerant, shooting black-backed jackal *Canis mesomelas* on a regular basis and using lethal control as the primary method of dealing with problem animals.

*The project collaborated with Namibia's Ministry of Environment and Tourism for the National Leopard Survey, a nation-wide survey aiming to produce regional density estimates for leopards that would be used for setting national hunting quotas. See section 2.3.2 for more details.

Gunsbewys (-26.158/16.309) is the smallest study farm at 100 km^2, and shares a 25 km border fence with the Namib-Naukluft National Park. The farm is entirely open plains habitat, with the south-eastern section of the farm turning to dune habitat at the start of the Namib Desert dune field (Fig 2.7). Gunsbewys rented grazing to the owner of 150 cattle at the start of the study, however all cattle were removed from the farm in April 2014, after spotted hyenas *Crocuta crocuta* allegedly predated upon an adult cow. The farm has just two water points, giving a density of 2.00 water sources/100 km^2. The farm owner is predator friendly and refused to allow the owner of the cattle to shoot a hyena following the predation, hence the removal of the cattle from the farm. Gunsbewys has a small camping site, self catering bungalow and private rooms.

Figure 2.6: Sheep being taken for grazing, NBR

Figure 2.7: Dune habitat border fence, Gunsbewys

Klein Aus Vista (-26.716/16.264) borders the Tsau//Khaeb (Sperrgebiet) National Park and is located 2 km west of Aus. It comprises the farms Paddaputs, Heinrichsfelde and Ausweiche. The main farming practice is cattle production, with approximately 400 cattle farmed on the 500 km^2 site. Approximately 20 % of the farm is mountain habitat with the remaining 80 % being open plains (Fig 2.8). Twenty artificial water points are located throughout the farm, giving a density of 4.00 water sources/100 km^2. Fifty domestic horses are also kept on the farm, although are not considered a main farming activity. The farm was originally three farms and most of the original border fences are still in place and are used as grazing camps for the livestock; however the wire in these fences is widely spaced allowing carnivores and smaller game passage through. The farmer is generally carnivore tolerant, although sporadic shooting of black-backed jackals does occur. Livestock is checked on once a week. The farm also houses a luxury tourist lodge, campsite and mountain bungalows.

Figure 2.8: Aerial view of mountains, KAV

Figure 2.9: Offal pit at Tsirub

Tsirub (-26.774/16.058) is a 400 km^2 game farm bordering the Tsau//Khaeb (Sperrgebiet) National Park, close to the Garub horse trough area. At the start of the study a small number of cattle were present on the farm, but were removed shortly after camera trap surveying began as the farmer wanted to concentrate solely on game farming. Oryx and springbok are hunted from a vehicle on a twice weekly basis and the meat sold wholesale in nearby Luderitz. Butchery occurs on-site with an open offal pit being used for disposing of offal, horns, skins and bones of game (Fig 2.9). Approximately 15 % of the farm is mountain habitat, the rest being open plains. Twenty-nine artificial water points are in operation, resulting in a water point density of 7.25/100 km^2, with no internal fences occur on the farm. The farmer is carnivore intolerant, shooting black-backed jackal on sight and considering lethal control of problem animals as a first solution.

2.2 Species descriptions

2.2.1 Focal species

2.2.1.1. Black-backed jackal

Black-backed jackal (Fig. 2.10) is listed as Least Concern by the International Union for the Conservation of Nature (IUCN), although no population estimates are currently available. The species is endemic to Africa, existing in two distinct sub-populations separated by at least 1000 km, one in east Africa and the other in southern Africa. Within South Africa and

Namibia they are widespread and common in protected areas, whilst considered vermin in livestock production areas (Hoffmann 2014a). Across southern Africa black-backed jackals occupy a variety of habitats including open and arid areas, preferring habitats with scattered bush (Estes 1992).

Black-backed jackals have a fox-like appearance with a long and pointed muzzle and pointed and erect ears. The species earns its name from the black stripe situated midway up each flank, sloping obliquely from behind the shoulder to the top of the rump. The back has a dark saddle, with reddish limbs and flanks and the tail is black and bushy (Loveridge and Nel 2004). Average body weight is 7.8 kg and 6.6 kg for males and females respectively (Estes 1992), with an average weight of 9.7 kg for jackals on Namibia's skeleton coast (Loveridge and Nel 2004), shoulder height ranges from 38 to 48 cm (Estes 1992).

The basic social unit of black-backed jackals is a monogamous mated pair, the pair bond between adults lasting for life (Loveridge and Nel 2004). If one member of the pair dies, the other usually looses the territory quickly. Adult pairs are often accompanied by the previous years' offspring who stay to help raise the next litter of pups (Estes 1992). Groups defend territories, which are usually temporally and spatially stable, using faeces and urine as markers (Loveridge and Nel 2004), as well as vocal advertisement in the form of a long, whining howl, which is also used to call group members together (Estes 1992). Home range has been found to vary across the range of the species (Loveridge and Nel 2004); Rowe-Rowe (1982) recorded an average home range size of 18.2 km^2 in KwaZulu Natal, South Africa, Kamler et al. (2012) recorded 17.75 km^2 in Benfontein, South Africa and Kaunda (2001) recorded a mean home range size of 15.9 km^2 in Botswana.

Figure 2.10: Black-backed jackal, Namtib Biosphere Reserve

Usually only the dominant individuals within a territory breed, with breeding by subordinates stopped by constant harassment from dominant jackals (Loveridge and Nel 2004). Breeding seems to be largely seasonal, with mating occurring between late May and August in southern Africa (Bernard and Stuart 1992). Between one and eight (mean 4.6) pups (Bingham and Purchase 2002) are born after a gestation period of 60 days in a burrow (Bernard and Stuart 1992). Alloparental care, in the form of food regurgitation and guarding of the pups whilst the parents are away, is usually given by the previous years' offspring (Moehlman 1978) and can drastically improve survival success of the litter (Estes 1992).

Black-backed jackals are generalist feeders, with the diet varying according to food availability at the time (Loveridge and MacDonald 2003). Many studies of diet have found mammals, in particular ungulates to be important dietary items in a range of locations; for example Kaunda and Skinner (2003) in Mokolodi, northern Botswana, Linh San et al. (2009) in the Great Fish River Reserve, South Africa, Klare et al. (2010) in Kimberley, South Africa, and Van de Van et al. (2013) in the eastern Karoo, South Africa. Black-backed jackals living at Van Reenen Bay seal colony, southern Namibia were largely dependent upon Cape fur seal pups as a food resource (Kotze and Swanson 1989). Whilst jackals are classed as mesocarnivores, a single animal was recorded killing an adult female impala *Aepyceros malampus*, which has a body mass of 45 kg, in Botswana (Kamler et al. 2009).

The IUCN states there are no major threats to the existence of this species, however they are persecuted for their role as livestock killers and rabies vectors (Hoffmann 2014a). It is noted that whilst the species is heavily persecuted on farmlands, for example in South Africa 317,787 bounties were paid for dead jackals between 1914 and 1923 (Bezuidenhout 2014), this seems be mostly ineffective, causing a temporary decrease in numbers only (Hoffmann 2014a).

2.2.1.2 Spotted hyena

The IUCN currently lists spotted hyena (Fig. 2.11) *Crocuta crocuta* as Least Concern, and is Africa's most abundant large carnivore, having an estimated global population of 27,000-48,000 adult individuals, with viable populations persisting in a number of countries. Sub-Saharan Africa has a widespread population of around 10,000 adults, the largest population occurring within the Serengeti ecosystem; the Tanzanian portion being home to between 7,200 and 7,700 individuals, and 500 - 1,000 individuals on the Kenyan side (Honer and Holekamp 2008). Population size in Namibia was recently estimated at 7,198 - 13,092 individuals in the Large Carnivore Atlas (Stein et al. 2012), although due to the methods used to produce this estimate, mail-in questionnaires to landowners, the Atlas recognises the need for a more detailed survey.

Figure 2.11: Spotted hyena, Namtib Biosphere Reserve

Spotted hyenas occur in a wide variety of habitats, often in close association with humans, but are usually absent or occur at low densities in extreme desert conditions and tropical rainforests (Honer and Holekamp 2008). In the Namib Desert, it is often found in areas of riverine growth along seasonal rivers. Density of adults can vary significantly throughout their range, from 0.006 to 1.7 individuals/ km^2 (Hofer and Mills, 1998). Territory size can also vary significantly and has been recorded at less than 40 km^2 in the Ngorongoro Crater (Kruuk 1972) to over 1,000 km^2 in the arid Kalahari (Mills, 1990).

Spotted hyena is African's second largest carnivore after the lion *Panthera leo*, with an average shoulder height of 70 - 91.5 cm and weighing up to 86 kg (Estes 1992). Females are 10 % larger than males (Frank 1997; Holekamp 2006). The species is the largest member of the hyena family, with a powerful, dog-like build, sloping back and short back legs (Mills and Hofer 1998). Young are born solid seal-grey, changing to a lighter grey with black spots, turning grey with age, and dark feet and muzzle when mature (Estes 1992). Spot patterns are individually unique. The female spotted hyena is unusual in having a pseudopenis; the female has no external vagina, instead the urogenital canal traverses the enlarged clitoris (Frank 1997). The females' enlarged clitoris and male penis are virtually indistinguishable, and the female gives birth, urinates and copulates through the pseudo penis (Holekamp 2006). Discussions are still on-going within the scientific community as to the purpose of the pseudopenis (Holekamp 2006), with two main theories in existence. Firstly the pseudopenis evolved as it serves as a signal in greetings ceremonies, where the anogenital region is exposed and sniffed and licked by the second individual (East et al. 1993). Secondly the competition-aggression hypothesis states that selection for adult aggressiveness, which confers advantages of better access to resources, favoured fetal androgen production which in turn resulted in male-like genitalia (Frank 1997).

Spotted hyenas live in social groups called clans, which can range in size from 3 to over 90 adult individuals (Estes 1992), and consist of multiple unrelated adult males and multiple, usually related matrilines and their young (Trinkel and Kastburger 2005; Holekamp 2006). In Namibia clan sizes in Etosha National Park range from 11 to 30 individuals (Trinkel 2003), whilst in the Namib-Naukluft National Park, clans are much smaller, ranging between three and eight individuals (Tilson 1984). Clans are defined as fission-fusion societies where individuals are likely to be found in smaller sub-groups (Holekamp et al. 1997). Strict linear hierarchies exist within clans with an individual's position within the hierarchy determining its access to resources (Tilson et al. 1984). A juveniles' social status is inherited from her mother and females are always socially dominant to males (Holekamp 2006).

Breeding is largely non-seasonal, with two young (range 1 - 4) being born after a 16 week gestation period (Estes 1992). Young are born into a secluded natal den (Kruuk 1972) and are then moved by the mother into the communal den (White, 2007). Sibling aggression is extremely common, especially in same sex litters and often commences within five minutes following birth (Frank et al. 1991). Females usually stay within the natal clan their entire lives whilst males disperse (Watts and Holekamp 2007) at 24 to 60 months old (Van Horn et al. 2003).

Spotted hyenas are well known for their rich repertoire of vocal communications (Mathevon et al. 2010), with ten distinctive call types being recognised (Kruuk 1972). Vocalisations can be used for long range communication, for example the 'whoop' which can be heard for up to 5 km, or close-range communication such as the 'giggle' which is used to indicate anxiety or fear (Estes 1992). Spotted hyenas also use olfactory communication, where individuals of both sexes also paste mark a fatty, smelly, white secretion from the anal gland on tall grass stalks throughout the territory (Burgener et al. 2008). Scent marks are thought to be individually recognisable and aid the maintenance of a social network within the fission-fusion community (Burgener et al. 2009).

Whilst traditionally known as a scavenger, spotted hyenas are adapted for hunting medium to large ungulate prey, and are capable are taking down prey three times their own body weight. Spotted hyenas feed primarily on prey they kill themselves, but will also scavenge opportunistically (Watts and Holekamp 2007). In the Kuiseb River Canyon area of the Namib-Naukluft National Park Tilson et al. (1984) recorded oryx remains in 79.6 % of scats and Hartmann's mountain zebra in 12.7 % of scats. In contrast, in the Etosha National Park, spotted hyenas were recorded as major predators of migratory ungulate species; springbok, plains zebra *Equus burchelli* and blue wildebeest *Connochates taurinus* (Trinkel 2010a).

Human persecution in the form of shooting, hunting and trapping in conflict situations and the decline of wild prey species due to increased human habitation and over-grazing by domestic livestock are the main threats faced by spotted hyenas (Honer and Holekamp 2008). Trophy hunting for the species is not especially common, as they are not traditionally seen as an attractive species; however they are used for food and traditional medicine in certain cultures (Hofer and Mills 1998).

2.2.1.3 Brown hyena

Brown hyena *Hyaena brunnea* (Fig 2.12) is listed by the IUCN as Near Threatened with an estimated global population of 5,000 - 8,000 individuals, with Botswana having the largest population with an estimated 3,900 individuals (Wiesel et al. 2008). The population for Namibia was estimated at 566 - 2440 individuals, with high occurrence mapped for most of the entire western coastline (Stein et al. 2012). The species is endemic to southern Africa and inhabits desert areas with an average annual rainfall of less than 100 mm, semi-desert, open scrub, and open woodland savannah with a maximum average annual rainfall of 700 mm (Wiesel et al. 2008).

Like spotted hyenas, brown hyena has a dog-like appearance, with powerfully built forequarters and the typical hyena sloping back (Mills 1998). Brown hyena has long, dark brown to black shaggy hair, which can reach 25 cm in length (Skinner 1976), and a golden mantle and yellow and black stripes on the fore and hind legs (Estes 1992), the patterning of which is unique to each individual. In contrast to spotted hyenas, the ears of brown hyenas are long and pointed (Mills and Hofer, 1998). Shoulder height is 78.7 cm, with a range 70.6 - 86.8 cm and the mean body weight is 39 kg (range 35 - 50kg) (Estes 1992).

Although brown hyenas are usually seen alone when foraging, social groups known as clans exist, consisting of kinship groups including sons and daughters (Estes 1992). Clan sizes of up to 10 individuals have been recorded (Mills 1990) with social structure ranging from a solitary female and her young to several females and their offspring of different ages. Females usually remain within their natal clan, whilst males remain in the natal clan, become nomadic mating with females from several clans or immigrate permanently into another clan (Mills 1998).

Figure 2.12: Brown hyena, Tsirub

Social interactions mainly occur at the den, which is the social meeting point of the clan (Mills 1983). Unlike spotted hyenas, brown hyenas communally suckle and provision young at the den (Estes 1992). Group members bring food back to the den whilst cubs are being raised, leading to accumulations of bones at den sites (Skinner and Aarde 1991). Clan females will mate with immigrant and nomadic males and produce an average of three cubs (range 1 - 5) after a gestation period of 97 days (Mills 1983). Cubs are born with eyes and ears closed (Mills and Mills 1978), with the denning period lasting 15 months, during which time the young are moved between several dens (Mills 1998).

Brown hyenas are primarily scavengers of large vertebrate carcasses, but will also supplement their diet with fruits, reptiles and insects and birds eggs (Mills 1998). In the Makgadikgadi area of Botswana brown hyenas living within the vicinity of pastoralists, domestic livestock carcasses was found to be an important food resource (Maude 2005), whilst on the Namib Coast brown hyenas feed mainly on Cape fur seal *Arctocephallus pusillus pusillus* pups and marine carrion (Wiesel 2010).

The distribution of food resources determines the size of a territory, whilst the type of food within a territory determines clan size (Mills 1982). In the southern Kalahari Mills and Mills (1982) recorded territory size from 285 km^2 to 480 km^2, with a density of 1.8 individuals/100 km^2. Density in the Makgadikgadi area of Botswana was estimated at 2.0/100 km^2 (Maude 2005), and 2.8/100 km^2 in Pilanseberg National Park, South Africa (Thorn et al. 2009), whilst a high density in Namibia is considered between 0.15 and 1.0 individuals/ 100 km^2 (Stein et al. 2012).

Brown hyenas defend territories through the use of olfactory communication (Estes 1992), through defecating at latrines and through a scent marking behaviour known as pasting, in which anal gland secretion are pasted onto vegetation and rocks through inverting the anal gland pouch (Mills 1998). During pasting, two types are paste are deposited; a white paste with a long lasting odour and a black paste with a much shorter lasting odour (Mills et al. 1980) The main threat to the survival of this species comes from human-wildlife conflict; animals are often shot, trapped or poisoned in response to alleged predation events (Wiesel et al. 2008), however the impact of brown hyenas on domestic livestock is usually small (Mills 1998, Maude 2005).

2.2.1.4 Leopard

Leopard *Panthera pardus* (Fig. 2.13) is listed as Near Threatened by the IUCN Red List, although currently no reliable population estimate for Africa exists (Henschel et al. 2008).

Leopards are the most widely distributed cat species in the world (Stein and Hayssen 2013), occurring throughout sub-Saharan Africa, India and southern Asia (Nowell and Jackson 1996), with relict populations in the Middle East and south-eastern Europe (Hunter et al. 2003). The Namibian population is believed to be part of a genetically diverse sub-species *P. p. pardus*, occurring across Africa (Uphyrkina et al. 2001). The species occurs widely throughout sub-Saharan Africa, but has disappeared from 36.7 % of its historical range across Africa (Ray et al. 2005). Namibia is believed to house between 13,356 and 22,706 individuals, with population increases occurring throughout many regions within the country (Stein et al. 2012). Leopards have the widest habitat tolerance of any old world felid, having been recorded in habitats ranging from tropical rainforests to deserts (Henschel et al. 2008) as well as alpine mountains and edges of urban areas (Balme et al. 2007). In Africa it seems to be most successful in woodland, grassland savannah and forest habitats (Henschel et al. 2008), preferring rocky hills and mountainous areas (Swanepoel 2008) however, it can survive in any environment where there is sufficient cover for concealment (Estes 1992). In Namibia the leopard is absent from the Skeleton Coast (Stein and Hayssen 2013), but is believed to have healthy populations throughout the rest of the country, primarily on farmlands (Stein et al. 2011).

Leopards are long and low cats with sexual dimorphism between the sexes (Estes 1992). There is variation in body size between geographical regions, with leopards in the Cape region being the smallest in Africa (Stein and Hayssen 2013). Shoulder height ranges between 60 - 70 cm and 57 -64 cm in males and females respectively, with average weight of males 35 - 65 kg and 28 - 58 kg for females (Estes 1992). Mature males develop a dewlap from the lower jaw to chest and have large and well-defined musculature on the forelimbs, shoulders and neck (Stein and Hayssen 2013). The coat is a pale tan colour with dark spots grouped into rosettes (Estes 1992).

Figure 2.13: Male leopard, Klein Aus Vista

Being a typical cat, leopard are both solitary and territorial; adults only coming together long enough to mate (Estes 1992). Home ranges of males encompass ranges of several females (Mizutani and Jewell 1998). Home range size and density have been found to be highly variable, and home range is largest where prey availability is lowest (Stein and Hayssen 2013). Stein et al. (2011) recorded densities of 1.0 leopards/100 km^2 in the Waterberg Plateau Park, Namibia, and 3.6 leopards/100 km^2 on adjacent commercial farmland. Marker and Dickman (2005a) recorded wet season home range sizes ranging from 55.9 km^2 to 1,099.1 km^2 in north central Namibia, with no significant differences between the sexes. Home ranges sizes for leopards in Namibia are larger than those recorded elsewhere in Africa (Marker and Dickman 2005a), with the exception of those recorded by Bothma et al. (1997) in the southern Kalahari, where males had a mean of 2,182.4 km^2 and females 488.7 km^2.

Territories are defended by vocal and olfactory communication, and the entire home range is moved through over a period of seven to ten days (Mizutani and Jewell 1998). The distance call of the leopard, known as ‘sawing’, is usually made at dawn and dusk whilst the animal moves through the territory (Estes 1992). Olfactory communication occurs in the form of urine marking trees, bushes and rocks throughout the territory and is especially used by males when mating (Bothma and Le Riche 1995), and by females hoping to attract a male (Bailey 1993). Trees are regularly used for sharpening claws, with Bothma and Le Riche (1995) believing this behaviour has the primary function of sharpening the claws rather than olfactory communication.

Between one and three cubs are born after a gestation period of 90 - 100 days, in concealed areas such as dense thickets, hollow trees or caves. Young usually become independent at 13 months and sexual maturity is reached at two years (Estes 1992). Infanticide by male leopards is common and observed and inferred rates are amongst the highest recorded for any mammalian carnivore (Balme and Hunter 2013).

Diet of leopard is highly catholic, with 92 prey items have been recorded from sub-Saharan Africa alone (Bailey 1993), although ungulate prey within the 10 - 40 kg range is preferred (Hayward et al. 2006). They are able to survive on smaller prey items if necessary (Stuart and Stuart, 1993), but have also been recorded taking much larger prey such as giraffe *Giraffa camelopardalis* calves (Scheepers and Gilchrist 1991). Ott et al. (2007) found domestic livestock contributed only a small part of leopard diet in the Baviaanskloof region, South Africa. The leopard is a typical ambush and stalk predator (Estes 1992) and has to approach prey extremely closely, for example Stander et al. (1997) found a leopard had to be within of 4.4 ± 0.25 m (mean ± SE) of prey to before initiating a charge to have a chance of success. To avoid competition with other carnivores leopards haul kills into trees (Estes 1992), and are able to carry carcasses more than double their own body weight (Scheepers and Gilchrist 1991).

Within Africa the major threats faced by leopards are habitat conversion and retaliatory killings following real or perceived livestock predation events (Ray et al. 2005). Henschel et al. (2008) noted an increasing number of leopards being removed through poisoning of carcasses for predator control. Trade in skins and canines domestically within some central and West African communities are additional threats faced (Henschel et al. 2008).

2.2.2 Non-focal species

2.2.2.1 Cape fox

Cape fox *Vulpes chama* (Fig. 2.14) is the smallest canid and only true fox in southern Africa, where is it endemic, occurring in South Africa, Namibia, Botswana and Angola, although its presence in Lesotho and Swaziland is still unconfirmed (Stuart and Stuart 2004). It is listed by the IUCN as Least Concern (Hoffmann 2014b), and is common to fairly abundant throughout its range (Stuart and Stuart 2004), although its populations are known to be suppressed by black-backed jackal (Kamler et al. 2013; Kamler and MacDonald 2014).

Cape foxes have grizzled silver-grey upperparts with the lower limbs, head and back of ears being reddish to tawny brown. The tail is thick and bushy with a black or dark brown tip (Stuart and Stuart 2004). Average shoulder height is 35 cm, with an average weight of 2.8 kg and 2.5 kg for males and females respectively (Skinner and Chimimba 2005). The species inhabits arid and semi-arid areas preferring open country, particularly grassland (Hoffmann 2014). It is strictly nocturnal and solitary (Skinner and Chimimba 2005), with members of the mated pair foraging solitarily but having high overlap of home ranges (Kamler and MacDonald 2014). Home range size was calculated at 27.68 km^2, with a density of 4.9 foxes/100 km^2 in South Africa (Kamler et al. 2012). Between one and six young (mean 2.8) cubs are born (Stuart and Stuart 2004), usually in spring and summer (Stuart 1981), and are defended by both parents (Stuart and Stuart 2004).

Figure 2.14: Cape fox, Klein Aus Vista

Whilst Cape foxes take a number of prey items (Stuart and Stuart 2004), Stuart (1981) found small mammals to be by far the most important prey item for Cape foxes in the Cape province, South Africa. They are considered a problem animal by farmers over most of their range (Hoffmann 2014), although little evidence of predation on domestic livestock exists (Skinner and Chimimba 2005). The IUCN states no major threats to this species exist (Hoffmann 2014).

2.2.2.2 Bat-eared fox

Bat-eared fox *Otocyon megalotis* (Fig. 2.15) has a disjunct range, occurring in southern and east Africa across arid and semi-arid regions (Nel and Maas 2004). The species is listed by the IUCN as Least Concern, and is common in conservation areas, only becoming uncommon on farmland in southern Africa where it is occasionally persecuted (Hoffmann 2014c). Bat-eared foxes are small, slight canids having slim legs, a long and bushy tail with conspicuously large ears. The backs of the ears, snout and face are black, whilst the rest of the body is uniform grey. Males are slightly larger than females, with an average body mass of 4.1 kg, compared to 3.9 kg for females (Nel and Maas 2004).

Figure 2.15: Bat-eared fox, Tsirub

Bat-eared fox prefers short grass with areas of open ground, light acacia woodland and overgrazed rangeland. Its habitat requirements and geopgraphic range are almost the same as its main prey item the harvester termite *Hodotermes mossambicus* (Estes 1992). The species is monogamous, although whether the pair bond lasts for life is still unknown (Estes 1992). Pairs forage as a unit (Nel and Maas 2004), with nocturnal foraging behaviour in summer turning to diurnal foraging in winter when sub-zero temperatures keep harvester termites below ground at night (Nel 1990). Mating usually takes place from July to September, where up to 10 copulations per day occur (Rosenberg 1971). Breeding occurs annually (Estes 1992) and between one and six cubs are born after a 60 - 75 day gestation period (Nel and Maas 2004). Males have been recorded spending significantly more time at the den than females, guarding, grooming and defending young against predators (Wright, 2006).

Whilst previously regarded as a dietary specialist of termites, the species has recently been recorded as having a much broader prey range, with termites only representing 12 - 40 % of biomass in a study by Klare et al. (2011). Prey abundance has an influence on bat-eared fox density; where termites, insects and insects are abundant densities can reach 280 foxes/100 km^2 (Estes 1992). Kamler et al. (2013) estimated density at 67.7 foxes/100 km^2 in Kimberley South Africa, with home ranges of 2.79 km^2, whilst Kamler et al. (2012) recorded a home range of 4.96 km^2 on a game farm in Kimberley, South Africa. No major threats to the survival of this species are listed by the IUCN, however it is acknowledged that they are persecuted in some areas of southern Africa where they are perceived as a predator of livestock (Hoffman 2014c).

2.2.2.3 Honey badger

Honey badger *Mellivora capensis* (Fig. 2.16) has a globally wide distribution occurring across Sub-Saharan Africa to southern Morocco and south-western Algeria and outside of Africa to Iran, Arabia and western Asia to Turkemenistan and the Indian peninsular. They are believed to exist at low density throughout most of their range and are listed as Least Concern by the IUCN Red List (Begg et al. 2008).

Figure 2.16: Honey badger, Tsirub

As the name suggests, honey badgers have a badger-like appearance with conspicuous white/grey upperparts and black underparts. They are a broad and powerfully built animal with stout legs, broad feet with long and curved foreclaws. Shoulder height ranges between 23 - 25 cm and adult weigh 12 kg (range 8 - 14 kg), with no obvious dimorphism between the sexes (Estes 1992). Despite the wide range of the species, extensive studies of honey badger are currently lacking (Begg et al. 2003a). Honey badgers are not known to have any ecological or dietary specialisation (Begg et al. 2008), having a catholic diet. Begg et al (2003a) recorded 59 species of prey items taken by honey badgers in the Kgalagadi Transfrontier Park. Kruuk and Mills (1983) noted rodents were the most important prey item for honey badgers in the Kalahari, followed by lizards and invertebrates, with larger mammals such as aardwolf and large snakes also being taken.

Honey badgers are believed to live in socially monogamous pairs (Estes 1992), with polygynous mating behaviour (Begg et al. 2008). A study by Begg et al. (2005) recorded an unusually small litter size of one cub being born after a gestation period of 50 - 70 days, with the mother raising the cub alone. Honey badgers living near to human habitation have been recorded as being strictly nocturnal, whereas those living in parks and remote areas are often active in the day (Estes 1992). Begg et al (2003b) described honey badgers releasing a foul smelling yellow liquid from the anal gland when threatened, and using olfactory communication in the form of defecting and urinating as a form of territorial defence. Threats to this species include direct persecution by apiculturists and smallstock farmers throughout their range and the use of body parts in traditional medicine (Begg et al. 2008).

2.2.2.4 Aardwolf

Aardwolf *Proteles cristatus* (Fig. 2.17) is listed by the IUCN as Least Concern. It occurs within Africa in two geographically distinct populations; one in east Africa and one in southern Africa; its distribution within southern Africa being largely determined by the range of its main prey species *Trinervitermes* termites. Within its range aardwolf is reasonably widespread and present in numerous protected areas (Anderson and Mills 2008).

Figure 2.17: Aardwolves, Weissenborn

Aardwolf is the smallest extant hyena (Watts and Holekamp 2007); with both males and females weighing on average 10 kg, and standing 40 - 50 cm at the shoulder (Estes 1992). The aardwolf has long slender legs and a long neck, having a less sloping back than other hyena species. The background colour of the body is yellowish white to rufous with three vertical, black stripes running vertically down the body. There are also one or two diagonal stripes on the fore and hind quarters (Richardson 1998).

Prime habitat for aardwolf is open grassy plains and they are absent from forests and pure desert (Anderson and Mills, 2008). Aardwolves are highly specialised carnivores, feeding almost exclusively on harvester termites of the genus *Trinervitermes* (Watts and Holekamp 2007), Matsebula et al. (2009) recorded the genus in 87 % of aardwolf scats in Swaziland; however a study by Vries et al. (2011) also recorded sun spiders (Arachnida: Solifuge) and scorpions (Arachnida: Scorpiones) in aardwolf diet suggesting they may opportunistically feed on larger prey items. Harvester termites stay underground on cold winter nights becoming inaccessible, at these times aardwolves have been recorded consuming the less abundant and energy rich *Hodotermes* termites, suggesting winter may be a time of metabolic stress for aardwolves (Williams et al. 1997).

Aardwolves are socially monogamous, foraging alone but coming together to cooperate in parental care and territorial defence (Watts and Holekamp 2007), but show polygynous mating behaviour (Kotze et al. 2012). A male and female pair will typically share a 1 - 2 km^2 home range with their most recent offspring (Estes 1992). Territories are defended via olfactory communication in the form of scent marks from the anal gland, urine and uncovered faeces away from established latrines (Sliwa 1996). Scent marks may also be used to synchronise mating behaviour (Sliwa and Richardson 1998). The aardwolf faces no major threats, although it if often mistakenly persecuted for livestock predation (Anderson and Mills 2008).

2.2.2.5 Cheetah

Cheetah *Acinonyx jubatus* (Fig. 2.18) is listed by the IUCN Red List as Vulnerable to extinction, with an estimated global population of 7,000 - 10,000 mature individuals (Durant et al. 2008). The species formerly ranged through the Near East to south India and throughout Africa, however it become extinct within India in the 1950's and is now scarce in Asia and north Africa (Estes 1992). Southern Africa is seen as a stronghold for the species, with a population of 4,500 adults estimated (Purchase et al. 2007). Purchase et al. (2007) estimated the Namibian population at 2,000 adults, whilst the Namibian Large Carnivore Atlas (Stein et al. 2012) estimated between 7,648 - 13,520 adults.

Cheetahs are built for speed, having a deep chest, wasp-like waist and comparatively long legs (Nowell and Jackson 1996). The body is a tawny colour with white underparts, small and solid black spots with the outer tail ringed black and white with a white tip. The backs of the ears, lips and nose are black and the face has distinctive black tear marks coming down from the eyes. The mean body weight is 50 kg (range 35 - 65 kg) with males on average being 10 kg heavier than females. The shoulder height is 78 cm (range 70 - 90 cm) (Estes 1992).

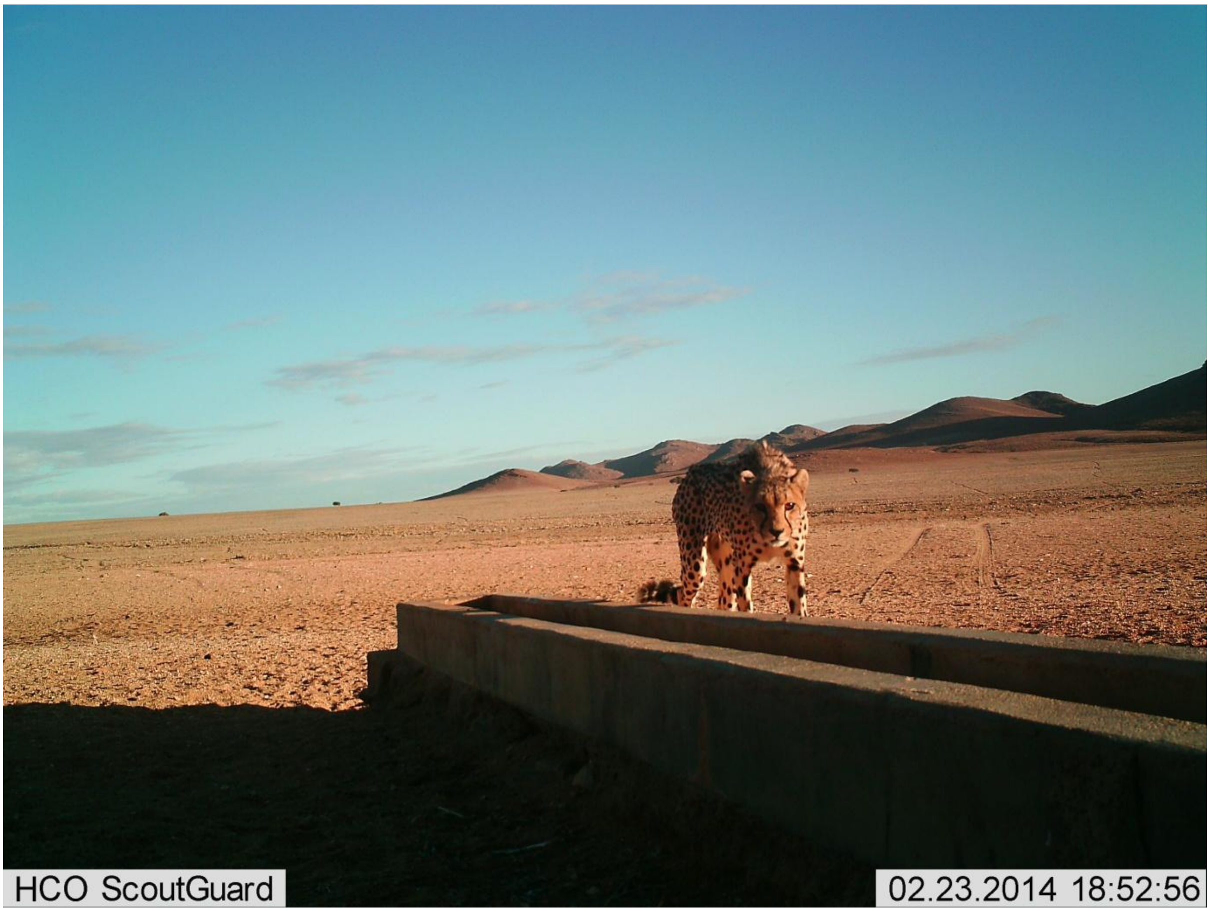


Figure 2.18: Cheetah, Tsirub

Female cheetahs are primarily solitary, whilst males are usually seen in coalitions (Estes 1992), 76.2 % of male coalitions recorded by Marker et al. (2003a) contained two males, with coalition size ranging between two and four individuals. Coalitions most often contain related males, usually brothers, formed by littermates staying together after separating from the mother. Between 3 and 4 young (range 1 - 8) are born after a gestation period of 90 - 95 days (Estes 1992). Cheetahs are mainly found in open, grassy habitats; however they also use dry forest, savannah woodland and semi-desert (Durant et al. 2008). Marker (2002) estimated a mean home range size of 1,642.3 km^2 ± 1,565 km^2, with a density of 0.25 cheetahs/100 km^2 on northcentral Namibian farmland, whilst Bissett et al. (2004) estimated home range size of 65.6 km^2 and 110.07 km^2 for single females and independent cubs respectively.

Cheetah's main prey is small to medium sized antelopes, with ground-dwelling birds and smaller mammals also being taken (Durant et al. 2008). The species suffers high levels of removals within southern Africa by farmers (Marker et al. 2003a), particularly from game farmers (Marker et al. 2003b), although are thought to rarely take domestic livestock (Marker 2002). Apart from persecution by humans and habitat fragmentation, it has been noted the species has a comparatively low genetic diversity which could threaten the survival of the species (Durant et al. 2008).

2.2.2.6 Caracal

Caracal *Caracal caracal* (Fig. 2.19) is widely distributed across Africa, central Asia and south-west Asia into India and is listed as Least Concern by the IUCN. Within Africa the caracal occurs widely, being only absent from the equatorial belt and much of the central Sahara (Breitenmoser-Wursten et al. 2008). It is believed most caracals live in arid bush country (Estes 1992), although they occur in a variety of habitats ranging from semi-desert to moist woodland. They are noted to be expanding their range into new and vacant areas in South Africa and southern Namibia (Breitenmoser-Wursten et al. 2008).

Figure 2.19: Caracal, Klein Aus Vista

Caracals are the largest of Africa's small cats, with average weights of 13 kg (max. 18 kg) and 10 kg (max. 16 kg) for males and females respectively (Nowell and Jackson 1996), with a shoulder height 40 - 45 cm (Estes 1992). Caracal have distinctive black backs to the ears and a 4.5cm tuft on the tip of the ear (Nowell and Jackson 1996), which are used in visual communication (Estes 1992). They are solitary and nocturnal, with adults only coming together to mate (Estes 1992). Bernard and Stuart (1987) noted a pronounced peak in birthday during summer, with a mean litter size of 2.2 young born after a 79 day gestation period.

Caracals have been recorded consuming a diverse range of prey items, ranging from 1 g insects to 31 kg antelopes (Avenant et al. 2002), with a number of studies finding small mammals, especially rodents as an important resource; e.g. Meville et al. (2004) and Braczkwoski et al. (2012). Home range size for male caracal on northcentral Namibian farmland was estimated at 312.6 km^2 on commercial farmlands (Marker and Dickman, 2005b). Whilst Avenant and Nel (1998) recorded much smaller home ranges of 29.6 km^2 ±

0.75 km and 7.39 km^2 ± 1.68 km for males and females respectively in arid scrub habitat on the west coast of South Africa.

The IUCN lists persecution by farmers due to human-wildlife conflict as a major threat to the survival of this species (Breitenmoser-Wursten et al. 2008). Indeed Meville et al. (2004) found domestic livestock in the diet of caracal in the Kgalagadi Transfrontier Park near the South African/Namibian border, and Meville and Bothma (2006) suggested during conditions of low prey availability, caracals moved from the park to neighbouring farmlands to feed upon livestock.

2.2.2.7 African wild cat

African wild cat *Felis silvestris lybica* (Fig. 2.20) is the most common and widely distributed wild cat in the world. It is listed by the IUCN as Least Concern, with a decreasing global population trend. Wild cats occurring in Africa are a subspecies of the wild cat *Felis silvestris*, and have an extremely wide range within Africa, occurring in almost every habitat, with the exception of tropical forest (Driscoll and Nowell 2010).

Figure 2.20: African wild cat, Namtib Biosphere Reserve

Appearance of African wild cats varies both geographically and individually (Estes 1992; Driscoll and Nowell 2010), however they are usually grey or tan with dark stripes on the upper limbs, the tail is ringed with a dark tip and stripes are present on the forehead and cheeks. Males are larger than females, at 5 kg (2.7 - 6.4) compared to 4 kg (3.2 - 5.4), shoulder height is 58 cm (Estes 1992).

Studies focusing on this species are lacking (Estes 1992), but individuals are known to be solitary and nocturnal with some crepuscular activity (Driscoll and Nowell 2010). Rodents are the main prey item with small birds, reptiles, amphibians and large insects also being taken. Springhare *Pedetes capensis* and African hare *Lepus microtis* are thought to be the largest prey items taken. Between two and five (mean 3.7) young are born in the rainy season, when small mammal abundance is at its peak (Estes 1992).

The major threat faced by this species is hybridisation with domestic cats *Felis catus* (Driscoll and Nowell 2010); it is thought the only genetically pure populations of African wild cat are likely to be found in remote protected areas, away from human habitation. It is also noted this species is killed as a pest across southern Africa (Nowell and Jackson 1996).

2.3 Methods

2.3.1 Camera traps

Camera traps provide the perfect solution for monitoring large terrestrial carnivores which are generally difficult to study, often being shy, elusive and solitary with large home ranges and naturally low densities (Balme et al. 2009). As a result, they have been used successfully to address a number of research questions with a wide range of carnivore species; for example brown hyena *Hyaena brunnea* (Thorn et al. 2009), leopard *Panthera pardus* (Balme et al. 2009b; Stein et al. 2011), Malagasy civet *Fossa fossana* (Gerber et al. 2011), puma *Puma concolor* (Kelly et al. 2008), tiger *Panthera tigris* (Karanth 1995; Karanth and Nichols 1998), and sun bear *Helarctos malayanus* (Linkie et al. 2007). Due to their advantages over more invasive methods such as capture and direct observations which have the disadvantages of being expensive, time consuming and costly (Weaver et al. 2005), and disturbance to the animals, camera traps were used as one of two main tools for surveying carnivores on the study farms.

During July and August 2012, 20 Scoutguard SG560 infra-red camera traps were set up across the three main study farms; Namtib Biosphere Reserve, Tsirub and Klein Aus Vista

(Figs 2.21 & 2.22). Due to the aridity of the environment and predicted low density of carnivores, camera traps were set up at artificial water troughs, natural springs and game trails leading to natural springs to maximise carnivore capture success. Fifteen camera traps were set up at artificial water troughs, two set up at permanent springs and the remaining three set up along game trails in gorges leading to permanent springs within mountains, in a variety of habitats. Camera traps were housed in metal protective cages and placed, due to the lack of trees, in column shaped chicken wire cages filled with rocks (Fig. 2.23), with the exception of the artificial water point at Namtib Biosphere Reserve where the camera trap was mounted 1.7 m from the ground after repeated interference and damage from spotted hyena (Fig. 2.24).

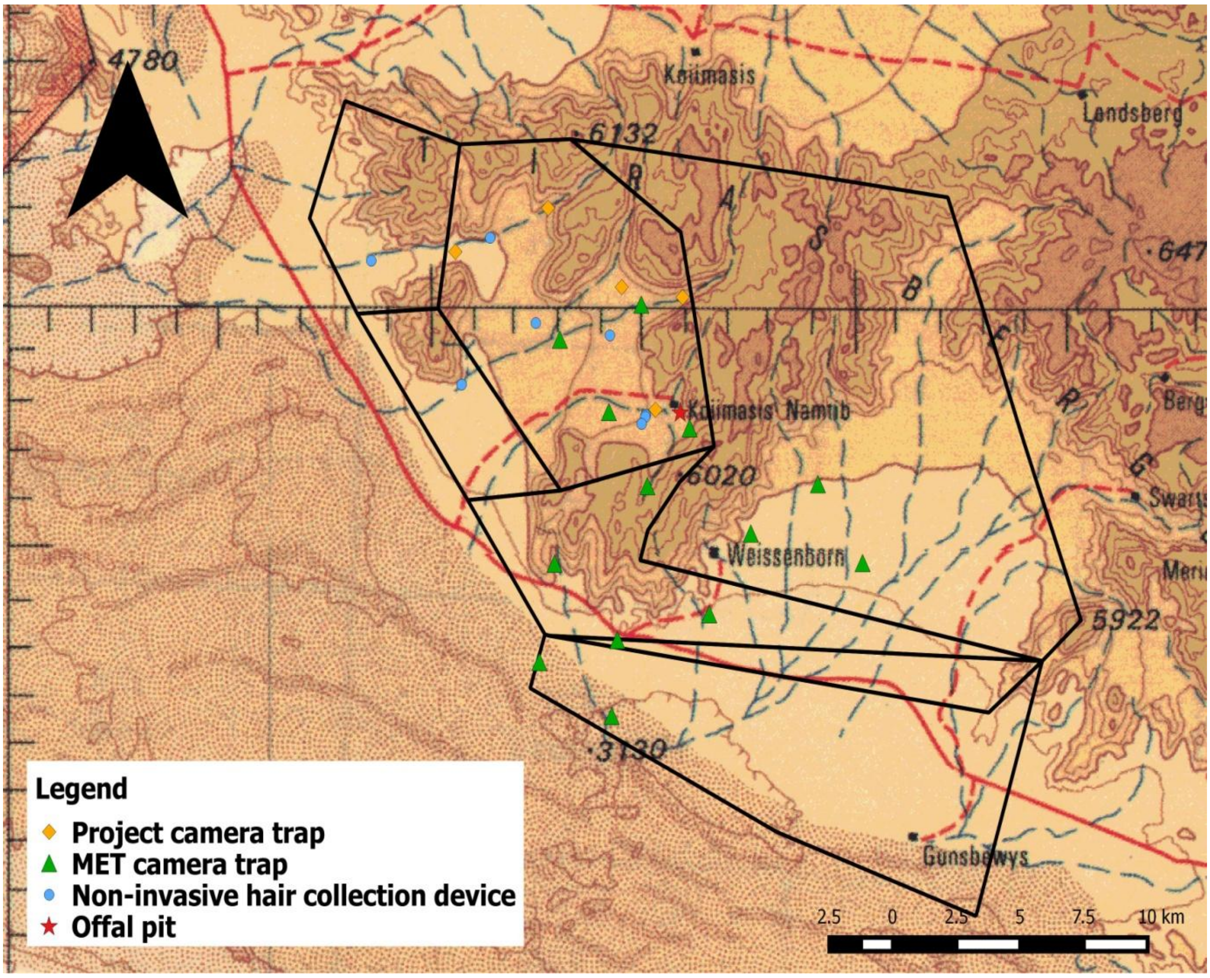


Figure 2.21: Locations of project and NLS/MET camera traps, offal pit and non-invasive hair collection devices on the northern study farms; Namtib Biosphere Reserve, Weissenborn and Gunsbewys

Camera traps at artificial water points and natural springs were set to be active 24 hours a day and to take one photo per firing with a minute interval between firings. Camera traps on game trails were programmed to take two photos at a time with 30 seconds between firings to increase the chance of capturing the animal triggering the camera trap. Two different set ups were used as animals coming to drink from water sources are more likely to stop and stand still, giving the camera trap enough time to fire, whilst animals walk past the camera traps on game trails without stopping. A spacing of approximately 4 km between camera traps was used to aid with density estimates as 4 km/h was approximately the average walking speed for cheetah (J. Melzheimer, personal communication, 12th June 2012.), spotted hyena (L. Hanssen, personal communication 3rd July 2012, Stratford and Stratford, 2011) and brown hyena (I. Wiesel, personal communication 5th June 2012). Therefore, for example, if two brown hyenas were captured by two different camera traps within an hour, it can be safely assumed it is two different individuals rather than the same animal as it is unlikely an animal would walk the 4 km between the two camera traps in less than an hour. Hence such spacing ensures that the camera trap locations can be considered to be spatially independent.

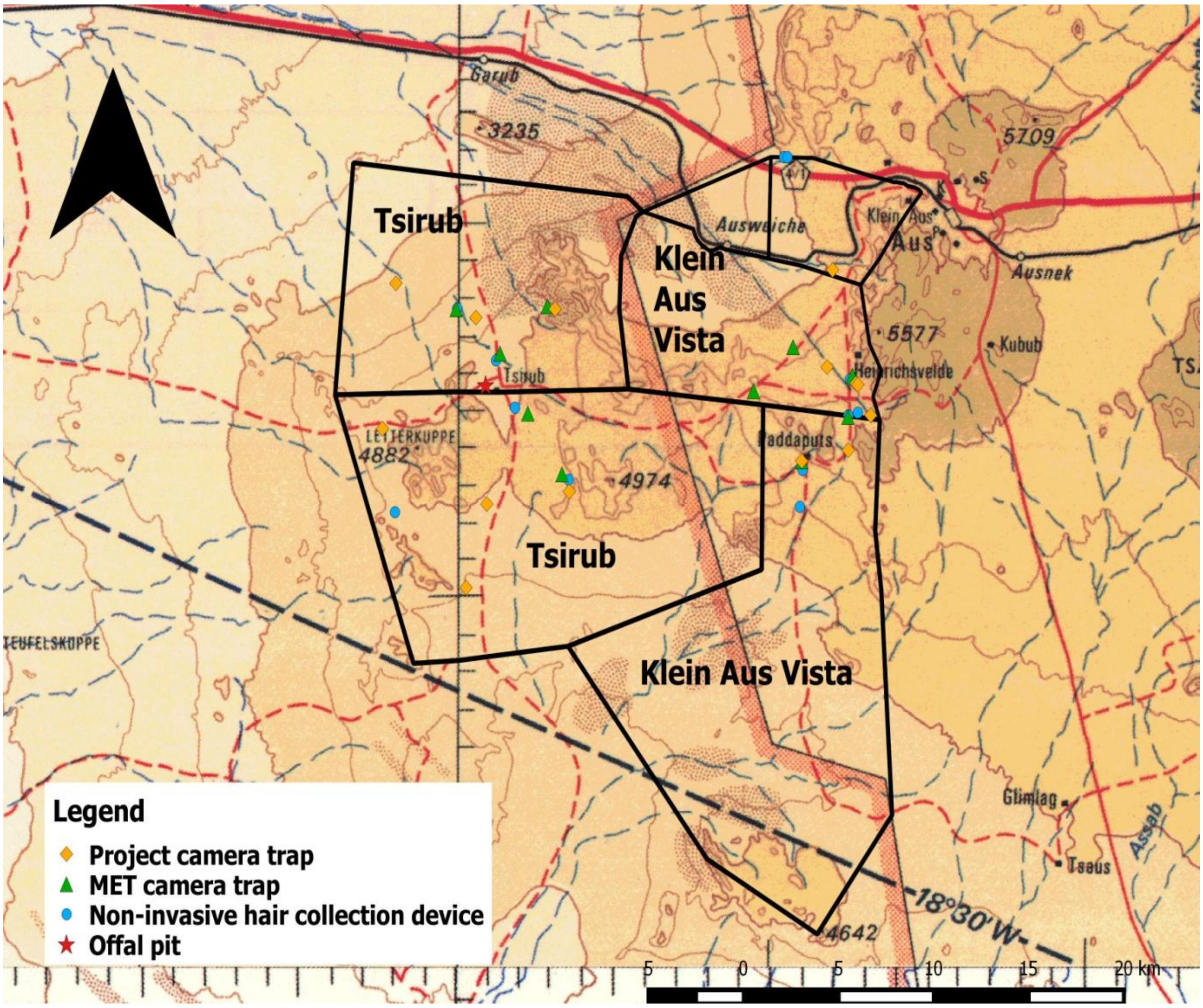


Figure 2.22: Locations of project and NLS/MET camera traps, offal pit and non-invasive hair collection devices on the southern study farms; Klein Aus Vista and Tsirub

Figure 2.23: Camera trap in chicken wire cage

Figure 2.24: Camera trap at Namtib mounted on pole with spotted hyena

Camera traps were checked once every two weeks, when SD cards and batteries were changed. Due to low battery voltage camera traps would occasionally not be active for the entire two week period between checks; as a result, the total number of camera trap nights varies between traps. During the first two months of camera trap operation, each location was evaluated and camera traps moved, to the nearest water source or game trail, within a 1 km radius, if carnivores were not being detected at a particular site. No baits or lures were used to attract carnivores to camera traps, and camera traps were in operation until the end of the project in May 2014.

Major problems were encountered with the original set of Scoutguards purchased for the project, 18 of the 20 camera traps were faulty and would drain batteries quickly, sometimes within a few hours. Initially 6 v external batteries were used and the decision was made to change to lithium and then rechargeable NiMH batteries as the issue was thought to be with the batteries rather than the camera traps. Due to these problems, and the time taken to replace the faulty traps, consistent data collection did not start until May 2013 and continued until May 2014. Once all camera traps were working properly four or eight (depending on the site) 2700 mAh rechargeable batteries were used, in conjunction with 8 GB SD cards.

From January to May 2014, Bushnell X-8 Trail camera traps were set up to monitor the offal pits at Tsirub and Namib Biosphere Reserve. Camera traps were mounted on the fence at Tsirub and on a metal pole at Namtib Biosphere Reserve and set to take one photo per triggering, with a one minute interval between firings. The Tsirub offal pit is a relatively large (10 x 10 m) fenced off area, approximately 400 m from the main farm house. Despite being entirely fenced, carnivores could gain access to the offal pit via a large hole under the gate, where a hair snare was set up. Offal along with skin, bones and horn from oryx and springbok were put into the pit on average three times a week. The offal pit at Namtib was a deep pit (5 x 5 m), with no fencing around located approximately 450 m from the main farm house. Remains from general refuse from the lodge were put in the pit after burning along with offal from domestic livestock and game culling for meat, although on a much less regular basis than at the Tsirub offal pit.

Camera trap data was entered in Excel databases, with the following information being recorded for each image; image number, time and date which were extracted using programme ACDSee (ACD Systems Ltd, 2004), species present, and the number of each species present (carnivores only). Individual inventories were produced for each species where individually unique markings were present; leopard, spotted and brown hyena and cheetah, however it should be noted that due to brown hyena leg stripe patterns often being blurred on images, the individual inventory for this species is not complete and would rather represent a catalogue of the minimum number alive. Although both aardwolf and African wild cat also have unique markings, such markings rarely showed up clearly on camera trap images and so the decision was made to not produce individual inventories for these species.

2.3.2 National Leopard Survey

In March 2013 the project started to collaborate with Namibia's Ministry of Environment and Tourism (MET) to start surveying the study area as part of the National Leopard Survey (NLS). The NLS was started in 2011 in three locations across Namibia; the Mount Etjo region, the Khomas Hochland Mountains and around the NamibRand Nature Reserve (Fig. 2.25). The NLS aimed to categorise each region of the country into high, medium and low density estimates which would then be used to generate national hunting quota recommendations (Stein et al. 2011). At the time of the collaboration no sites further south than the NamibRand site had been included as part of the NLS; as a result density estimates for the project study in the NLS final report (medium to high) were based on farmer questionnaires rather than ecological data (Stein et al. 2011).

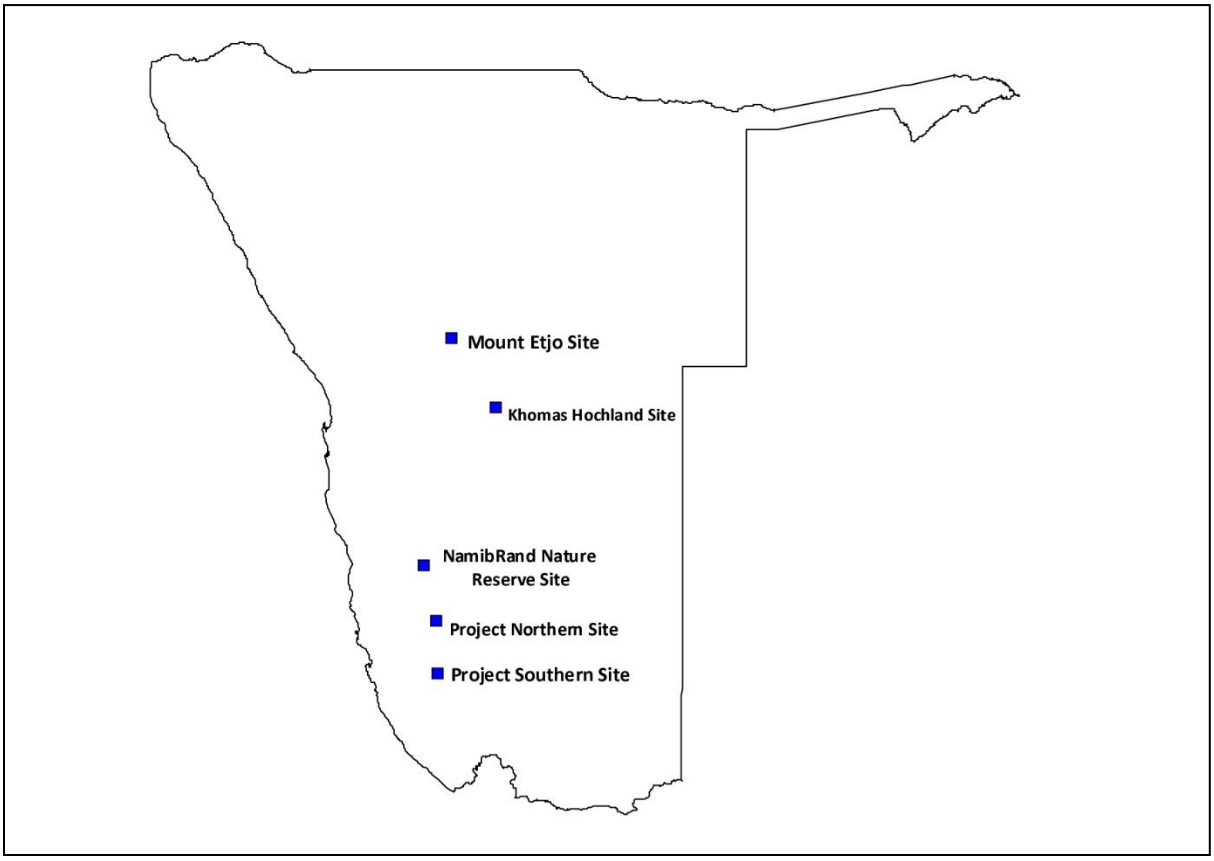


Figure 2.25: Locations of previous National Leopard Survey study sites and the two project study sites

A total of 23 camera trap stations were set up for the NLS in March 2013 (Figs 2.21 & 2.22), each station consisting of two Reconyx HC 600 infra-red camera traps facing each other on opposite sides of roads, game trails or riverbeds, offset by approximately one metre to avoid the flash from one camera trap interfering with the other trap (Fig. 2.26). Having two camera traps set up in such a manner should ensure identification photographs of both and left and right flanks of the animal as it passes between the camera traps. As there were very few trees in the study site, cameras were housed in metal protective boxes and mounted on metal fence poles or where possible on large logs at approximately 40 cm from the ground. Reconyx camera traps were set to be active 24 hours a day, with five consecutive photos being taken per firing, with no interval between firings. A set of 12 lithium batteries were used in each camera trap, with either 2 or 8 GB memory cards. Like the project camera traps, no baits or lures were used to attract carnivores to the traps. National Leopard Survey methodology had camera traps spaced approximately 3.5 km apart meeting the capture-recapture theory assumption of every animal in the area having a more than zero chance of being captured, and is based on the home range size of a female leopard with cubs from northern Namibia (Stein et al. 2011).

Figure 2.26: Camera trap station for National Leopard Survey showing camera traps mounted on metal fence poles on either side of a road, Namtib Biosphere Reserve

At the start of the survey in March 2013, ten camera trap stations were set up across Tsirub and Klein Aus Vista with a further 13 set up across Namtib, Gunsbewys and Weissenborn. In August 2013, a decision was made to move all traps to the northern area (Namtib, Gunsbewys and Weissenborn) to cover a larger area rather than two smaller sites. Due to problems with some camera traps not functioning properly, a total of nineteen stations were then used across the northern farms from August 2013 to May 2014.

2.3.3 Non-invasive hair collection

Non-invasive hair collection is becoming a frequently used tool for study rare and elusive carnivores, being both time and cost efficient, sensitive and reliable (Schwartz et al. 2006). Non-invasive hair collection involves the use of hair snagging devices which target animals come into contact naturally, or via the use of attractants (Kendall and McKelvey 2008). Such devices have been mainly developed and used in North America and have so far rarely been used in Africa, with the exception of Hanke and Dickman (2013) who used rough-sawn wooden stakes baited with tuna-emulsion oil to detect wild felids, African wild cat, black-footed cat *Felis nigripes* and feral felids *Felis catus*, in the Namib Desert.

Non-invasive hair collection devices were used as an alternative method to camera trapping for constructing a carnivore species inventory through identification of hair samples to species level and collecting hair for stable isotope analysis of diet. Two methods were used to collect hair from carnivores; hair snares and rub stations. Hair snares are passive devices that snare the hair from animals usually with barbed wire or glue, using no bait or lure to attract the animal and have the advantage of not changing the natural behaviour of the animal (Kendall and McKelvey 2008). Whilst many studies have used barbed wire hair snares around trees in conjunction with a bait or lure in the centre on target animal travel routes (black bear *Ursus americanus* Dixon et al. 2006; brown bear *Ursus arctos* Kendall et al. 2009; mesocarnivores in California, USA Zielinski et al. 2012), few studies have used passive hair snares along holes in fence lines where animals are likely to pass through (Amur tiger *Panthera tigris altaica* Sugimoto et al. 2012).

Hair snares were set up across Namtib Biosphere Reserve (*n* = 3), Klein Aus Vista (*n* = 3) and Gunsbewys (*n* = 4) during October 2012, at holes under internal and farm border fences where carnivores were likely to pass through. No hair snares were set up at Tsirub as the owner performed a weekly fence check patrol and filled any holes present. Not only does this method show which carnivores are present on farmland, but for those snares set up along national park border fences, which species are crossing between farmland and Park.

Hair snares consisted of two strands of barbed wire (1 cm barbs at 12 cm intervals) running parallel to the bottom strand of fence lines over holes and attached to the bottom fence line with wire (Fig. 2.27). Initially a single strand of barbed wire was used, however this method snared only a small amount of hair, therefore the decision was taken to add a second strand placed so the barbs from the two strands were staggered; this adaption resulted in a greater amount of hair being snared. Hair snares were checked on a bi-weekly basis, when any snared hair was removed and stored in envelopes and condition of barbed wire checked.

Figure 2.27: *Left*: Hair snared on hair snare (Klein Aus Vista). *Right*: Hair snare set up along hole under fence line (Gunsbewys)

In contrast to hair snares, rub stations are classed as active devices using baits or lures to induce face or neck rubbing behaviour in carnivores, resulting in hair being deposited on carpet pads attached to trees or poles (Kendall and McKelvey 2008). A number of studies have used such devices to collect hair from a range of carnivore species; margays *Leopardus wiedii* and mountain lions *Puma concolor* (Downey et al. 2012), Eurasian lynx *Lynx lynx* (Schmidt et al. 2006; Heurich et al. 2012), ocelots *Leoparus pardalis* (Weaver et al. 2012) and felids in Namibia (Hanke and Dickman 2013).

Rub stations were set up across Namtib Biosphere Reserve (*n* = 5), Klein Aus Vista (*n* = 4) and Tsirub (*n* = 5) (not on Gunsbewys due to a lack of trees) in October 2012, and consisted of three 10 x 10 cm carpet pads nailed to trees. To maximise chances of carnivores encountering rub stations, they were positioned on trees within five metres of a road where carnivores were known to travel along, as Schmidt et al. (2006) found this to be an effective distance for the placement of rub stations for Eurasian lynx. As the study had focal carnivores ranging in size from Cape fox, with a shoulder height of 30 cm to spotted hyena, shoulder height 70 - 90 cm (Walker 1996), the first rub station was positioned approximately 15 cm from the ground and the third approximately 50 cm from ground level (Fig. 2.28).

Figure 2.28: *Left* Close up shot of rub station with hair snared on barbed wire. *Right* Rub station attached to tree

Nails were used to attach rub stations to trees, with one positioned in each corner and a fifth through the centre of the carpet pad. Additional nails were added if needed, usually when the tree trunk was not straight. Rub stations were initially baited with catnip (Johnsons Veterinary Products, UK), a commercial scent lure 'Canine Call' (Russ Carman, USA) and beaver castoreum. In August 2013, the frequency of hair samples collected by rub stations decreased and a decision was made use a new additional lure, in case habituation to the scents was causing the decrease. A lady's perfume 'Designer Notes - Once Upon a Time' (Designer Group, South Africa) was used from August 2013 until rub stations were taken down in May 2014. All lures were mixed with glycerin (Allied Drug Company Ltd, South Africa) to decrease evaporation rate and stop freezing, in a ratio of 1 : 6 (lure to glycerine). A single drop of each lure was applied directly onto each carpet pad during each check.

Originally nails were placed protruding out from each carpet pad in addition to iron wool which was attached to carpet pads to increase chances of hair being caught, however all iron wool from each rub station was removed at each study site by an unknown species. To counter this problem, two 8 cm strands of barbed wire were inserted through each carpet pad so that the barb on each strand was on the outside (Fig. 2.28). This method worked well, with hair often being found on both the barbed wire and carpet pad. Rub stations were checked once every two weeks, during which any hair collected was removed and stored in envelopes or plastic tubes and lures refreshed. Occasionally rub stations were removed completely from trees on Namtib and from spoor present at the time, it is likely spotted hyena were responsible.

Hair samples were stored in envelopes or plastic tubes and initially it was tried to identify to species level using cuticle pattern identification with a microscope, following the methods described by De Marinis and Agnelli (1993) using clear nail polish (Revlon, Charlie, South Africa) to produce an imprint of the cuticle pattern for examination under the microscope. Hair samples were identified using guides (Keogh, 1980, Seiler, 2010) as well as making reference slides from hair samples taken from carnivores killed on the road, in a conflict situation or found dead on the study sites. However, due to difficulties in distinguishing between cuticle patterns of closely related species, the decision was made have the samples genetically analysed to species level. Therefore all samples, along with seven 'blind' samples, i.e. those with species identity known, were sent to the Cheetah Conservation Fund genetic laboratory in Otjiwarango, Namibia for analysis.

2.3.4 Farmer questionnaires

One of the most commonly utilised tools for assessing the human perspective of human-wildlife conflict is the questionnaire, examples include Herrmann et al. (2001), Wang and Macdonald (2006), Gusset et al. (2007), Dickman (2008) and Swanpoel (2008). Despite being such a frequently used research approach, data obtained in this way should be regarded with some caution; livestock owners often deliberately over-inflate losses (Herrmann et al. 2001; Polisar et al. 2003), might not actually know the species of carnivore responsible, or be able to distinguish between the proximate and ultimate cause of predation (Herrmann et al. 2001) which will ultimately lead to misleading and subjective information being given (Graham et al. 2004).

Despite such a wide spread use of questionnaires in ecological studies, a review by White et al. (2012) of 168 questionnaires, found less than 10 % of these actually carried out ground-truthing to validate facts. To gain a better insight into the conflict situation in southern Namibia, a questionnaire was used with farmers within the south west Karas region to gain an understanding of the human perspective of the conflict situation. This data will be compared to ecological gained from camera trapping, non-invasive hair collection and stable isotope analysis to see how accurately the farmers are perceiving the problem.

Due to the relatively poor response rate to a 2004 postal questionnaire (16 %) by the Brown Hyena Research Project, a decision was made to conduct the questionnaire face to face whilst visiting farmers at their homes. However it soon became clear this approach would not work well; appointments made with farmers just a few days beforehand would often not be upheld, with the farmer not even being present on the farm at the arranged time. Therefore the postal questionnaire approach was used, with some of the farmers being visited for the questionnaire. The questionnaire used is included in Appendix four.

3.0 Modelling conflict-causing carnivore occupancy on arid commercial farmlands in southern Namibia

3.1 Abstract

Non-protected areas such as farmlands, are being increasingly acknowledged as essential sites for the conservation of a range of carnivore species. However, due to the perceived or real involvement of carnivores with livestock predation, they are largely unsafe areas for carnivores if lethal removal is practiced in response to such predation. Identification of the microhabitat features associated with carnivore activity on farmlands is likely to be useful in pre-emptive carnivore conflict mitigation methods. This study used a modern occupancy analysis approach to identify the microhabitat features affecting site occupancy and detection probability for four problematic carnivores species in southern Namibia. Camera traps were used across five (three northern sites, two southern sites) commercial farmlands bordering the Namib-Naukluft and Tsau//Khaeb (Sperrgebiet) National Parks, over a wet summer and a dry winter period. Results showed each species to have a unique combination of environmental features affecting both occupancy and probability of detection, and that this combination changed between sites and seasons for each species. Presence of water was the most frequently seen covariate within top-fitting models, and was seen to always increase both probability of occupancy and detection. Open plains/mountain transition habitat was associated with an increase in detection probability for most species. Such results might suggest concentrating mitigation efforts in areas closer to water, and in open plains/mountain transition habitat. Conversely, such areas might wish to be avoided for grazing livestock without protection, or as sites for kraals.

3.2 Introduction

Protected areas are now acknowledged to be largely inadequate for the conservation of many wide-ranging terrestrial carnivores (Woodroffe and Ginsberg 1998; Kent and Hills 2013) as a result non-protected areas such as farmland are increasingly recognised as important habitats for a variety of species (Smith et al. 2011). However, in areas where carnivores and livestock coexist, human-wildlife conflict frequently occurs, often resulting in the lethal removal of carnivores (Woodroffe et al. 2005). Such lethal removal can have major consequences for species survival, for example conflict with farmers has been cited as a main reason for population declines of cheetah (Marker et al. 2003c) and spotted hyena (Kissui 2008). The reduction of human-wildlife conflict may be key to the persistence of viable carnivore populations outside of protected areas (Ogada et al. 2003).

Depredation of livestock is likely to be affected by habitat features, and the identification of such features may be crucial for pre-emptive conflict mitigation (Abade et al. 2014). For example Holmern et al. (2007) found distance from the Serengeti National Park fence line affected chance of depredation by large carnivores in Tanzania, for example predation by large felids was only seen to occur within a 3 km boundary strip along the Park border. Kolowski and Holekamp (2006) found the level of vegetation cover to affect probability of spotted hyena attack in Kenya, with increases in vegetation being associated with an increased risk of predation. Farmlands house anthropogenic habitat features such as artificial water points and these features may also affect depredation, for example, Schuette et al. (2013) found human land use to affect occupancy patterns of 10 out of 12 carnivore species in Kenya.

Previous human-wildlife conflict studies have examined the habitat features associated with livestock depredation by large carnivores in Brazil (De Azevedo and Murray 2012), Bhutan (Sangay and Vernes 2008), Kenya (Kolowski and Holekamp 2006), Tanzania (Holmern et al. 2007; Abade et al. 2014) and South Africa (Thorn et al. 2012), using data collected from livestock owners concerning depredation events. However, within the study area investigated here, actual incidences of human-carnivore conflict were rare, meaning insufficient data would be available for such an approach. Additionally problems regarding inaccuracy and deliberate over-inflation of livestock losses by farmers whilst using a questionnaire based approach (Herrmann et al. 2001), could potentially lead to biased and/or false data.

Identifying which habitat features are preferred by carnivore species across the farmlands could be an alternative approach for conflict mitigation, as increased predation pressure is often associated with increased predator activity (Šálek et al. 2010). Habitat preferences of carnivores have previously been addressed by using photographic rates from camera traps (e.g. large mammals in Brazil Goulart et al. 2009 and carnivores in Patagonia Lantschner et al. 2012). However, due to problems associated comparing relative abundance indices, when probability of detection is not constant between sites (Sollmann et al. 2013) (as discussed in Chapter eight), such an approach is likely to be unsuitable.

However the occupancy modelling approach, developed by MacKenzie et al. (2012) accommodates for differences in detection probability and has been used by a number of studies to examine habitat preferences for a range of species, for example American martens *Martes americana* (Baldwin and Bender 2008), Sumatran tigers *Panthera tigris sumatrae* (Sunarto et al. 2012), small carnivores in the Western Ghats, India (Kalle et al. 2014) and for six species of bats in US pine forests (Bender et al. 2015). It can be used at a number of scales from habitat use within the home range to landscape scale. To date no studies in the literature exist regarding the habitat features preferred by carnivores on farmlands in arid environments

Occupancy modelling allows the affect of environmental covariates on probability of occupancy to be assessed (MacKenzie et al. 2006), and can be used for any species as individual identification is not required. Modern occupancy analysis allows for the counting of patches, or sites, potentially occupied by a species, rather than counting individual animals (Ramesh and Downs 2014). It estimates the probability of a site being occupied whilst correcting for imperfect detection, i.e. the probability of detecting a species at an occupied site being <1 (MacKenzie et al. 2006). Occupancy modelling also produces estimates of detection probability and also allows the effect of environmental covariates on probability of detection to be examined (MacKenzie et al. 2006).

This chapter aims to use an occupancy model approach to investigate the microhabitat features preferred by black-backed jackal, spotted and brown hyena and leopard. The specific objectives to be met by this chapter are; to produce a list of environmental variables/microhabitat features, as identified by the best fitting models as increasing occupancy and probability of detection for each focal carnivore species. To compare these aforementioned lists between species, sites and seasons. And lastly, to use information regarding the preferences of focal carnivore species to make informed recommendations regarding conflict resolution, by identifying areas preferred by carnivores, which should be avoided for grazing and kraaling. It is hypothesised that, as water is a rare and essential resource across all study sites, it will be a microhabitat feature preferred by all species. Additionally, due to their known preferences for denning in mountainous areas, it is hypotheised sites within mountain habitat will be preferred by brown and spotted hyena. Due to their preference for hunting in areas with cover, it is hypotheised leopard will prefer sites with cover, specifically mountain and open plains/mountain transition habitat. Finally, is is hypothesised being a more opportunistic species, no microhabitat preferences will be seen for black-backed jackal.

3.3 Methods

3.3.1 Sampling design

Two camera trap set ups where used (see sections 2.3.1 and 2.3.2 for full details), one where camera traps were set up at water sources, or game trails leading to water sources when water was in mountain areas not easily accessible to humans, and another set up where camera traps were placed along roads for the National Leopard Survey.

3.3.2 Occupancy modelling

Occupancy models are based on two parameters; the probability of a site being occupied by a species (ψ), whilst correcting for imperfect detection, and the probability (p) that the species will be detected at a site, given that it is occupied during a sampling occasion, based on repeated detection/non-detection data (MacKenzie et al. 2006). Occupancy can alternatively be defined as the proportion of the area occupied by at least one individual during the sampling period (MacKenzie et al. 2006), but for the purposes of this study the former definition was used. Sites with higher occupancy estimates were interpreted as being preferred by species, as sites preferred by species are more likely to be occupied than those sites not preferred by a species, following Sunarto et al. (2012).

Non-detection of a species at a site could result from the species being truly absent, or present and failing to be detected. To allow for this possibility, repeated visits (sampling occasions) to a site are used to estimate detection probability (MacKenzie et al. 2006). Sollmann et al. (2011) noted that the occupancy state of a site may be dependent upon whether an individual is available for sampling within the given time frame considering within-home range movements of an individual. They countered this problem by using longer sampling occasions. Given the scale of this study and the potential home range sizes of spotted hyena, six consecutive 14 day sampling occasions were used, giving a total sampling period of 84 days.

Programme PRESENCE (Hines 2006) was used to estimate occupancy, with the occupancy model ‘single-season’ which estimates occupancy and detection of probability over a single season, and assumes demographic closure within the sampling period, i.e. occupancy status of a site will not change (MacKenzie et al. 2006). A period of 2 - 3 months has been recommended for demographic closure for big cats (Karanth and Nichols, 1998; Silvers et al. 2004) and Thorn et al. (2011) used a period of five months for brown hyena occupancy,

. Therefore, this study’s sampling period of 84 days (~3 months) should meet the closure assumption for leopards, brown and spotted hyena. However, little information regarding closure periods exists for mesocarnivores, therefore to enable comparisons between species possible, the same sampling period was used for black-backed jackal.

In order to make comparisons between winter and summer seasons, two sampling periods were used in the northern sites. The winter period started 29th May and ran until 6th August 2013, with the summer period starting 11th December 2013 and ending 4th March 2014. The summer period included the onset of the rains in late December 2013, and the presence of temporary water sources is considered to be one of the main differences between the seasons. Such seasonal differences could effect mitigation priorities, for example the presence of water sources within mountain habitat in summer could make this a habitat more likely to be occupied by leopard which are known to favour mountainous areas for hunting. A lack of such water sources in winter, may mean leopards are more likely to move into different habitats, in search of water, where they may encounter livestock. Due to MET camera traps being moved in August 2013 from the southern sites, only the winter period was analysed.

Standard detection matrices, consisting of binary variables, were constructed separately for each species, season and site. For each site and sampling occasion a '1' indicated detection of a species, i.e. at least one independent event (refer to Chapter four) of that species recorded, and a '0' indicated non-detection during each sampling occasion. Detection matrices were then imported into PRESENCE 7.0 (Hines, 2006).

For each site, a total of five environmental site covariates were recorded (Table 3.1) which were hypothesised to affect the distribution of focal species across the sites and could potentially affect occupancy estimates and/or probability of detection. The focal species are known to have habitat preferences, which may effect the probability of a site being occupied. Leopards, for example, are known to favour habitat containing cover for concealment, whilst black-backed jackals are known to inhabit a wide variety of habitats but prefer areas with scattered bush (Estes, 1992). Therefore habitat was deemed important and three habitat classifications were identified (see Table 3.1). For similar reasons, distance from mountain habitat was determined as important, especially for leopard which rely on cover for concealment when hunting, and for brown and spotted hyenas which often den in mountainous habitats (Estes 1992; Mills and Hofer 1998).

Neither of the National Parks (NPs) bordering the study farms provides artificial water for wildlife, which may therefore represent a block of unsuitable habitat for focal species which are dependent upon drinking water. Therefore, distance from the border fence was considered important. Species are likely to include important resources such as water within their home ranges, and home range size has been shown to vary with water availability (Bowers et al. 1990; de Beer and van Aarde 1998). Therefore, areas near to the National Parks border could be less likely occupied than those further towards the interior of the farms where there are permanent water sources. Similarly, the distance from the nearest water source could have a similar effect on the probability of a site being occupied. All distances were converted to standardised Z scores, as when the range of a continuous covariate is known to vary over several magnitudes of order, the numerical optimisation algorithm used by PRESENCE may fail to find the correct parameter estimates (Cooch and White 2006).

Lastly, the presence of water at a site was included as a covariate as it is likely to affect probability of occupancy and detection in an arid environment where permanent water is scarce. Camera traps set up along roads could have a lower detection probability than those set up at water. At water a carnivore is likely to stop and drink in front of the camera trap, increasing the probability it will actually be detected. In comparison, a carnivore passing a camera trap on a road is less likely to stop, and if moving quickly it is possible the reaction time of the camera would be too slow to capture the animal moving through.

Table 3.1: Environmental covariates used for occupancy modelling, which were predicted to have an effect on occupancy and/or probability of detection for focal carnivores

Covariate	**Definition**	**Method**
Habitat	Three habitat types; mountain, open plains and open plains/mountain transition (Below).	
Mountain	Camera trap site surrounded totally by, or a maximum distance of 500m from, mountain/rocky habitat, e.g. mountain gorge.	Determined when visiting the site
Open plains	Camera trap site located a minimum of 1km away from mountain habitat. Characterised by open, grass or gravel plains.	Distance measured on Google Earth
Open plains/mountain transition	Camera trap site located between 0.5 and 1km from mountain habitat/base of mountain.	Distance measured on Google Earth
Distance to mountain	Straight line distance from edge of nearest mountain habitat including the 500m distance defined in mountain habitat above, measured in km.	Distance measured on Google Earth
Distance to National Park (NP) fence line	Straight line distance from nearest National Park fence line, measured in km.	Distance measured on Google Earth
Nearest water distance	Straight line distance from nearest water source, either artificial or natural, measured in km.	Distance measured on Google Earth
Presence of water	Presence of water, artificial or natural at the camera trap site. If water is present, camera trap is focused on water.	Determined when visiting the site

In order to compare occupancy and probability of detection between species, sites and seasons, PRESENCE was used to generate maximum likelihood estimates using the model $\psi(.)$, $p(.)$, where occupancy and detection probability are held constant, using the single-season analysis. Next, candidate models were constructed where both occupancy and probability of detection were allowed to vary using individual and then additively combined environmental covariates. Candidate models were ranked using Akaike Information Criterion (AIC) (Burnham and Anderson 2002), with candidate models with the lowest AIC values indicating the most parsimonious models. Low values in ΔAIC indicate the two models in question showed a similar fit for the data.

As the AIC does not provide a measure of goodness of fit for the candidate models, this was examined using the goodness of fit procedure in PRESENCE. Goodness of fit testing was applied to the global model, i.e. the one containing all covariates, with 10,000 parametric bootstraps. A variance inflation factor ($\hat{c}$) is produced along with a *p* value indicating the probability of the test statistic being greater than or equal to the observed. The variance inflation factor is a measure of variation in the data, showing if there is under or over dispersion. A $\hat{c}$ of over or under 1 would be deemed a poor fit for the data with the test statistic and associated standard deviations being distorted (Cooch and White 2006). The suggested procedure for correcting for over-dispersion is to inflate standard errors by a factor of $\sqrt{\hat{c}}$ and use a quasi-corrected AIC for model selection (Burnham and Anderson 2002) however for under-dispersion ($\hat{c} < 1$) no procedure is currently suggested for correction (MacKenzie et al. 2006).

3.4 Results

3.4.1 Constant occupancy and detection probability estimates

In order to make direct comparisons regarding the occupancy and probability of detection between sites and species, models where firstly ran which excluded all environmental covariates.In these models, brown hyena had the highest occupancy and spotted hyena had the highest detection probability in the northern summer period (Table 3.2). For the northern sites where comparison between winter and summer periods was possible, occupancy was higher in summer for black-backed jackal and higher in winter for both spotted hyena and leopard. Probability of detection was higher in summer for all three focal carnivore species where between season comparisons were possible (i.e. all species except brown hyena). Comparing the winter periods for the north and south for black-backed jackal and leopard, it can be seen that both occupancy and probability of detection are higher in the southern sites (Table 3.2).

Table 3.2: Constant occupancy (ψ) and probability of detection (p) across sites and seasons for focal carnivores, i.e. model results where environmental covariates were not included within models

Species	**Site**	**Season**	**ψ ± 1 S.E.**	**p ± 1 S.E**
Black-backed jackal	North	Winter	0.44 - 0.68	0.48 - 0.60
Black-backed jackal	North	Summer	0.62 - 0.75	0.51 - 0.75
Black-backed jackal	South	Winter	0.72 - 0.9	0.70 - 0.78
Spotted hyena	North	Winter	0.04 - 0.18	0.44 - 0.72
Spotted hyena	North	Summer	0.01 - 0.11	0.68 - 0.98
Brown hyena	South	Winter	0.8 - 1.0	0.27 - 0.35
Leopard	North	Winter	0.41 - 0.67	0.27 - 0.41
Leopard	North	Summer	0.13 -0.35	0.24 - 0.46
Leopard	South	Winter	0.74 - 0.74	0.50 - 0.74

3.4.2 Model fit

Before examining candidate occupancy models for species across sites, goodness of fit for the global model, i.e. the model containing the most parameters, was examined. Results suggest there was no evidence to suggest any of the global models were a poor fit for the data, i.e. probability of the test statistic being greater than the observed being over 0.05 (Table 3.3). Three models showed under-dispersal (ĉ), with all three ĉ values being close to 0, hence correction was not possible.

Table 3.3: Goodness of fit statistic for the global occupancy models, i.e. the models with the most parameters included in them

Site	**Season**	**Species**	**Probability of test statistic ≥ observed from 10,000 parametric bootstraps**	**ĉ**
North	Winter	Black-backed jackal	0.27	1.07
North	Summer	Black-backed jackal	0.96	0.79*
South	Winter	Black-backed jackal	0.06	1.42

North	Winter	Spotted hyena	0.37	1.61
North	Summer	Spotted hyena	0.67	0.78*
South	Winter	Brown hyena	0.17	1.17
North	Winter	Leopard	0.41	1
North	Summer	Leopard	0.05	1.56
South	Winter	Leopard	0.61	0.91*

** under-dispersal is indicated when $\hat{c} < 1$, however currently no convention for correcting this is suggested (MacKenzie et al. 2006)*

3.4.3 Occupancy models with environmental covariates

3.4.3.1 Black-backed jackal

When examining differences in the candidate models, where ψ and p were allowed to vary with environmental covariates, the most parsimonious model, i.e. with the highest AIC weight, for winter was found to be the ψ (Distance to mountain and Presence of water, p (Habitat) (Table 3.4) for winter in the northern sites. This model showed black-backed jackals preferred to occupy sites further away from the mountains, however sites with water were always preferred and had more weight in the model than distance from mountain, irrespective of distance from the mountain. Probability of detection was highest in the open plains/mountain transition habitat and lowest in the mountain habitat. The low difference in AIC weights between the top two models, shows either model would be a good fit for the data. For summer at the northern sites the model ψ (Distance from NP fence), p (Presence of water) was the best fit, with black-backed jackals preferring sites further from the National Park fence line. Probability of detection varied with the presence of water with sites with water having a higher detection probability than sites without. In the southern sites the model ψ (Presence of water), p (Presence of water) proved to be the best fitting model, where black-backed jackals preferred sites where water was present and also had a higher chance if being detected there.

Table 3.4: Black-backed jackal top-fitting occupancy models, across sites and seasons. K= number of covariates, W=Water, NW=No water. O=Open plains, M=Mountain, O/M=Open plains/Mountain transition

Model	**AIC**	**ΔAIC**	**AIC Weight**	**Model likelihood**	**K**	***ψ* (S.E.)**	***p* (S.E.)**
North winter							
ψ (Distance to mountain and Presence of water), *p* (Habitat)	104.47	0	0.32	1	3	From 0.25 (0.11) to 1.0 (0.0)	O = 0.63 (0.10), M = 0.26 (0.11), O/M = 0.72 (0.11)
ψ (Distance to mountain and Presence of water), *p* (Presence of water)	104.47	0.22	0.29	0.89	3	From 0.25 (0.11) to 1.0 (0.0)	W=0.58 (0.14), NW=0.50 (0.0)
ψ (Distance to mountain), *p* (.)	106.84	2.37	0.1	0.31	3	From 0.32 (0.10) to 0.97 (0.05)	0.55 (0.06)
North summer							
ψ (Distance from NP fence), *p* (Presence of water)	111.13	0	0.89	1	2	From 0.29 (0.20) to 0.63 (0.14)	W = 1.0 (0.0), NW = 0.5 (0.0)
ψ (Distance to Mountain), *p* (Presence of water)	111.72	0.4	0.4	0.74	2	From 0.46 (0.07) to 0.62 (0.24)	W=1.0 (0.0), NW=0.5 (0.0)

ψ (Distance from NP fence), *p* (Habitat)	117.82	3.85	0.07	0.15	4	From 0.34 (0.17) to 0.65 (0.17)	O=0.55 (0.12), O/M=0.54 (0.10), M=0.20 (0.08)
South winter							
ψ (Presence of water), *p* (Presence of water)	118.53	0	0.64	1	2	W = 1.0 (0.0), NW = 0.5 (0.0)	W= 0.83 (0.04), NW 0.5 (0.0)
ψ (Habitat and Presence of water), *p* (Presence of water)	120.23	1.71	0.29	0.42	5	From 0.0 (0.0) to 1.0 (0.0)	W= 0.83 (0.04), NW 0.5 (0.0)
ψ (Habitat), *p* (Presence of water)	128.6	10.08	0.001	0.01	4	O=0.76 (0.22), O/M=0.73 (0.13), M=1.0 (0.0)	W= 0.83 (0.04), NW 0.5 (0.0)

3.4.3.2 Spotted hyena

Spotted hyena was the least frequently detected focal carnivore species with a total of 142 independent events across the northern sites. In the south, just 16 events were recorded for spotted hyena. Due to the long time periods between events (up to six months) they were not believed to be resident, rather transient individuals passing through and were therefore not included for occupancy analysis. AIC weight comparison showed the most parsimonious model, when allowing environment covariates to vary was *ψ* (.), *p* (Habitat) winter, where (.) gives a constant estimate. The best fitting model therefore shows no environmental covariates affected the probability of a site being occupied. Probability of detection results was highest in the open plains/mountain transition habitat and lowest for mountain habitat. In summer the model *ψ* (.), *p* (Distance to NP fence) proved the best fit for the data and showed no environmental covariates affected site occupancy. Probability of detection results showed sites nearer to the National Park fence line had a higher probability of detection (Table 3.5).

Table 3.5: Spotted hyena northern sites winter and summer top-fitting occupancy models across sites and seasons. K= number of covariates, W=Water, NW=No water. O=Open plains, M=Mountain, O/M=Open plains/Mountain transition

Model	**AIC**	**ΔAIC**	**AIC Weight**	**Model likelihood**	**K**	***ψ* (S.E.)**	***p* (S.E.)**
Winter							
ψ (.), *p* (Habitat)	23.36	0	0.61	1	4	0.11 (0.07)	O=0.0 (0.0), M=0.07 (0.09), O/M=1 (0.0)
ψ (.), *p* (Presence of water)	24.82	1.46	0.29	0.48	2	0.11 (0.07)	W=1.0 (0.0), NW=0.50 (0.0)
ψ (Habitat), *p* (Habitat)	27.54	4.18	0.08	0.12	2	O=0.20 (0.18), M=1.0 (0.0), O/M=1.0 (0.0),	O=0.0 (0.0), M=0.07 (0.09), O/M=1 (0.0)
Summer							
ψ (.), *p* (Distance to NP fence)	16.35	0	0.45	1	2	0.09 (0.08)	From 0.007 (0.02) to 0.99 (0.02)
ψ (.), *p* (Distance from mountain)	16.71	0.38	0.38	0.82	2	0.09 (0.08)	From 0.0 (0.0) to 0.92 (0.12)
ψ (.), *p* (Distance from NP fence and Presence of water)	17.69	1.36	0.19	0.51	3	0.09 (0.08)	From 0.0 (0.0) to 0.99 (0.1)

3.4.3.3 Brown hyena

Brown hyena was only detected in the southern sites, where it was the most frequently detected large carnivore and had a naive occupancy of 0.81. The most parsimonious occupancy model where occupancy and probability of detection were allowed to vary with environmental covariates was ψ (Presence of water), p (.), where (.) produces a constant estimate, meaning no micro-habitat features were found to affect probability of detection (Table 3.6). Sites with water present had a higher occupancy estimate than sites without water.

Table 3.6: Brown hyena southern sites top-fitting occupancy models, across sites and seasons. W=Water, NW=No water

Model	**AIC**	**ΔAIC**	**AIC Weight**	**Model likelihood**	**K**	**ψ (S.E.)**	**p (S.E.)**
ψ (Presence of water), p (.)	152.06	0	0.42	1	2	W=0.81(0.0, NW=0.5(0.0)	0.33(0.04)
ψ (.), p (.)	153.85	1.79	0.19	0.41	2	0.90 (0.11)	0.33(0.04)
ψ (Habitat + presence of water), p (.)	154.3	2.24	0.9	0.33	5	From 0.0 (0.0) to 1.0 (0.0)	0.33(0.04)

3.4.3.4. Leopard

The most parsimonious model for the northern sites in winter was ψ (Distance to mountain), p (.), where sites closer to mountain habitat were preferred by leopard. In summer the northern sites most parsimonious model was ψ (Distance from mountain), p (Habitat), where sites further away from the mountain were preferred, and probability of detection was highest in the open plains/mountain transition habitat (Table 3.7). For the southern sites AIC weights showed occupancy varying with presence of water and distance to the National Park fence line, with probability of detection varying with habitat type was the best fit. Sites further away from the National Park fence line were preferred, however sites with water were always preferred, irregardless of distance from the National Park, whilst probability of detection was highest in mountain habitat and lowest in the open plains.

Table 3.7 Leopard southern sites top-fitting occupancy models, across sites and seasons. K = number of covariates, O=Open plains, M=Mountain, O/M=Open plains/Mountain transition

Model	**AIC**	**ΔAIC**	**AIC Weight**	**Model likelihood**	**K**	ψ **(S.E.)**	p **(S.E.)**
North winter							
ψ (Distance to mountain), p (.)	91.47	0	0.42	1	2	From 0.004 (0.01) to 0.81 (0.13)	0.33 (0.07)
ψ (Distance to mountain and Distance to NP), p (.)	91.75	0.28	0.22	0.87	3	From 0.001 (0.009) to 0.99 (0.03)	0.33(0.07)
ψ (Habitat and Presence of water), p (.)	91.84	0.37	0.21	0.83	4	From 0.00 (0.00) to 1.0 (0.00)	0.33(0.07)
North summer							
ψ (Distance to Mountain), p (Habitat)	53.64	0	0.23	1	4	From 0.22 (0.13) to 0.99 (0.007)	O=0.22 (0.13), M=0.30 (0.15), O/M=0.66 (0.20)
ψ (.), p (Habitat)	54.22	0.58	0.17	0.75	4	0.26 (0.12)	O=0.22 (0.13), M=0.30 (0.15), O/M=0.66 (0.20)
ψ (.), p (.)	54.26	0.62	0.17	0.78	2	0.26 (0.12)	0.35 (0.11)
South winter							
ψ (Presence of water and Distance to NP fence), p (Habitat)	124.4	0	0.25	1	5	From 0.17 (0.17) to 0.89 (0.13)	O=0.06 (0.06), M=0.40(0.09), O/M=0.35 (0.09)
ψ (Presence of water and Distance to NP fence), p (.)	124.8	0.4	0.82	0.82	3	From 0.17 (0.17) to 0.89 (0.13)	0.35 (0.06)
ψ (Distance from NP fence and Habitat), p (.)	126.1	1.61	0.45	0.45	3	From 0.12 (0.15) to 0.96 (0.07)	0.35 (0.06)

3.4.3.5 Summary of occupancy results

In summary, it can be seen from the Table 3.8 that each species has a unique set of environmental covariates affecting occupancy and probability of detection. Furthermore, the set of covariates changed between seasons for all species, and differences were seen for species between sites.

Table 3.8: Summary of top-fitting occupancy model results for all species, with covariates included assumed as being preferred by each species.

Species	Site	Season	Occupancy/Preference	Probability of detection
Black-backed jackal	North	Winter	Sites further from the mountain, with sites with water present always preferred	Highest in open plains/mountain transition, lowest in mountain
Black-backed jackal	North	Summer	Sites further from NP fence line	Highest at sites with water present
Black-backed jackal	South	Winter	Sites with water present preferred	Highest at sites with water present
Spotted hyena	North	Winter	Not affected by habitat features	Highest in open plains/mountain transition, lowest in open plains
Spotted hyena	North	Summer	Not affected by habitat features	Highest at sites nearer to the NP fence line
Brown hyena	South	Winter	Not affected by habitat features	Highest at sites with water present
Leopard	North	Winter	Sites closer to mountains	Not affected by habitat features
Leopard	North	Summer	Sites further from mountains	Highest in open plains/mountain transition, lowest in open plains
Leopard	South	Winter	Sites further from NP fence line, with sites with water present always preferred	Highest in mountains, lowest in open plains

3.5 Discussion

The results of this study identified the key microhabitat features preferred by problem causing species on commercial farmlands. Occupancy modelling showed each species had a unique combination of environmental covariates affecting both probability of occupancy and detection probability, with differences also seen between sites and seasons for each species. As predicted, the presence of water was included as an environmental covariate in the best fitting models, affecting probability of a site being occupied for black-backed jackal and leopard, and was included as a covariate in the best fitting models as increasing probability of detection for black-back jackal and brown hyena. In every case, the presence of water increased probability of occupancy and probability of detection. The open plains/mountain transition habitat was included the best fitting model as increasing probablity of detection for black-backed jackal, spotted hyena and leopard, which was hypothesised for leopard. It is interesting to note, environmentals did not affect probability of occupancy in the best fitting models for either hyena species, which contradicts the intial hypothesis of both hyena species preferring sites within mountain habitat.

In Kenya, Schuette at al. (2013) found unique environmental covariates combinations contained in the best fit models for each carnivore when conducting occupancy analysis. Results for the Kenyan carnivores also showed the occupancy of the smallest species were affected by the fewest parameters. However, this study showed when taking the mean number of parameters from the top models for each season, brown hyena had the fewest, whilst spotted hyena was affected by the most parameters. The combination of effecting environmental covariates also changed between seasons for all species.

Presence of water was an environmental covariate included in the top candidate model for occupancy for black-backed jackal in winter for both the northern and southern sites, and for both brown hyena, and leopard in the south. For each species, the presence of water was associated with the highest occupancy estimates, showing these species preferred sites with water. Schuette et al. (2013) found across all species, the distance to water had an effect on occupancy. It is worth noting here that the bordering National Park provides no artificial water, with the exception of the artificial water point at Garub near the southern study sites, and that distance from the National Park fence line was an environmental covariate affecting occupancy for black-backed jackal and spotted hyena across the northern sites in the summer, and for leopards in the south during winter. For black-backed jackal and leopard, the probability of a site being occupied increased with increasing distance from the fence line, whilst the reverse was seen for spotted hyena. Spotted hyena were believed to be denning within the National Park, as spoor was continually seen coming from the Park to the farm (*pers. obs*.) and an approximately five month old cub seen for the first time on NBR in December 2013 (Fig 3.1), which could explain such a result. For black-backed jackal and leopard, it is possible whilst distances between neighbouring water sources on the farms are too small to influence occupancy, distance from the National Park, where water is extremely scarce is more likely to affect occupancy.

Figure 3.1: Spotted hyena adult and cub at Namtib Biosphere Reserve water trough, this spotted hyena clan were believed to be denning within the National Park near to this water trough.

Previous studies have shown a negative relationship between distance to water and occupancy (Kalcounis et al. 2005; Pasinelli et al. 2013), whilst Sunarto et al. (2012) found tiger occupancy to increase with increasing distance from water. This result was believed to be due to concentrations of human activity at water sources, and given the high annual rainfall, water availability not to be an issue within forest habitat for tigers. As water availability is scarce for carnivores across the study sites, and not particularly associated with higher levels of human activity, occupancy estimates would be expected to be higher nearer sites where water is present.

Distance from nearest mountain habitat affecting occupancy was included in the best fitting model for black-backed jackal in winter across the northern sites with black-backed jackal preferring sites away from the mountains, and for leopard across the northern sites for both summer and winter. Leopard occupancy changed between season with regard to distance from mountain habitat; in winter leopards preferred mountains, whilst in summer a preference for sites away from mountains was seen. As leopards are normally associated with rocky hills and mountainous habitats (Swanepoel, 2008), relying on cover for concealment when hunting (Balme et al. 2007), a preference for mountains is not surprising. However a preference for sites away from mountains in summer was not expected; leopards are known to favour mountainous habitats (Estes 1992) and Balme et al. (2007) found leopards to actively avoid open grassland habitat on Phinda Private Game Reserve, South Africa. Such a change in preference for distance from mountain between seasons could suggest differences in space use between seasons, and such differences have been observed for both cheetah (Marker 2002) and spotted hyena (Trinkel et al. 2004; Stratford and Stratford 2011) in other regions of Namibia. Stratford and Stratford (2011) observed hyenas moving to different areas of Ongava Game Reserve between seasons, with one female hyena using a different set of waterholes in the wet season.

Changes in space use and home range size between seasons by carnivores have been associated with changes in density and distribution of prey. Marker (2002) and Stratford and Stratford (2011) found home range size to decrease in the wet season, with Marker (2002) postulating such contraction being due to the onset of the rains leading to increases in vegetation density, aggregations of prey in these areas and the birthing season of prey species, and general increased prey availability. However, Trinkel et al. (2004) found spotted hyena to enlarge home range size in the wet season in Etosha National Park, where prey is migratory, in response to increased dispersion of prey. When environmental covariates were modelled, occupancy was higher in winter for black-backed jackal and spotted hyena, and higher in summer for leopard. During summer across both sites, a total of six new locations for leopard were detected, all in open plains or open plains/mountain transition habitats. Such results could suggest utilisation of different areas during the wet season, possibly in relation to prey movements, or increases in home range sizes.

Due to the known behavioural traits of the leopards, it was not expected for them to show a preference for sites away from mountains, as discussed above. Black-backed jackal having a microhabitat features included within the best-fitting models was not predicted, given its opportunistic nature and known ability to persist in a variety of habitats (Estes 1992). Black-backed jackals in the northern sites preferred sites further from mountains in winter and sites further from the National Park border fence in the summer. It is possible the preference for sites away from mountain habitats in winter may have been affected by leopards preference for mountain in winter, and may have represented spatial partitioning between the two species, to decrease the potential for intraguild predation (for a thorough discussion of intraguild predation see Chapter four). Another surprising result given the known behavioural traits of both hyena species using mountainous areas for denning, was the absence of environmental covariates in the top fitting models for either hyena species. Given the low density of both species in the area, it is possible those camera traps located within mountain habitat were not close to hyena dens, and therefore may not have detected this preference.

Habitat type was also a frequently seen environmental variable for probability of detection in top models, being seen for black-backed jackal and spotted hyena for the northern sites in winter and for leopard in the northern sites in summer and southern sites during winter. Black-backed jackal was most likely to be detected in the open plains/mountain transition habitats and least likely detected in the mountains. For spotted hyena and leopard in the north, the probability of detection was highest in open plains/mountain transition habitat and lowest in open plains. However leopard in the southern sites were most likely to be detected in the mountains and least likely in open plains habitat. Thorn et al. (2009) also found habitat type to influence probability of detection for brown hyena in Pilanesberg National Park, South Africa, recommending camera traps be placed in habitats where probability of detection was highest. Royle and Nichols (2003) suggested probability of detection is usually positively correlated with abundance. Therefore habitat preferences will be associated with higher detection probabilities for species. This study shows open plains/mountain transition habitat to be a preferred habitat for black-backed jackal, spotted hyena and leopard in the northern sites, whilst mountain habitat is preferential for leopards in the south.

The results of this occupancy analysis show the micro-habitat features associated with occupancy for carnivores that are defined by local farmers as the main problem animals on commercial farmlands in southern Namibia. Data like this could be important when choosing which grazing areas/camps to use and when, locations for kraaling livestock at night, and which artificial water sources to maintain in order to minimise risk of livestock depredation by avoiding areas preferred by carnivores. However, occupancy analysis revealed unique combinations of environmental features affect each species, with changes between seasons. For example, in the northern study sites, leopards preferred sites close to mountains in winter, yet sites further away from mountains in summer. Such a finding might suggest for a farmer experiencing problems with leopard, would want to consider locating his livestock further from mountains in winter and closer to mountains in summer. Therefore, how landowners plan livestock management will depend on the carnivore species most problematic to them. Small stock farmers often find black-backed jackal problematic (see Chapter seven), whereas cattle farmers have problems with larger carnivore species.

Whilst differences have been identified in the combinations of micro-habitat features associated with occupancy and probability of detection between species, a few general findings can be seen. Presence of water when included in the best fitting model always increased occupancy and probability of detection. This is not surprising given the scarcity of water across the study sites. For spotted hyena, black-backed jackal and in some seasons, leopard, open plains/mountain transition habitat was associated with higher detection probabilities and therefore abundance (Royle and Nichols 2003). Increasing distance from the National Park fence was associated with higher occupancy estimates for both black-backed jackal in the north in summer and leopard in the south. Therefore as a general guide sites for grazing or kraaling should be those close to the National Park fence in open plains habitats. Sites for maintaining water, however, could be more difficult to choose, as occupancy in the presence of water, at least for black-backed jackal and leopard, was always highest, irrespective of habitat type.

4.0 Spatio-temporal resource partitioning within a carnivore guild and between carnivores and prey, at waters on commercial farmlands, southern Namibia.

N.B. This chapter has been adapted and published as a full research paper in Journal of Zoology, see Appendix one

Additionally, Bonferroni corrections have been made to the data following discussions in the viva, and these results can be found in Appendix six.

4.1 Abstract

Water sources in arid environments are both rare and essential, making them attractive areas for a number of species. Such a phenomenon can result in such areas being associated with higher predation risks, for both carnivores through intraguild predation and herbivores via the more traditional form of predation between trophic levels. How species avoid each other at such sites is of interest as it is likely to affect which species are able to coexist in an area, and where domestic livestock species are concerned is especially important as predation of livestock by carnivores is the main reason for human-wildlife conflict globally. This study examined the degree of both spatial and temporal resource partitioning at permanent, spatially fixed water sources on arid, commercial farmlands in southern Namibia. Camera traps were used over the period of a year at 14 water sources across three farmlands to construct temporal and spatial patterns of use for carnivores, wild game and domestic livestock. Results showed within the carnivore guild, temporal rather than spatial partitioning to be the main mechanism used to avoid other guild members. Carnivores and herbivores also used temporal partitioning, as shown by all carnivore species having nocturnal peak activity times at water sources and herbivores mostly having diurnal peak activity times. Significant associations between the difference in body mass between each species pair and spatial overlap within the carnivore guild, and temporal overlap between carnivores and herbivores were also seen. These results show that whilst in arid environments water is rare and used by a number of carnivore species, resource partitioning allows a guild of carnivores, including species of conservation concern, to coexist outside of protected areas. Additionally, and especially encouraging is that domestic livestock species, whose anti-predator natural behaviour has often been questioned, were able to use

temporal resource partitioning to avoid water sources at peak activity times and do so in a way which reflects risk of predation relative to body mass.

4.2 Introduction

As water is an essential component of life, an animal's water requirements are expected to have implications for many aspects of its ecology and behaviour (Hayward and Hayward 2012). Water is known to be a key determinant of herbivore distribution (Chamaillé-Jammes et al. 2007a), and when surface water is scarce, for example in dry seasons, aggregations of numerous species occur around permanent water holes (Thrash et al. 1995; Valeix et al. 2007). In arid ecosystems, herbivores are forced to access water to complement forage consumption, effectively limiting the daily distances they are able to move (Chamaillé-Jammes et al. 2007b). Permanent water sources therefore in arid environments, where little standing water occurs, represent spatially fixed and important resources for a number of species.

One result of many species and individuals visiting water points is that they become high risk areas for predation (Valeix et al. 2009a; Hall et al. 2013). However, predation in such locations is not limited to traditional predation between trophic levels (Fedriani et al. 2000). In ecosystems with multiple carnivore species, this can include intraguild predation, an extreme form of interference competition (Holt and Polis 1997), occurring when one species kills and sometimes eats another species which uses similar resources (Polis et al. 1989). Such predation is largely asymmetrical (Woodward and Hildrew 2002), with larger species often killing both adult and young of smaller species (Palomares and Caro 1999). Intraguild predation can have important consequences for the distribution and abundance of carnivores (Tannerfeldt et al. 2002), and unlike traditional predation, also reduces potential competition with competing species (Polis et al. 1989).

Intraguild predation among mammalian carnivores is common and has been documented for 97 species pairs (Linnell and Strand 2000), for some species accounting for up to 68 % of recorded mortalities (Palomares and Caro 1999). Within the African carnivore guild, Caro and Stoner (2003) estimated the average species to be vulnerable to predation from 15 guild members. Palomares and Caro (1999) stated that bat-eared fox and cheetah are the most commonly killed species, with leopard being a frequent killer. Other examples include lions and spotted hyena as frequent causes of wild dog mortality (Mills and Gorman

1997) and black-backed jackal killing both Cape and bat-eared fox (Kamler et al. 2012). Water points, which are spatially fixed, limited and essential, are therefore areas where direct encounters between carnivore species are likely to occur, which could have lethal consequences.

Species at risk of intraguild predation often avoid intraguild predators (Polis and Holt 1992). Ecological separation is known to occur along the three axes of habitat, food and time (Schoener 1974) although when considering avoidance at water points, only habitat and time can be considered to be relevant. Hayward and Slotow (2009) examined temporal overlap between cheetah, wild dog, spotted hyena and lion and postulated that subordinate members of the guild use temporal resource partitioning, and have evolved activity patterns which minimise overlap with dominant species, to avoid both kleptoparasitism and intraguild predation. Schoener (1974) argued temporal resource partitioning is relatively rare in ecology, however it is seen more often in carnivores than other groups. Spatial partitioning however, is also seen between carnivores, for example Tannerfeldt et al. (2012) recorded spatial segregation between red fox *Vulpes vulpes* and Arctic fox *Alopex lagopus*, and Kamler et al. (2012) found spatial avoidance of black-backed jackal by Cape fox.

How carnivore species potentially at risk from intraguild predation share essential water sources has received little attention (but see Atwood et al. 2011), however this could have important consequences for species conservation, and the number of carnivore species an area can support. Intraguild predation is believed to have the ability to reduce the carrying capacity of an area below densities predicted from prey abundance alone (Linnell and Strand 2000). It is well known that the densities of both wild dog and cheetah, two species of conservation concern, show a negative association with the densities of lions and spotted hyenas (Creel and Creel 1996; Durant 2000; Mills and Gorman 1997).

The coexistence and avoidance of intraguild predation between carnivore species has important consequences for carnivore conservation. Similarly, the avoidance of carnivores by both wild prey and domestic game on farmlands has implications for carnivores through involvement in human-wildlife conflict. Human-wildlife conflict, caused when an animal injures, destroys or damages human life or property and that animal is killed, injured or otherwise harmed as a result (Jones and Barnes 2006), can have serious consequences for those species involved. Inskip and Zimmerman (2009) estimated 75 % of all felid species are thought to be involved in HWC, with 43 % of which being of conservation concern, and it is believed the substantial drop in large carnivore numbers and distributions in recent years has been mainly due to conflict with settlers and pastoralists (Herrmann et al. 2001).

Water holes are considered risky places for herbivores as they have no option but to aggregate at these essential resources (Valeix et al. 2009a). As a result, the encounter rate of prey by predators is predicted to be higher at water sources (Valeix et al. 2009b). Predators are known to take advantage of these aggregations by concentrating hunting activity there (Hopcraft et al. 2005; Valeix et al. 2009). However, prey species are known to use both spatial (Muhly et al.2010) and temporal resource partitioning to avoid predators, thus lowering risk of predation, and are known to increase vigilant behaviour whilst visiting water sources (Valeix et al. 2009a). Avoidance of predators by domestic livestock presents a case of special interest for two reasons. Firstly, predation upon domestic species by carnivores is a major cause of human-wildlife conflict globally (Fontúrbel and Simonetti 2011). Secondly, because anti-predator behaviour is believed to be reduced in domestic species (Mignon-Grasteau et al. 2005), and therefore can be considered easy prey for carnivores (Polisar et al. 2003). This second point is especially true for southern Namibian, where large domestic livestock are largely left unattended.

This study investigated spatial and temporal resource partitioning between carnivores, domestic livestock (cattle and horses) and wild game (oryx and springbok) at water sources on commercial farmlands bordering the Namib-Naukluft and Tsau//Khaeb (Sperrgebiet) National Parks, southern Namibia. Being the only continent with an intact carnivore guild, Africa presents the perfect opportunity to study carnivore guild interactions (Cozzi et al. 2012). Furthermore, Namibia, with its low rainfall (mean annual of just 270 mm), and the driest climate in sub-Saharan Africa (Sweet 1991), is an ideal place to study resource partitioning at spatially fixed resources as farmers are forced to provide domestic livestock and game with water in artificial troughs, and these are often the only water available for wildlife in the local area.

This chapter aims to examine the degree of temporal and spatial partitioning both within the carnivore guild and between focal carnivore species and domestic livestock and wild game, given the potential for such sites to be centres for activity for all wildlife species. The specific objectives for the chapter are; to use camera traps at water points to identify the temporal and spatial patterns of activity at water points by carnivores, wild game (specifically oryx and springbok) and domestic livestock (specifically cattle and horses). To compare and identify differences in temporal activity patterns at water points between each species pair, with significant differences in activity patterns being indicative of temporal partitioning. Thirdly, to compare and test for associations between the proportion of visits between species pairs at water points, with a significant, negative association taken as suggesting spatial partitioning as occurring. Lastly, to test for an association between difference in body mass and degree of both temporal and spatial partitioning between species pairs, both within the carnivore guild and between carnivores and herbivores.

Based on previous studies, it is hypothesised the carnivore guild will show mainly nocturnal activity, with the exception of cheetah, which will show mainly nocturnal activity, and honey badger and black-backed jackal which are hypothesised to show crepuscular activity patterns. It is also hypothesied, as carnivores are expected to mainly show nocturnal activity at water points, it is predicted herbivores, both wild game and domestic livestock would show diurnal activity. As water points are rare and occur at a low density, it is hypothesised temporal, rather than spatial, would be the main mechanism used, both within the carnivore guild and between carnivores and herbivores, to avoid direct encounters at water points. Finally, as body mass has been cited as a predictor of predation, it is hypothesised associations between difference in body mass between species pairs and the degree of temporal partitioning will be seen. Species pairs with larger differences in body mass, will show a greater degree of temporal partitioning.

4.3 Methods

A total of 14 water sources were monitored by camera trap from May 2013 to May 2014 over Tsirub, Klein Aus Vista (KAV) and Namtib Biosphere Reserve (NBR), shown in Figures 4.4 - 4.11. Thirteen of the water sources were artificial, having water pumped from underground sources to stone troughs often located next to large dams. The remaining water source on KAV was a permanent, natural spring in mountainous habitat. All camera traps were set to operate 24 hours a day, at normal sensitivity, with one photo being taken per triggering with a minute interval between triggers. Camera traps were checked on average once every two weeks when SD cards were changed and new batteries put in if needed.

4.3.1 Data analysis

4.3.1.1 Temporal resource partitioning between carnivores

Data from camera trap images were entered in Excel spreadsheet databases, with the location, date, time, image number, species and number of each carnivore species present in the image being recorded. Images were then classed into independent events to avoid pseudo replication. Images were classed as independent if a minimum of 30 minutes passed between consecutive photos of the same species, or where individual identification was possible, each photo showed a different individual (O'Brien et al. 2003; Thorn et al. 2009). For example, multiple photos of the same species within a 30 minute period would be classed as a single event. A period of thirty minutes was decided upon after conducting observation sessions at the hide at the Namtib Biosphere Reserve water point. During observations it was seen that black-backed jackal, the most frequently recorded carnivore species at water points, would have a minimum of thirty minutes between different individuals visiting the same water point. Individual identity was assumed from physical characteristics and direction of approach to the water point.

To assess the degree of temporal resource partitioning between carnivore species, two statistical analyses were conducted; the Mardia-Watson-Wheeler test, a non-parametric test which tests for homogeneity between two or more samples of circular data, and Pianka's index, a measure of niche overlap between species. Mardia-Watson-Wheeler tests were performed, and histograms produced in Oriana 4.02 (Kovach Computing Services) and conducted separately for each study site, using a significance level of $P = 0.05$. The test requires a minimum of ten data points in each variable, meaning not every carnivore species detected was included in data analysis. To perform the test, all independent events from all locations within a study site were pooled for each species.

Pianka's index (Pianka 1973) was calculated using R 3.1.1 (R Development Core Team, 2014), using package 'pgirmess' version 1.5.9 (Giraudoux 2014). The number of carnivore events per two hour time period were calculated for each species and the proportion of events in each time period were compared using Pianka's index. Pianka's index runs from 0 meaning no overlap, to 1 representing complete overlap between species. Spearman's rank correlation was used to examine the association between difference in body mass between species and Pianka's index for temporal overlap in R 3.1.1. The body mass of species were taken from Estes (1992).

In order to examine if different carnivore species avoid using water points on the same day, a re-sampling procedure was used to see if the observed number of nights carnivores were recorded at the same camera trap location on the same night significantly differed from the expected number of nights this would occur randomly. To calculate the number of nights that joint occurrence of two species was likely to occur by random at the same camera trap, two sets of random numbers were generated, one for each species in the pair. The *n* of the first set of random numbers was equal to the number of nights the first species was recorded at the camera trap and the *n* for the second sample was equal to the number of nights the second species was recorded at the camera trap. Random numbers were generated between one and the total number of camera trap nights. The number of times the same number was seen in the first and second set of randomly generated numbers was seen was equal to the number of joint occurrences likely to occur by random. This procedure was then repeated 10,000 times, each time with newly generated sets of random numbers and the mean number of joint occurrences taken.

This re-sampling procedure was then repeated at every camera trap location for each pair of carnivore species, using R 3.1.1. Wilcoxon paired tests were then performed, also in R 3.1.1, to test for significant differences between the observed and expected numbers of joint occurrences for each species pair for each study site. As Namtib Biosphere Reserve only had one water point, this analysis could not be performed for this study site.

An association between degree of temporal partitioning and difference in body mass between species pairs were tested for by calculating the difference in body mass between carnivores species pairs using were average body mass cited in Estes (1992). Differences in body mass were then plotted against Pianka’s indices of temporal overlap and Spearman’s rank correlation analyses performed in R 3.1.1., to test for associations between temporal overlap and differences in body mass.

4.3.1.2 Spatial resource partitioning between carnivores

As for temporal resource partitioning data analysis between carnivores, camera trap images of carnivores were classed into independent events, using a criterion of 30 minutes or more passing between consecutive photos of the same species, or for species with individually unique markings, a different individual was shown on each photo. The proportion of independent events at each camera trap location was calculated for each species on Tsirub and KAV. Namtib Biosphere Reserve was not included in this analysis as only one water point was present on the farm. To assess the degree of overlap between species, Pianka's index of niche overlap was performed using statistics programme R 3.1.1.

Additionally to further examine spatial overlap; association analysis between the relative abundance indices (RAIs) of carnivores at each water point was performed. Relative abundance was calculated using the formula from Negroes et al. (2010):

$RAI_i = (g_i \sum jP_{ij} / \sum_j tn_j)*100$

Where g_i = average group size for the $_{ith}$species, P_{ij} = number of independent events for the ith species, tn_j = total number of trap nights at the$_{jth}$ location. RAI therefore is a measure of the number of events per 100 trap nights, an index commonly reported in camera trap surveys allowing for comparisons to other studies. This equation incorporates group size which is important for social species such as black-backed jackal, bat-eared fox and spotted and brown hyena. Group size for carnivores was determined from literature and where possible through direct observation of carnivores on the study sites. As the number of water points at each study site was small (seven on Tsirub and six on KAV), data from the two study sites were combined for correlation analysis. Data was not normally distributed, therefore Spearman rank correlations were performed in R 3.1.1. As larger members of the guild are known to dominate smaller species (Palomores and Caro 1999), the dominant species, and therefore dependent variable was classed as the species with the higher body mass. Spearman's rank correlation was used to examine the association between difference in body mass and Pianka's index for spatial overlap.

In order to show the proportion of events at each water point in relation to habitat features, maps were made in Google Earth placing a buffer around each camera trap location, the radius of the buffer being related to the proportion of events at that camera trap by the species. The same scale was not used in all figures, and was adjusted each time to fit best on the map.

An association between degree of spatial partitioning and difference in body mass between species pairs were tested for by calculating the difference in body mass between carnivores species pairs using were average body mass cited in Estes (1992). Differences in body mass were then plotted against Pianka's indices of spatial overlap and Spearman's rank correlation analyses performed in R 3.1.1., to test for associations between temporal overlap and differences in body mass.

4.3.1.3 Temporal resource partitioning between carnivores, domestic livestock and game

As black-backed jackal, spotted hyena, brown hyena and leopard are perceived to be the main problem-causing species by farmers in the area, this section focuses on temporal resource partitioning between these carnivore species and domestic livestock and game only.

Data from camera trap images was entered into Excel spreadsheets as described in section 4.2.1.1. Due to game and domestic livestock standing at water points for sometimes several hours at a time (personal obs.) the previous method of classifying images as independent events, i.e. a minimum of thirty minutes had passed between consecutive photos, could not be used without evoking pseudo replication. Additionally, springbok and oryx could not be identified to individual level from camera trap images. Instead, the proportion of images falling into each two hour time period was used, with a minimum of 24 hours passing between photos. For example, each two hour time period could only contain one event per day, meaning the proportions calculated represented the proportion of days that particular species was present at a particular water point. To make comparisons between species possible, the same method was used for carnivores, domestic livestock and game.

Differences in body mass between carnivores, domestic livestock and game were then calculated using average body mass cited in Estes (1992). Differences in body mass were then plotted against Pianka's indices and Spearman's rank correlation analyses performed in R 3.1.1., to test for associations between temporal overlap and differences in body mass. Positive values for differences in body mass represented the domestic livestock or game having a higher body mass than the carnivore and negative differences represented carnivores with a larger body mass than the domestic livestock or game species.

4.3.2.4 Spatial resource partitioning between carnivores and game

As for temporal resource partitioning between carnivores, domestic livestock and game, camera trap photos were classified into independent events using the criteria of a minimum of 24 hours between photos, or for carnivores with individually unique markings, a new individual was captured. However, because domestic livestock on KAV were rotated through grazing camps and, therefore, could not control which water points they used on a spatial scale, these could not be included in spatial resource partitioning analysis. To assess the degree of spatial overlap between species Pianka's index for niche overlap was perform on the proportion of independent events at each camera trap location.

To further examine the spatial resource partitioning, correlation analysis was used to look at the association between the relative abundance indices of carnivore and game species at water points. Relative abundance was calculated from the number of operational camera trap nights, using the formula from Negroes et al. (2010) (see above). As for carnivores, buffer maps were produced for springbok and oryx where the size of the buffer around a camera trap location relates to the proportion of independent events by that species at that particular camera trap.

4.4 Results

4.4.1 Temporal resource partitioning between carnivores

A total of 6,648 independent records of nine carnivore species were captured at 14 water points across the three study sites over 4,879 trap nights; eight species were captured at seven water points over 2,500 trap nights on Tsirub, six species at six water points over 2,007 trap nights at Klein Aus Vista (KAV) and three species at a single water point over 372 trap nights at Namtib Biosphere Reserve (NBR).

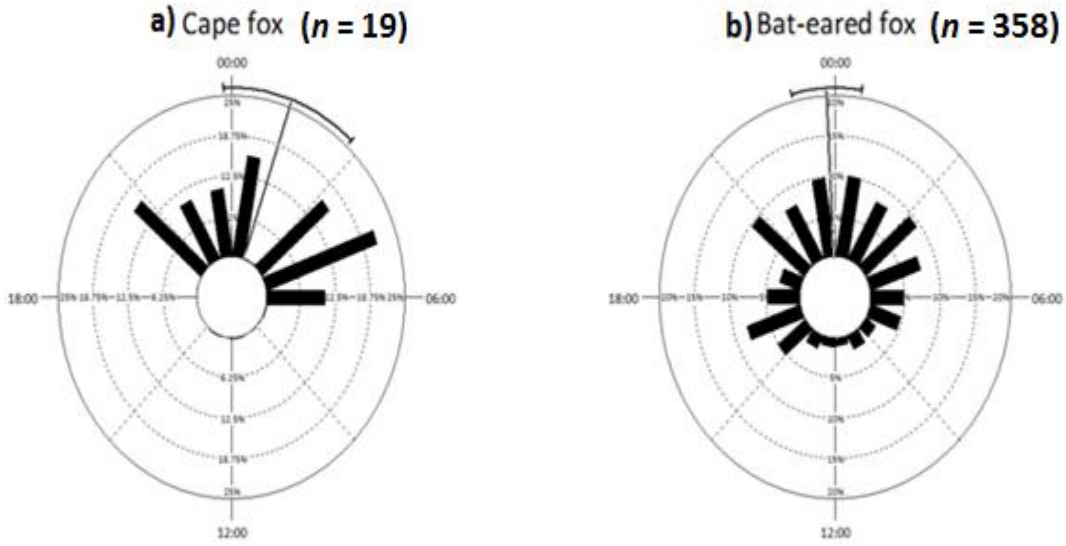
Mean activity time, concentration of activity and circular variance of activity differed between carnivores (Table 4.1). Cape fox was detected at Tsirub and KAV water points only and showed strict nocturnal activity across both sites (Fig. 4.1 and 4.2) with mean activity times of 01:17 h and 01:26 h for Tsirub and KAV respectively. Bat-eared fox was also captured at Tsirub and KAV only, at Tsirub activity was detected throughout the day with a mean activity time of 23:48 h, whilst at KAV activity was mainly nocturnal (Fig. 4.2), with a mean activity time of 22:21 h. Black-backed jackal was detected at all three sites, where it showed activity throughout the day (Figs. 4.1, 4.2 & 4.3) with mean activity times of 00:47 h, 23:57 h and 05:14 h for Tsirub, KAV and NBR, respectively. Honey badger was only present at Tsirub and KAV; at Tsirub it showed bimodal activity peaks, being mainly nocturnal with some crepuscular activity (Fig. 4.1) and a mean activity time of 02:11 h, whilst at KAV honey badger showed mainly nocturnal activity with a mean activity time of 02:33 h.

Table 4.1: Circular statistics of temporal activity patterns for carnivore species across the three study sites, Tsirub, Klein Aus Vista and Namtib Biosphere Reserve, statistics gained using programe Oriana

	Tsirub								**KAV**						**NBR**		
Variable	**Cape fox**	**Bat-eared fox**	**Black-backed jackal**	**Honey badger**	**Brown hyena**	**Leopard**	**Cheetah**	**African wild cat**	**Cape fox**	**Bat-eared fox**	**Black-backed jackal**	**Honey badger**	**Brown hyena**	**Leopard**	**Black-backed jackal**	**Spotted hyena**	**Leopard**
# of independent observations	19	358	3332	34	265	55	22	51	121	18	1150	12	134	93	768	196	20
# of water points recorded	5	7	7	7	7	5	6	6	1	2	6	4	5	5	1	1	1
Mean vector	01:17	23:48	00:47	02:11	01:23	01:03	02:14	23:23	01:26	22:21	23:57	02:33	01:42	00:18	05:14	00:52	00:02
Length of mean vector	0.69	0.36	0.25	0.08	0.63	0.32	0.45	0.55	0.63	0.8	0.18	0.73	0.58	0.4	0.91	0.64	0.69
Concentration	1.96	0.78	0.51	0.15	1.63	0.68	1.02	1.32	1.65	2.83	0.36	1.66	1.43	0.88	0.39	1.67	1.95
Circular variance	0.31	0.64	0.76	0.93	0.37	0.68	0.55	0.45	0.69	0.2	0.82	0.27	0.42	0.6	0.81	0.36	0.31
Standard error of mean	00:45	00:22	00:11	06:09	00:13	01:06	01:11	00:37	00:20	00:36	00:26	01:00	00:21	00:39	00:30	00:15	00:44
95% confidence interval	23:48-02:45	23:03-00:33	00:25-01:09	14:06-14:16*	00:56-01:50	22:53-03:12	23:53-04:35	22:09-00:37	00:46-02:06	21:10-23:32	23:05-00:50	00:35-04:31	01:00-02:25	23:00-01:36	04:15-06:13	00:21-01:24	22:35-01:28

* *Oriana cautioned value may be unreliable due to low concentration/uniform distribution*

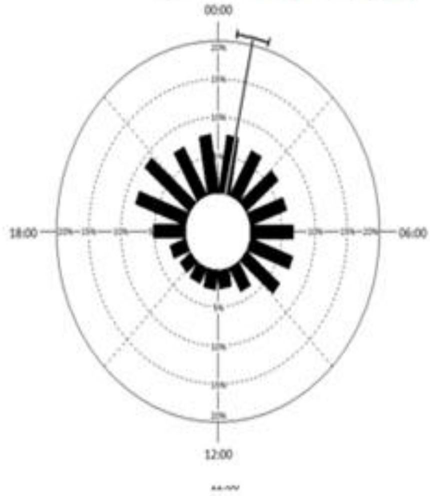
Brown hyena was detected at Tsirub and KAV only and at both sites showed primarily nocturnal behaviour (Figs. 4.1 & 4.2) with mean activity times of 01:23 h and 01:42 h respectively. Spotted hyena was detected at all three sites, however too few events were recorded at Tsirub and KAV in include in analysis. At NBR spotted hyena showed strict nocturnal behaviour (Fig. 4.3) and had a mean activity time of 00:52 h. Leopard was present at all three sites and showed activity throughout the day at Tsirub and KAV (Figs. 4.1 & 4.2), with mean activity times of 01:03 h and 00:18 h respectively, whilst at NBR behaviour was nocturnal with a mean activity time of 00:02 h. Cheetah was present at both Tsirub and NBR, the number of events at NBR were too low for data analysis. Cheetah on Tsirub showed primarily nocturnal behaviour, with some activity between 06:00 h and 09:00 h, with a mean activity time of 02:14 h (Fig. 4.1). African wild cat was detected at Tsirub and showed activity throughout the day, although this was mostly nocturnal (Fig. 4.1) and had a mean activity time of 23:23 h.



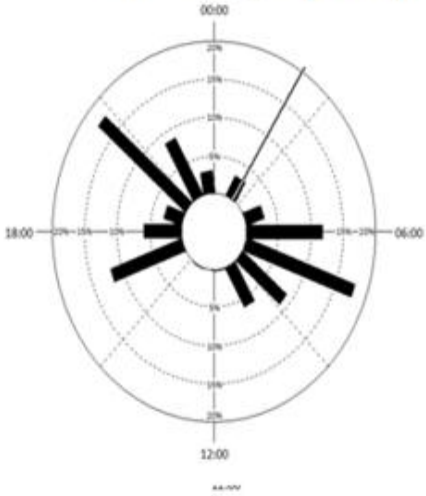
a) Cape fox (*n* = 19)

b) Bat-eared fox (*n* = 358)

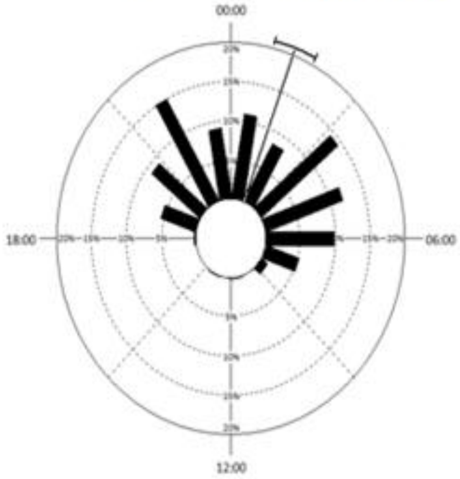
c) Jackal **(*n* = 3332)**



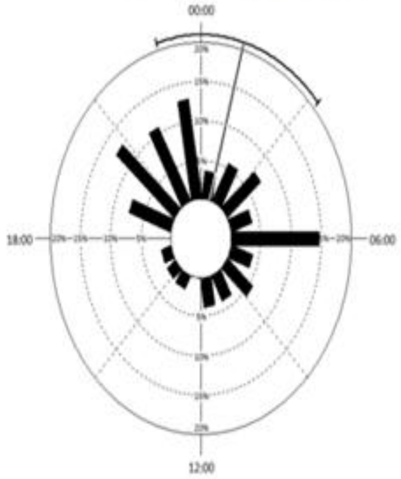
d) Honey badger **(*n* = 34)**

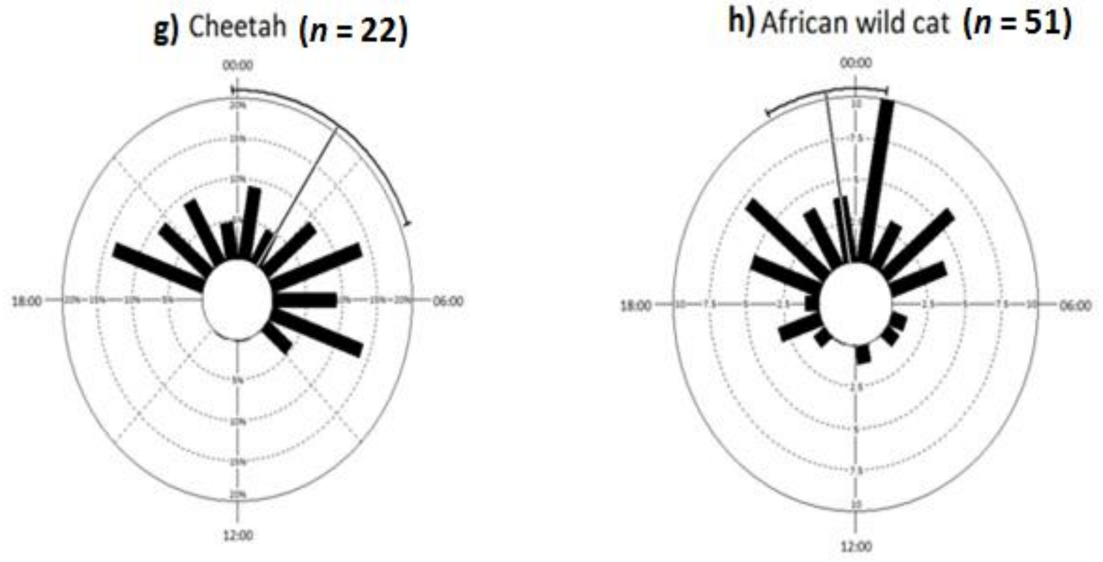


e) Brown hyena **(*n* = 265)**



f) Leopard **(*n* = 55)**

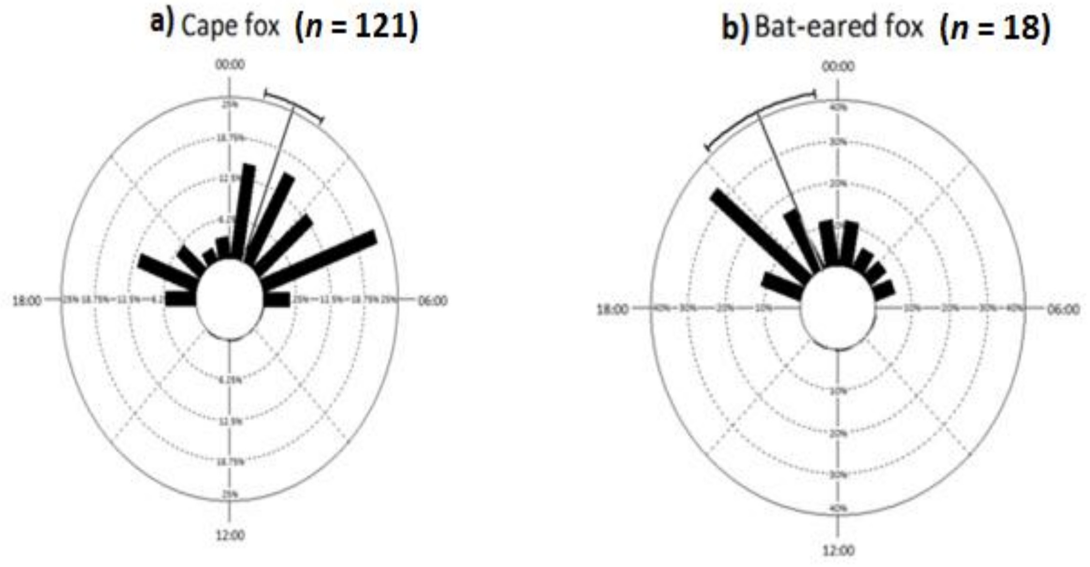




g) Cheetah (*n* = 22)

h) African wild cat (*n* = 51)

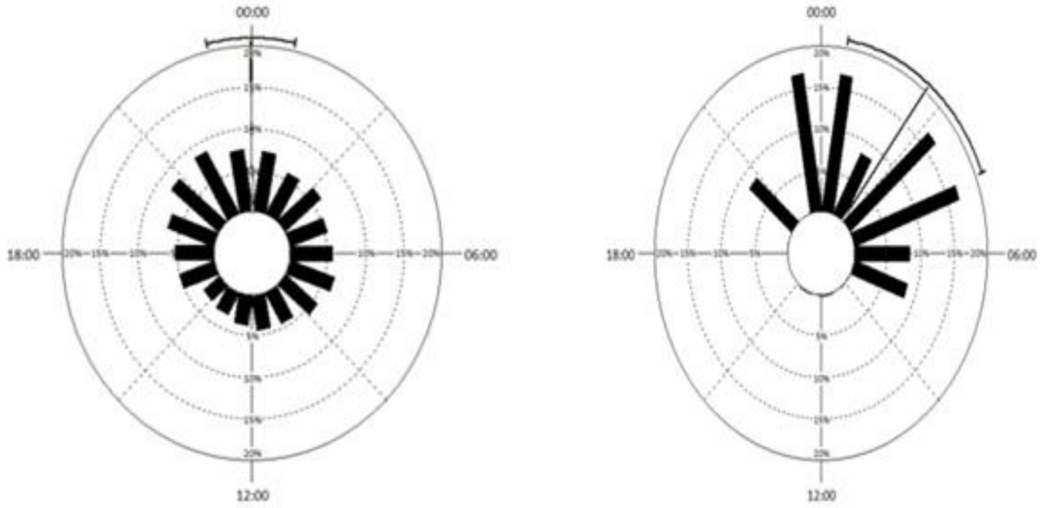
Figure 4.1: Temporal activity of carnivores on Tsirub, black bars show activity seen throughout the 24 hour period, with time shown on the outer region of the figure, with the length of black bars representing the proportion of activity seen. Longer bars represent peak times of activity.



a) Cape fox (*n* = 121)

b) Bat-eared fox (*n* = 18)

c) Jackal **(*n* = 1150)** **d)** Honey badger **(*n* = 12)**



e) Brown hyena **(*n* = 134)** **f)** Leopard **(*n* = 93)**

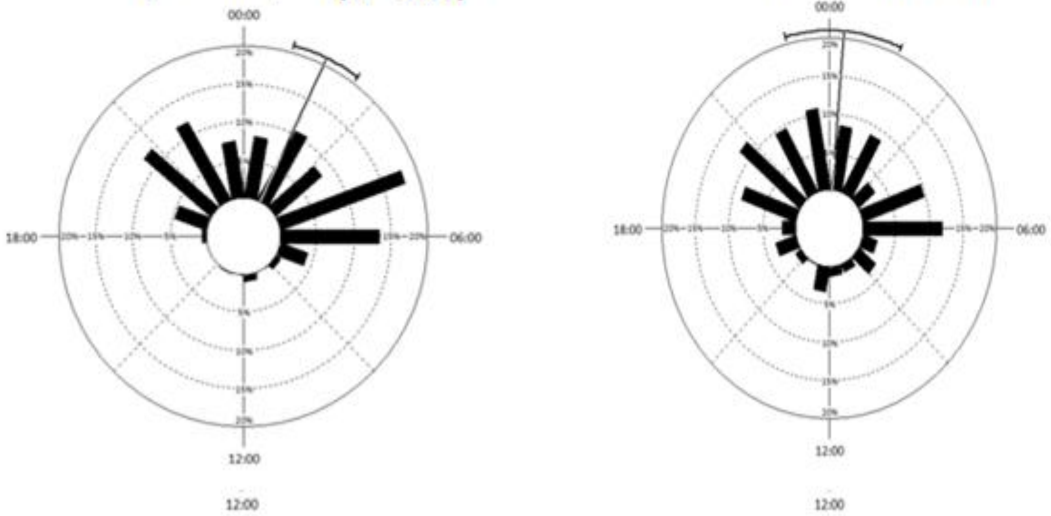


Figure 4.2: Temporal activity of carnivores on KAV, black bars show activity seen throughout the 24 hour period, with time shown on the outer region of the figure, with the length of black bars representing the proportion of activity seen. Longer bars represent peak times of activity

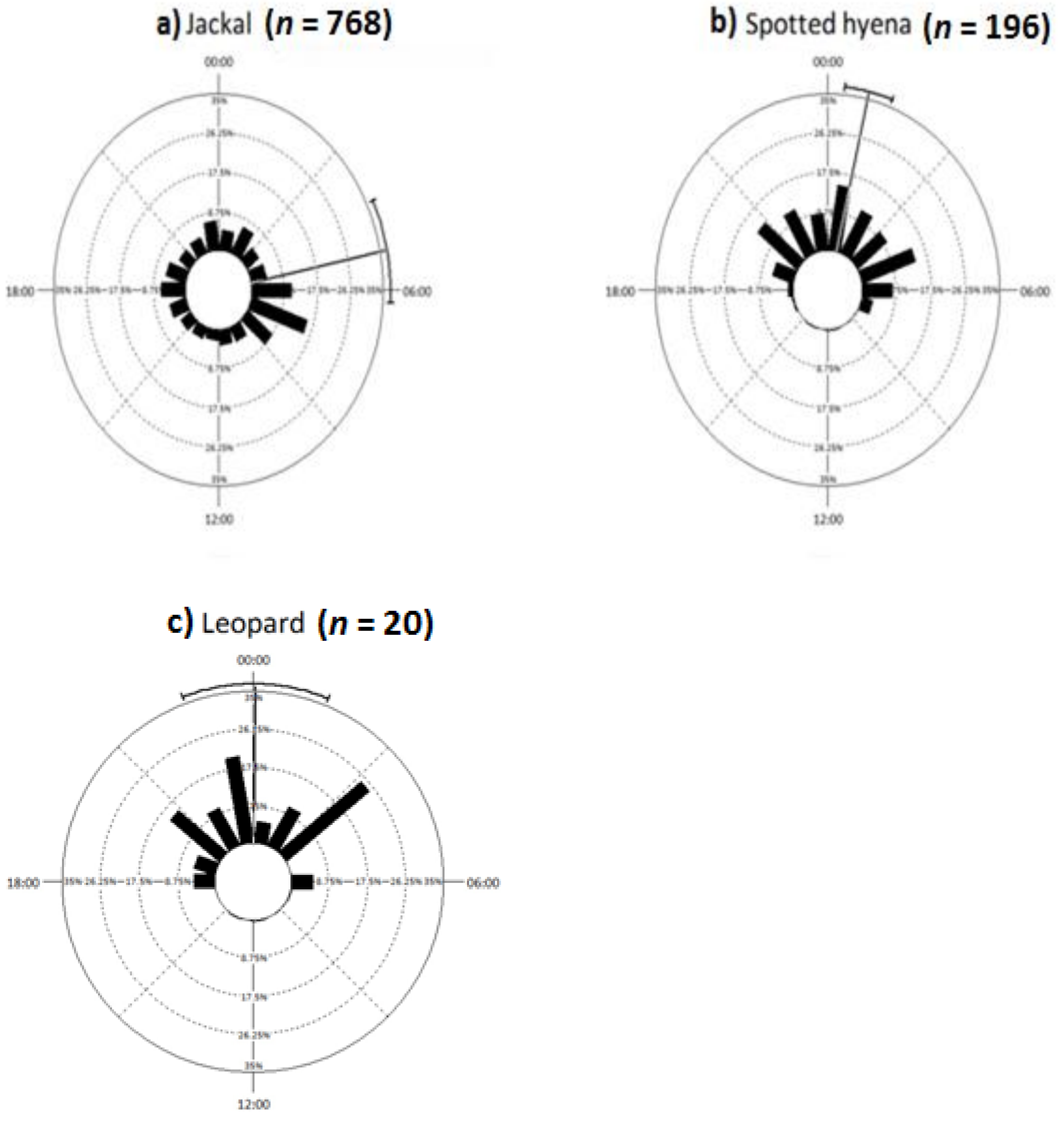


Figure 4.3: Temporal activity of carnivores on NBR, black bars show activity seen throughout the 24 hour period, with time shown on the outer region of the figure, with the length of black bars representing the proportion of activity seen. Longer bars represent peak times of activity

Mardia-Watson-Wheeler tests revealed significant differences in temporal activity between species at water points at Tsirub; brown hyena temporal activity being significantly different to the temporal activity of leopard, black-backed jackal, bat-eared fox and honey badger. Leopard temporal activity was significantly different from Cape fox and honey badger, black-backed jackal was significantly different from African wild cat, bat-eared fox and Cape fox and honey badger temporal activity was significantly different from African wild cat, bat-eared fox and Cape fox (Table 4.2). Pianka’s index showed the highest level of overlap occured between brown hyena and leopard, and black-backed jackal and cheetah (both at 0.94), whilst the lowest level of overlap was seen between Cape fox and honey badger, at 0.30) (Table 4.2).

At Klein Aus Vista, there were significant differences in temporal activity at water points between all carnivore species, with the exception of brown hyena and honey badger and honey badger and Cape fox. Pianka’s index showed the highest level of overlap to occur between black-backed jackal and leopard (0.92), and the lowest level to occur between black-backed jackal and honey badger (0.44) (Table 4.2).

Meanwhile, on Namtib Biosphere Reserve, significant differences in temporal activity patterns at water points were seen between black-backed jackal and spotted hyena and black-backed jackal and leopard. Pianka’s index showed overlap was highest between spotted hyena and leopard (0.92) and lowest between black-backed jackal and leopard (0.57) (Table 4.2).

Spearman’s rank correlation showed no significant association between difference in body mass and Pianka’s index of temporal overlap for data combined from all three study sites (r_s = -0.15, P = 0.33).

Table 4.2: Results of Mardia-Watson-Wheeler tests and Pianka's indices, as tests for examining the degree of temporal resource partitioning between carnivores, significant results are shown in bold

	Tsirub		**KAV**		**NBR**	
Species	**Mardia-Watson-Wheeler test**	**Pianka's Index**	**Mardia-Watson-Wheeler test**	**Pianka's index**	**Mardia-Watson-Wheeler test**	**Pianka's index**
Cape fox & bat-eared fox	2.34	0.68	**8.08**	0.53		
Cape fox & black-backed jackal	**10.08**	0.64	**52.87**	0.68		
Cape fox & honey badger	**20.92**	0.30	0.07	0.81		
Cape fox & brown hyena	0.20	0.79	**8.00**	0.84		
Cape fox & leopard	**6.74**	0.84	**20.09**	0.72		
Cape fox & cheetah	2.49	0.64				
Cape fox & African wild cat	0.48	0.60				
Bat-eared fox & black-backed jackal	**20.53**	0.93	**15.54**	0.73		

Bat-eared fox & honey badger	**13.54**	0.62	**7.33**	0.64		
Bat-eared fox & brown hyena	**12.52**	0.91	**8.83**	0.71		
Bat-eared fox & leopard	1.36	0.89	**8.92**	0.83		
Bat-eared fox & cheetah	1.12	0.88				
Bat-eared fox & African wild cat	2.33	0.85				
Black-backed jackal & honey badger	4.66	0.74	**10.26**	0.44		
Black-backed jackal & spotted hyena					**136.96**	0.71
Black-backed jackal & brown hyena	**94.61**	0.86	**43.64**	0.78		
Black-backed jackal & leopard	0.76	0.88	**8.41**	0.92	**20.60**	0.57
Black-backed jackal & cheetah	2.32	0.94				
Black-backed jackal & African wild cat	**10.60**	0.80				
Honey badger & brown hyena	**36.30**	0.54	1.63	0.81		
Honey badger & leopard	**6.44**	0.62	**6.69**	0.73		
Honey badger & cheetah	2.49	0.85				
Honey badger & African wild cat	**12.03**	0.46				
Brown hyena & leopard	**13.17**	0.94	**6.98**	0.91		
Brown hyena & cheetah	3.64	0.88				
Brown hyena & African wild cat	1.67	0.72				
Leopard & spotted hyena					0.65	0.92
Leopard & cheetah	1.22	0.89				
Leopard & African wild cat	2.75	0.63				
Cheetah & African wild cat	3.74	0.72				

Re-sampling procedures showed significant differences in the number of observed and expected numbers of joint occurrences for Cape fox and honey badger, Cape fox and leopard and Cape fox and African wild cat on Tsirub and honey badger and leopard on KAV. This meant the number of days the two species were seen at the same water source was significantly different than would be expected to happen at random. Observed number of joint occurrences for significant results were always less than expected. As Cape fox was only recorded at one location on KAV, Wilcoxon paired test could not be performed for this species.

Table 4.3: Wilcoxon paired test results for joint occurrences of carnivores, to test if the number of nights each species pair were detected together significantly differed from that expected by chance alone, bold value indicate significant results at 0.05 level.

Species	**Tsirub**	**KAV**
Cape fox & bat-eared fox	12	NA
Cape fox & black-backed jackal	10	NA
Cape fox & honey badger	4	NA
Cape fox & brown hyena	0	NA
Cape fox & leopard	0	NA
Cape fox & cheetah	4	NA
Cape fox & African wild cat	0	NA
Bat-eared fox & black-backed jackal	15	4
Bat-eared fox & honey badger	11	0
Bat-eared fox & brown hyena	0	3
Bat-eared fox & leopard	6	0
Bat-eared fox & cheetah	11	
Bat-eared fox & African wild cat	**0**	
Black-backed jackal & honey badger	17	4
Black-backed jackal & brown hyena	17	7
Black-backed jackal & leopard	5	7
Black-backed jackal & cheetah	20	
Black-backed jackal & African wild cat	8	
Honey badger & brown hyena	18	4
Honey badger & leopard	0	1
Honey badger & cheetah	**0**	
Honey badger & African wild cat	**0**	
Brown hyena & leopard	8	9
Brown hyena & cheetah	6	
Brown hyena & African wild cat	**0**	
Leopard & cheetah	0	
Leopard & African wild cat	4	
Cheetah & African wild cat	5	

4.4.2 Spatial resource partitioning between carnivores

A total of seven water points were monitored on Tsirub and six water points were monitored on KAV. Differences were seen in the number of independent events for each species at each water point, as shown by Figures 4.4 - 4.11. On Tsirub, Cape fox ranged from 0 events to 8, bat-eared from 1 to 109, black-backed jackal from 73 to 1,029, honey badger from 1 to 10 and brown hyena from 1 to 71. Leopard on Tsirub ranged from having one independent event to 25 at water points whilst cheetah ranged from 0 to 11 and African wild cat from 0 to 33. On Klein Aus Vista Cape fox was only recorded at a single water point, having 121 independent events at Pad House, bat-eared fox ranged from 0 to 13, black-backed jackal from 9 to 439, honey badger from 0 to 4, brown hyena from 0 to 50 and leopard from 0 to 30 (Table 4.4).

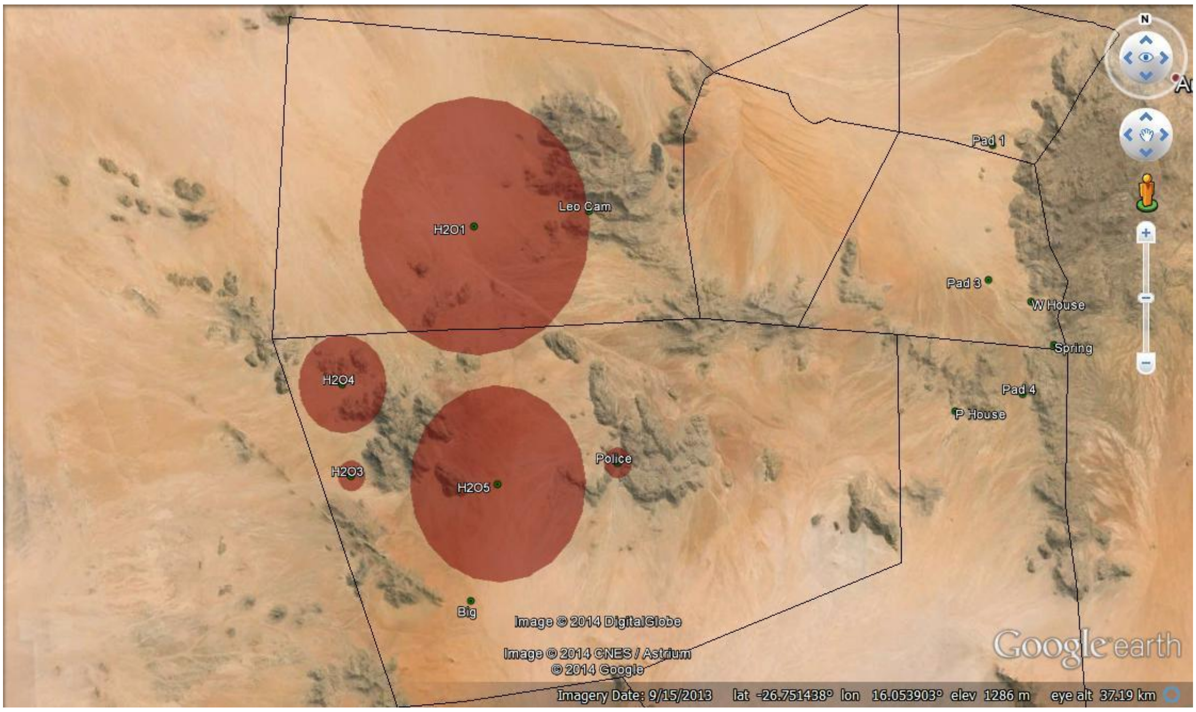


Figure 4.4: Buffer map showing proportion of independent events of Cape fox at water points on Tsirub

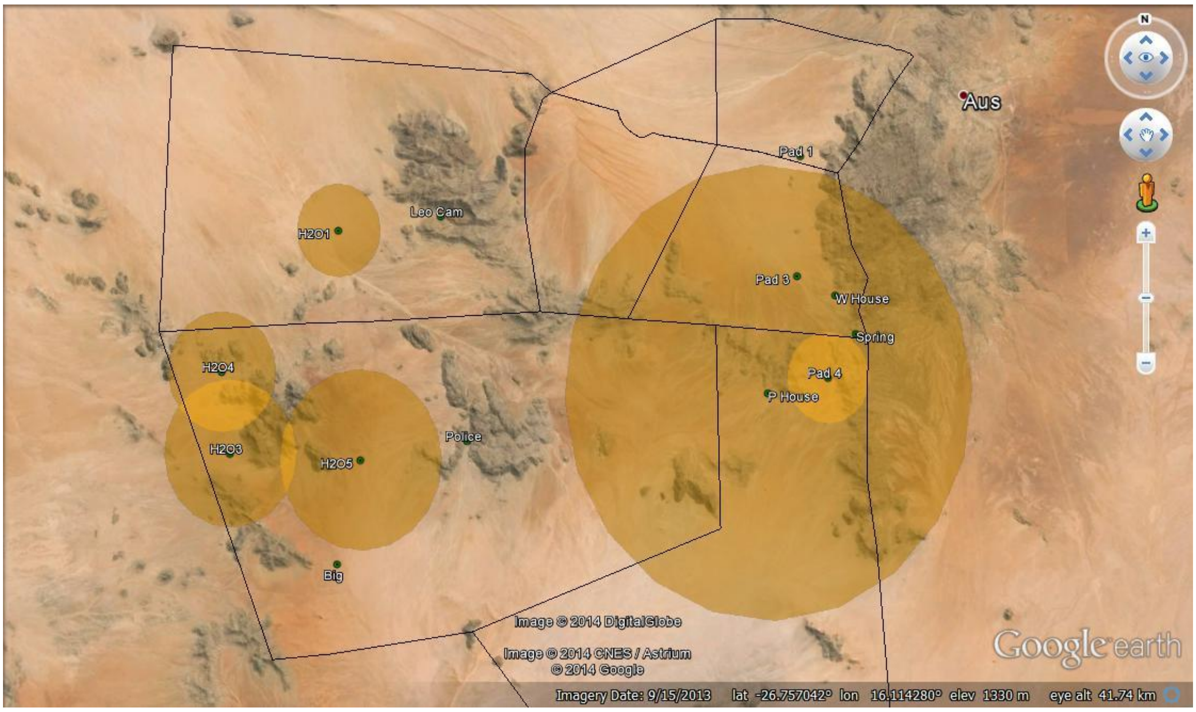


Figure 4.5: Buffer map showing proportion of independent events of bat-eared fox at water points on Tsirub and KAV

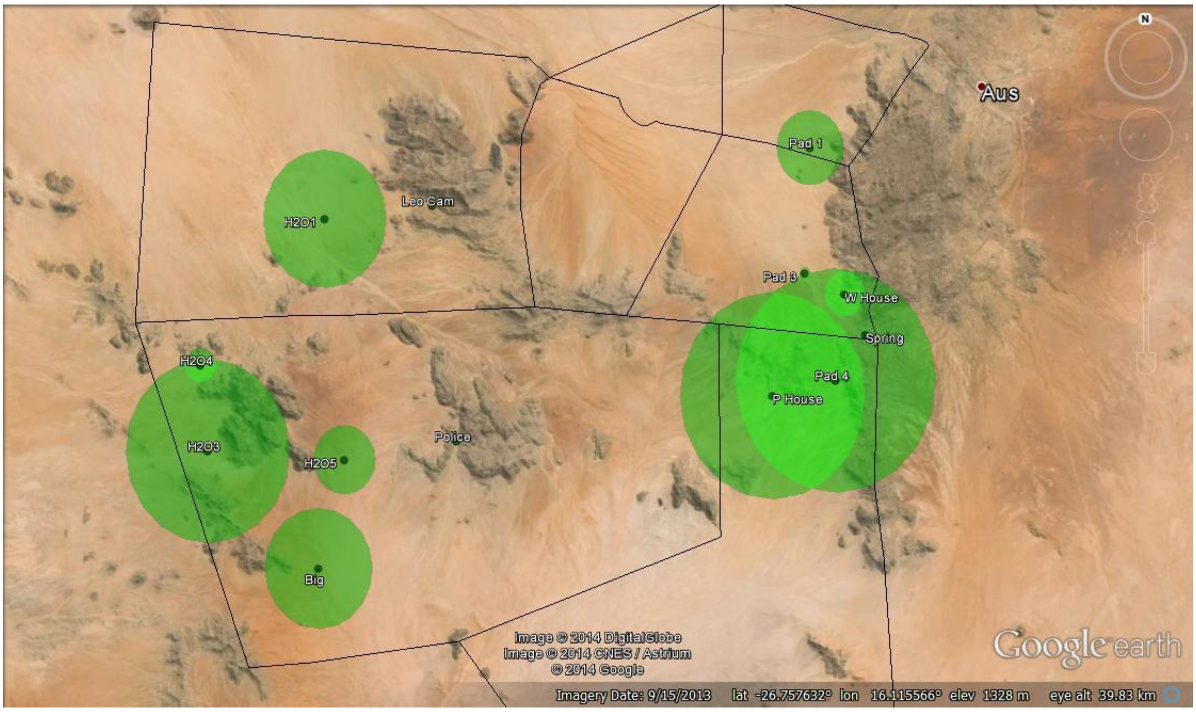


Figure 4.6: Buffer map showing proportion of independent events of black-backed jackal at water points on Tsirub and KAV

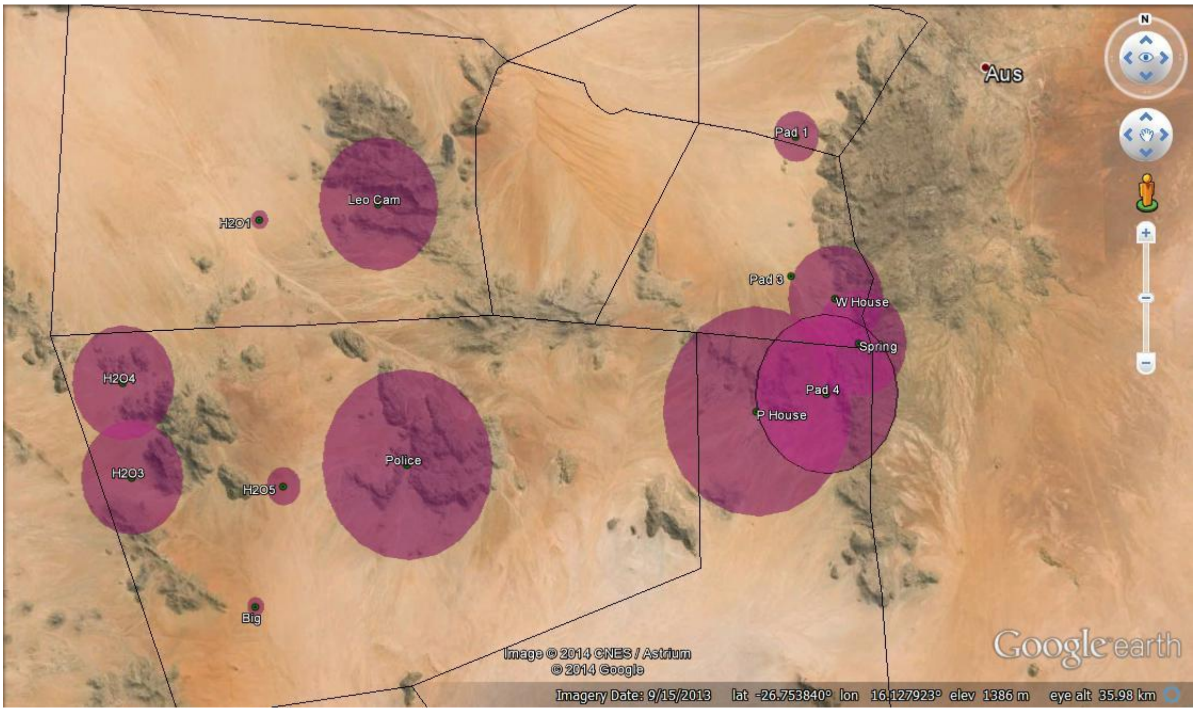


Figure 4.7: Buffer map showing proportion of independent events of honey badger at water points on Tsirub and KAV

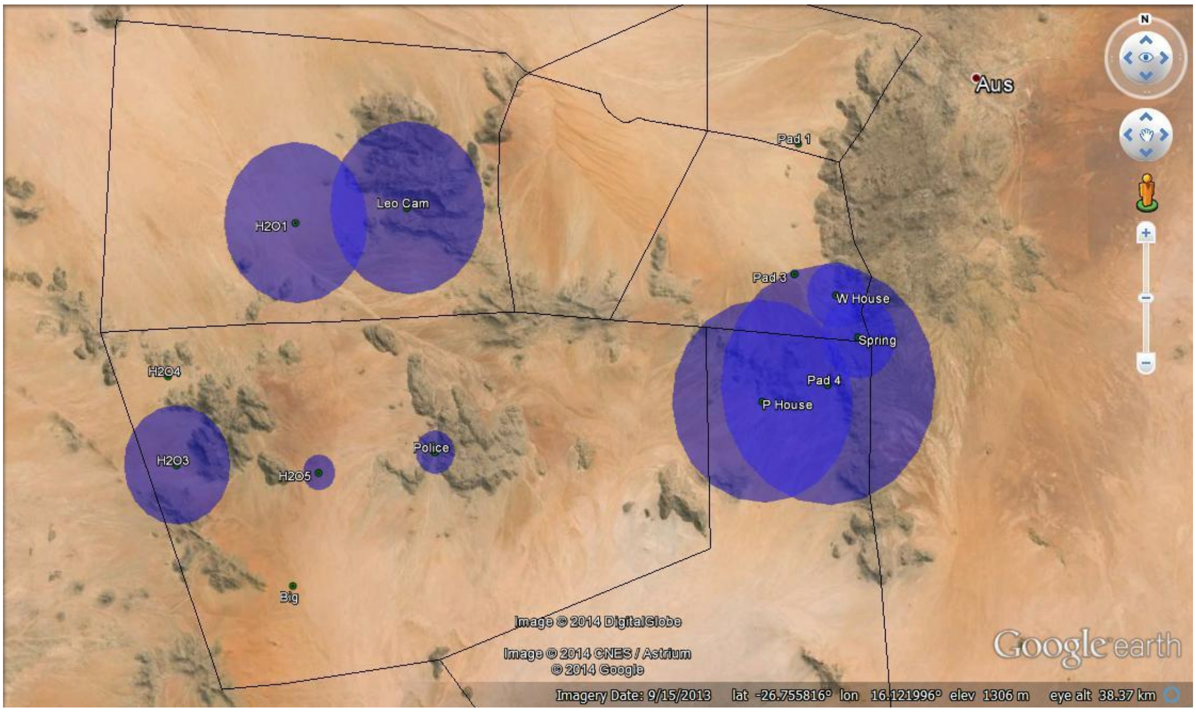


Figure 4.8: Buffer map showing proportion of independent events of brown hyena at water points on Tsirub and KAV

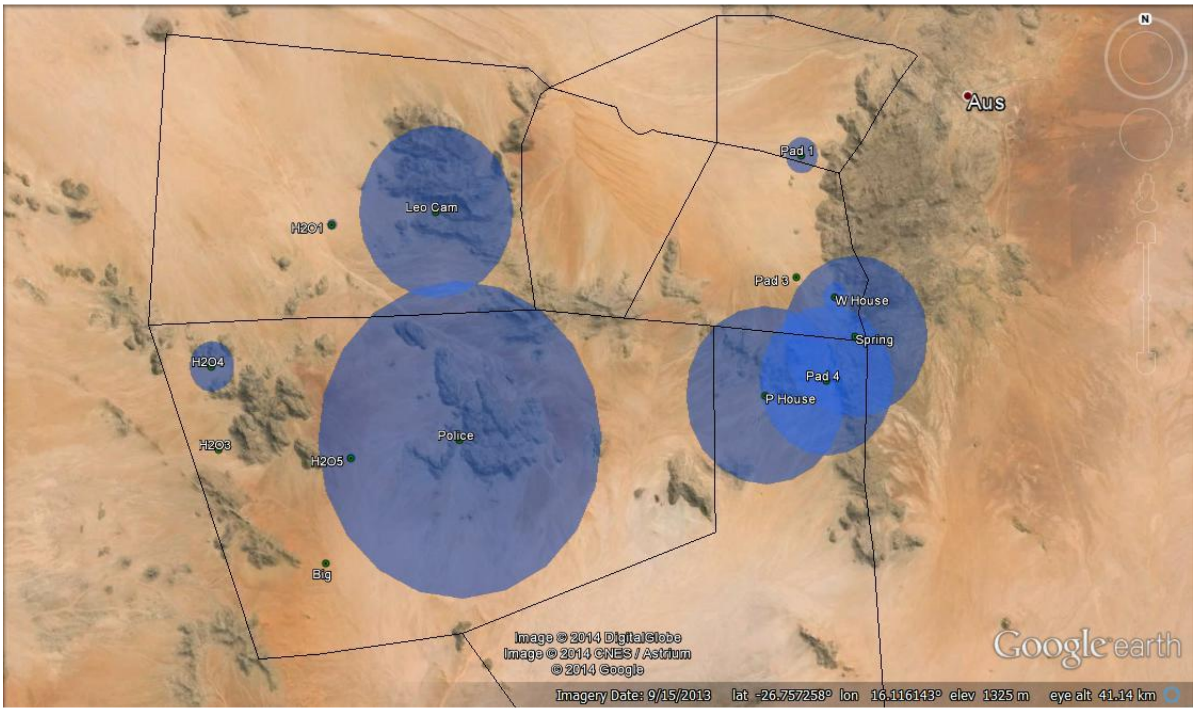


Figure 4.9: Buffer map showing proportion of independent events of leopard at water points on Tsirub and KAV

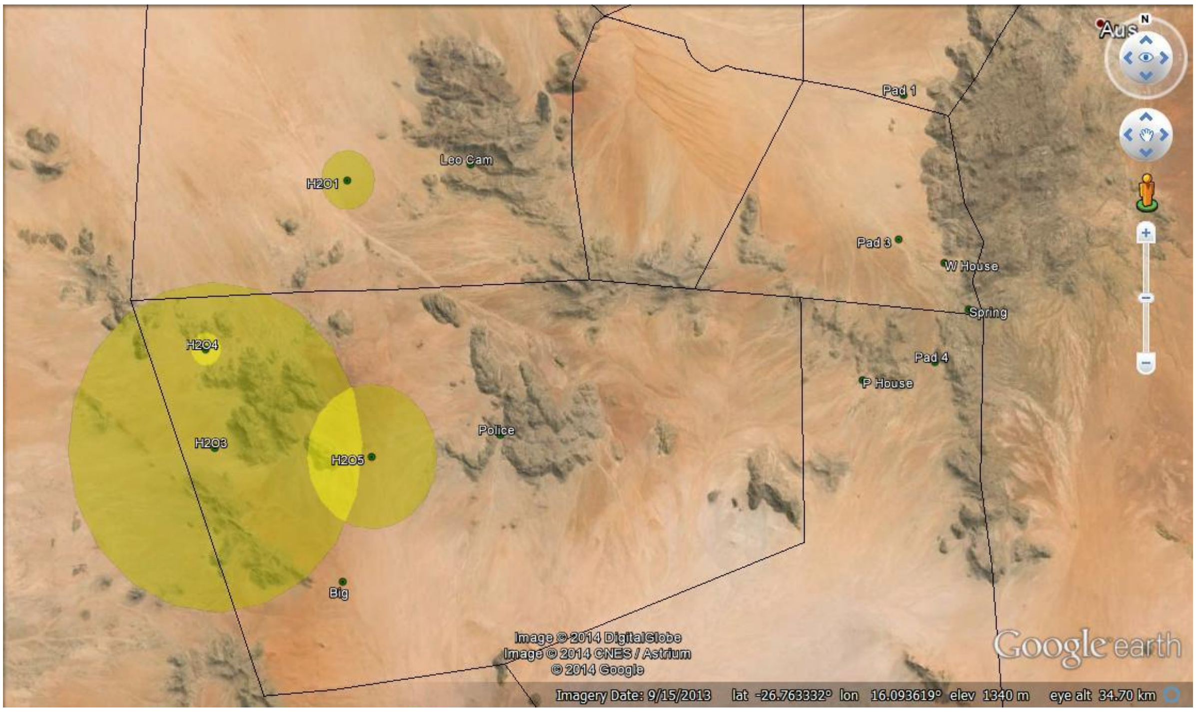


Figure 4.10: Buffer map showing proportion of independent events of cheetah at water points on Tsirub

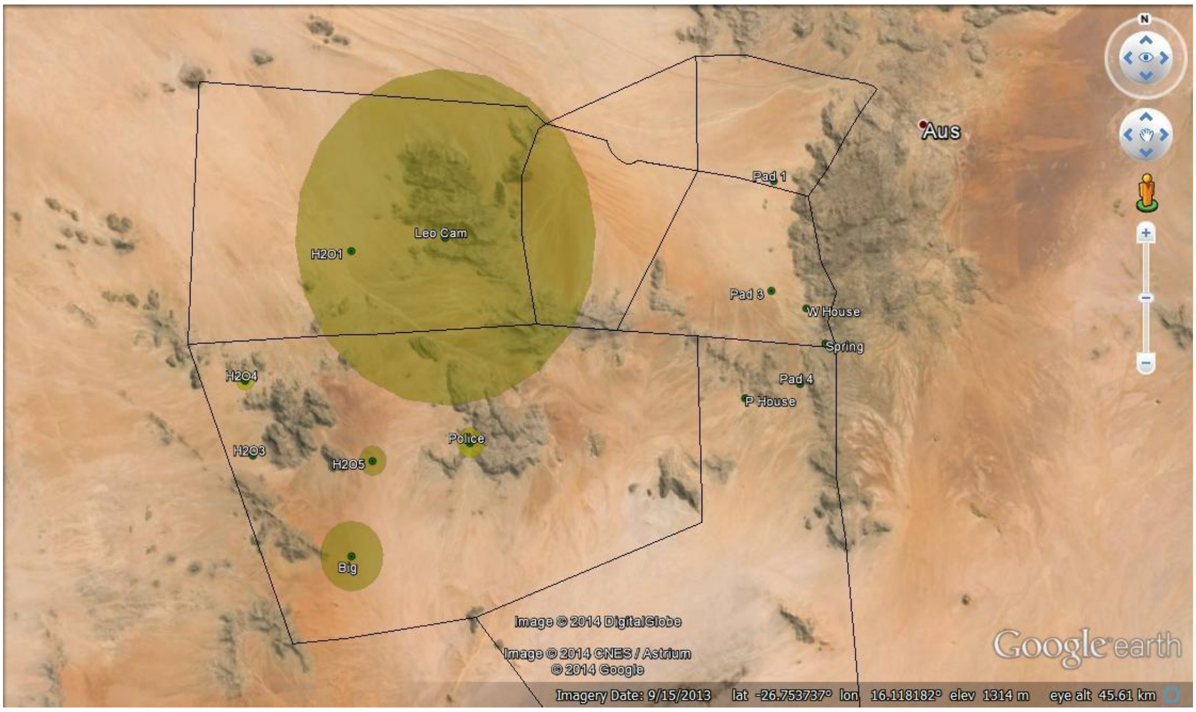


Figure 4.11: Buffer map showing proportion of independent events of African wild cat on Tsirub

Table 4.4: Total number of independent events of each carnivore species detected at each water point on Tsirub and KAV

Location	Cape fox	Bat-eared fox	Black-backed jackal	Honey badger	Brown hyena	Leopard	Cheetah	African wild cat
Tsirub								
H2O1	8	56	803	1	67	1	2	1
H2O3	1	88	1,029	6	50	0	11	0
H2O4	3	71	219	6	25	4	1	2
H2O5	6	109	390	2	14	1	5	3
Big	1	3	669	2	1	0	2	7
Police station	0	1	85	10	18	25	0	3
Leo cam	0	1	73	6	71	14	1	33
Total	**19**	**329**	**3,268**	**33**	**246**	**45**	**22**	**49**
KAV								
Pad 1	0	0	148	1	0	6		
Pad 3	0	0	26	0	5	0		
Pad 4	0	3	439	3	50	25		
Pad House	121	15	416	4	42	5		
W House	0	0	88	2	13	30		

Spring	0	0	9	2	17	27
Total	**121**	**18**	**1,126**	**12**	**127**	**93**

Pianka’s index of niche overlap showed varying degrees of spatial overlap between carnivores on Tsirub and KAV. Pianka’s index ranged from 0.07 for leopard and cheetah to 0.86 for Cape fox and honey badger, black-backed jackal and cheetah and honey badger and leopard on Tsirub (Table 4.5). In comparison, on KAV all indices were above 0.61, Cape fox and brown hyena showed a Pianka’s index of 0.61, with Cape fox and bat-eared fox showing the highest degree of overlap with a Pianka’s index of 0.98 (Table 4.5).

Spearman’s rank correlation tests showed significant, positive associations between Cape fox and bat-eared fox, black-backed jackal and bat-eared fox, bat-eared fox and cheetah, and black-backed jackal and cheetah (Table 4.5). Spearman’s rank correlation analysis showed a significant, negative association between difference in body mass and Pianka’s index of spatial overlap for all data combined ($r_s = -0.43$, $P = 0.004$) (Figure 4.12).

Table 4.5: Results of Pianka’s index of spatial overlap and Spearman rank correlation between carnivores for Tsirub and KAV combined, significant Spearman's rank correlation results are shown in bold

Species	**Pianka's index**		**Spearman's rank correlation**
	Tsirub	**KAV**	r_s
Cape fox & bat-eared fox	0.8	0.98	**0.78**
Cape fox & black-backed jackal	0.65	0.66	0.44
Cape fox & honey badger	0.86	0.66	0.16
Cape fox & brown hyena	0.63	0.61	0.28
Cape fox & leopard	0.17	0.62	-0.38
Cape fox & cheetah	0.47		0.42
Cape fox & African wild cat	0.09		-0.18
Bat-eared fox & black-backed jackal	0.76	0.78	**0.61**
Bat-eared fox & honey badger	0.5	0.9	0.38

Bat-eared fox & brown hyena	0.6	0.74	0.47
Bat-eared fox & leopard	0.1	0.71	-0.53
Bat-eared fox & cheetah	0.82		**0.63**
Bat-eared fox & African wild cat	0.1		-0.4
Black-backed jackal & honey badger	0.49	0.9	-0.2
Black-backed jackal & brown hyena	0.69	0.94	0.24
Black-backed jackal & leopard	0.11	0.83	**-0.79**
Black-backed jackal & cheetah	0.86		**0.61**
Black-backed jackal & African wild cat	0.19		-0.53
Honey badger & brown hyena	0.71	0.94	0.15
Honey badger & leopard	0.86	0.94	0.25
Honey badger & cheetah	0.49		0.05
Honey badger & African wild cat	0.56		-0.07
Brown hyena & leopard	0.49	0.92	0.03
Brown hyena & cheetah	0.59		**-0.79**
Brown hyena & African wild cat	0.65		-0.11
Leopard & cheetah	0.07		**-0.79**
Leopard & African wild cat	0.55		0.12
Cheetah & African wild cat	0.15		-0.34

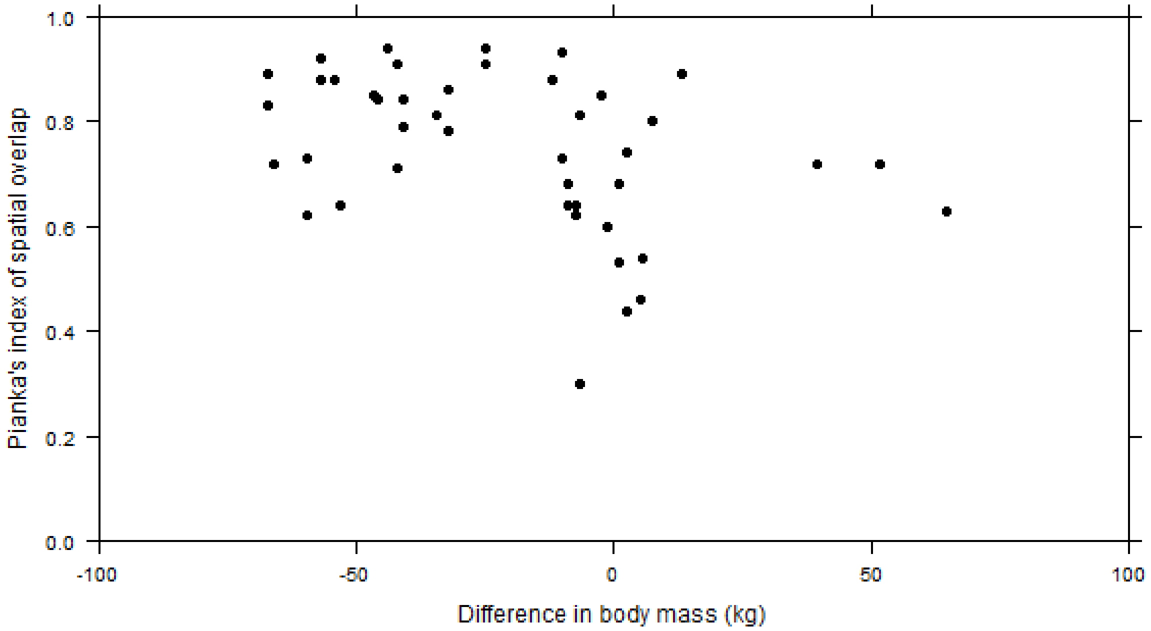


Figure 4.12: Negative association between difference in body mass and Pianka's index for spatial overlap for carnivores on Tsirub and KAV (*n* = 43, Spearman's rank correlation; r_s = -0.43, *P* = 0.004).

4.4.3 Temporal resource partitioning between carnivores, domestic livestock and game

A total of 28,360 independent events of focal carnivores, domestic livestock and game were recorded across the three sites, consisting of 4,898 carnivore events, 20,094 domestic livestock events and 3,368 game events (Table 4.6). Across all sites, black-backed jackal was the most frequently recorded carnivore and had differing peak time intervals across the three sites; 18:00 - 20:00 h at Tsirub, 22:00 h - 00:00 h at KAV and 06:00 h - 08:00 h at NBR (Figs. 4.4, 4.5 & 4.6). Brown hyena showed similar peaks in time interval at Tsirub and KAV; 02:00 h - 04:00 h and 04:00 h - 06:00 h respectively. Spotted hyena on NBR showed a peak during the 00:00 h - 02:00 h time period. Leopard showed similar peaks in time period at both Tsirub (22:00 h - 00:00 h) and KAV (20:00 h -22:00 h), whilst showed a later peak of between 02:00 h and 04:00 h at NBR.

Table 4.6: Summary of temporal activity of focal carnivores, domestic livestock and game at water points across the three study sites, showing the number of independent observations for each species and their peak activity time at water points, given as the period where the highest proportion of independent events occured.

	Tsirub		KAV		NBR	
Species	**# of independent observations**	**Peak time period**	**# of independent observations**	**Peak time period**	**# of independent events**	**Peak time period**
Black-backed jackal	2702	18:00-20:00	980	22:00-00:00	567	14:00-16:00
Spotted hyena					158	00:00-02:00
Brown hyena	222	02:00-04:00	121	04:00-06:00		
Leopard	40	22:00-00:00	92	20:00-22:00	16	02:00-04:00
Horse			1546	10:00-12:00	286	14:00-16:00
Springbok	4853	12:00-14:00	2526	08:00-10:00	853	10:00-12:00
Oryx	5729	12:00-14:00 & 18:00-20:00	3928	00:00-02:00	2205	12:00-14:00
Cattle			297	14:00-16:00	1239	14:00-16:00
Total	**13,546**		**9,490**		**4,471**	

Domestic livestock were only present at KAV and NBR. Horse was the most frequently recorded domestic livestock species at KAV and had a peak during the 10:00 h - 12:00 h time period, whilst on NBR horse showed a peak in the 14:00 h - 16:00 h time period (Figs. 4.14 & 4.15). Cattle were the most frequently recorded domestic livestock species on NBR (as horses were only introduced onto the farm in November 2013) and at both KAV and NBR showed a peak in activity at water points between 14:00 h and 16:00 h (Table 4.6).

Across all three sites oryx was the most frequently recorded game species, having a bimodal distribution at Tsirub showing peaks in both the 12:00 h - 14:00 h and 18:00 h - 20:00 h time periods (Fig 4.13). Oryx at NBR also showed a peak at 12:00 h - 14:00 h, whilst oryx at KAV showed a peak at 00:00 h - 12:00 h (Figs. 4.14 & 4.15). Springbok showed daytime peaks across all three sites with 12:00 h - 14:00 h, 08:00 h - 10:00 h and 10:00 h - 12:00 h for Tsirub, KAV and NBR respectively (Table 4.6).

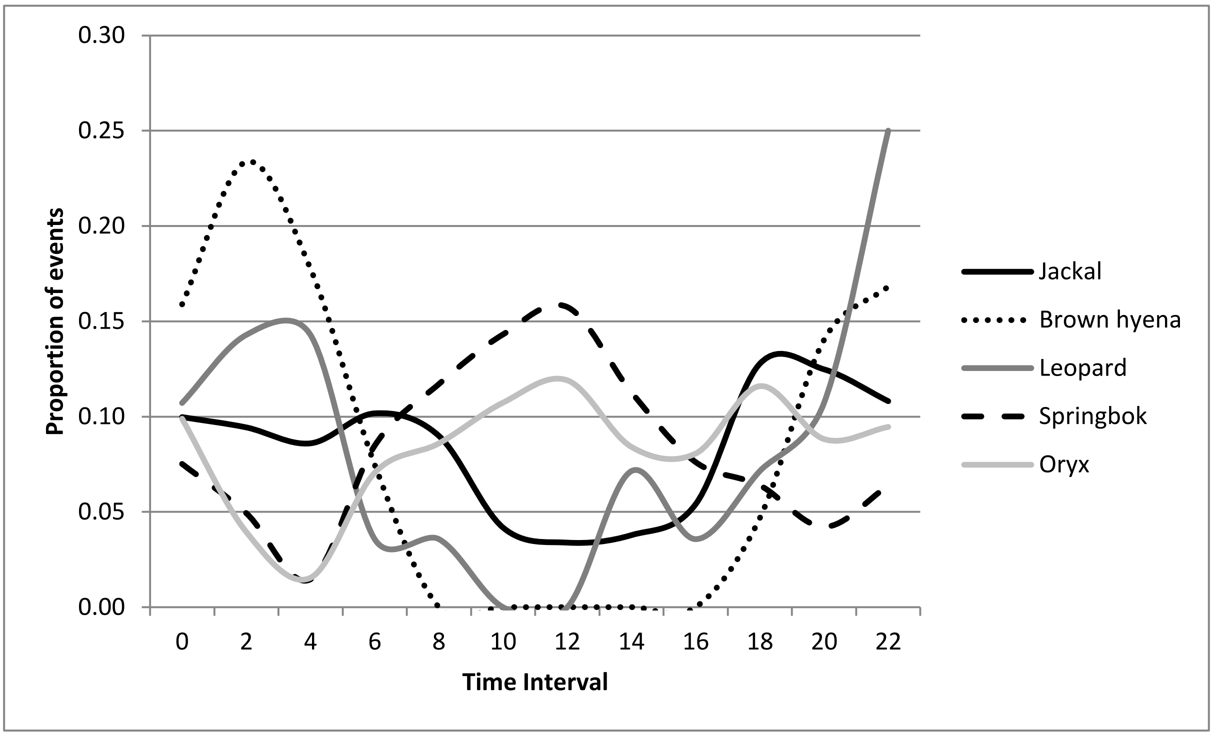


Figure 4.13: Temporal activity patterns of focal carnivores and game on Tsirub, showing the proportion of total activity in each time interval. Time interval represents time of day, with 12 showing midday, i.e 12:00 h

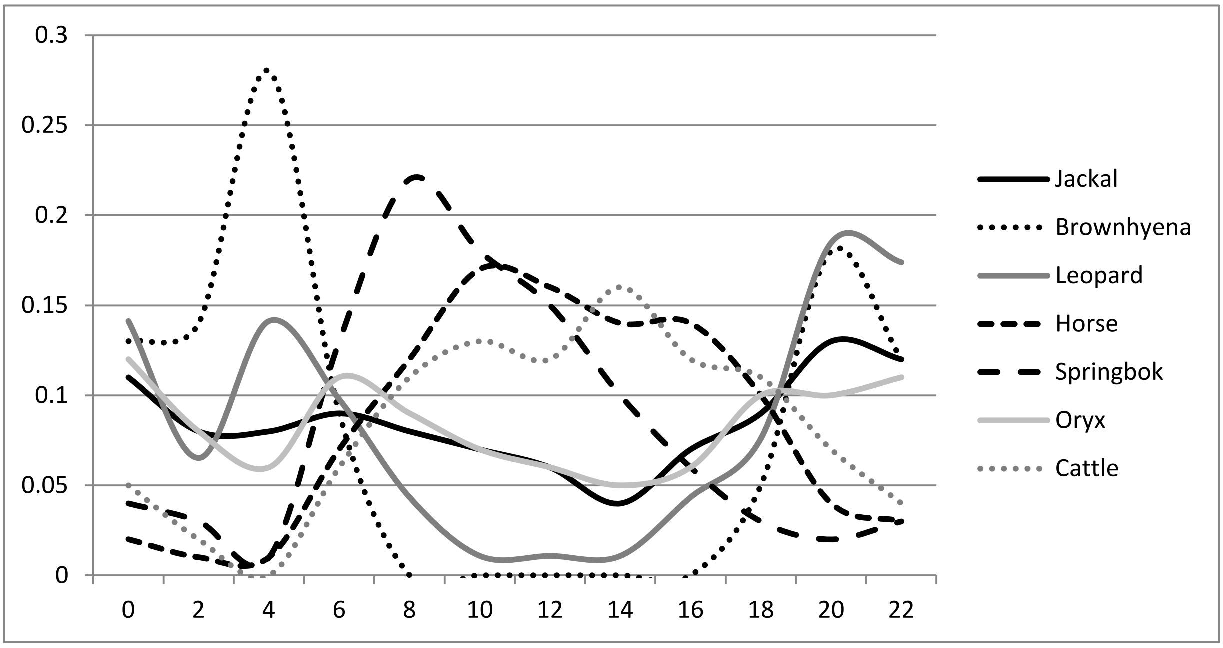


Figure 4.14: Temporal activity patterns of focal carnivores, domestic livestock and game on KAV showing the proportion of total activity in each time interval. Time interval represents time of day, with 12 showing midday, i.e 12:00 h

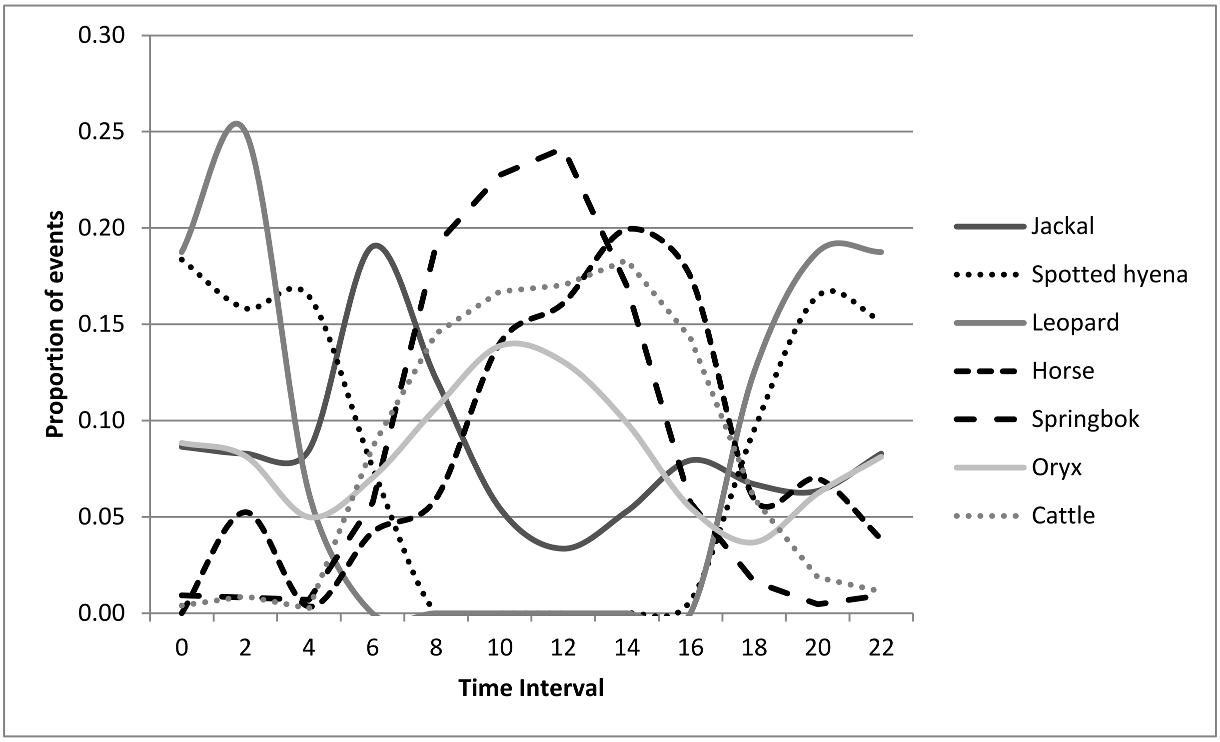


Figure 4.15: Temporal activity patterns of focal carnivores, domestic livestock and game on NBR showing the proportion of total activity in each time interval. Time interval represents time of day, with 12 showing midday, i.e 12:00 h

Pianka's index showed cattle to have the highest degree of overlap with black-backed jackal across both sites when comparing all carnivore species; 0.71 at KAV and 0.64 at NBR (Table 4.7). Horses also shared the highest degree of temporal overlap with black-backed jackals out of all four carnivore species; 0.68 at KAV and 0.59 at NBR. At KAV cattle shared the lowest degree of temporal overlap with brown hyena (0.28), whilst on NBR cattle had the lowest overlap with leopard at just 0.09 (Table 4.7).

Oryx and black-backed jackal had the highest temporal overlap at water points out of any carnivore/herbivore combination as determined by Pianka's index; 0.89 at Tsirub, 0.99 at Klein Aus Vista and 0.82 at NBR. Oryx and leopard had a Pianka's index of 0.75 at Tsirub, 0.88 at KAV and 0.54 at NBR, whilst oryx and brown hyena had a Pianka's index of 0.60 at Tsirub and 0.72 at KAV. In comparison oryx and spotted hyena had a Pianka's index of 0.58 at NBR (Table 4.7).

Springbok and black-backed jackal had differing degrees of temporal overlap at water points across Tsirub, KAV and NBR, with Pianka's indices of 0.75, 0.66 and 0.56 respectively. Springbok and brown hyena had Pianka's indices of 0.43 and 0.22 at Tsirub and KAV respectively, whilst springbok and spotted hyena at NBR had a Pianka's index of just 0.07. Springbok had the lowest degree of temporal overlap with leopard at NBR (0.05) followed by KAV at 0.37 and lastly at Tsirub with 0.56 (Table 4.7).

Table 4.7: Pianka's index of temporal overlap and difference in body mass of focal carnivores, domestic livestock and game across the three study sites

Species	Pianka's index	Difference in body mass/kg
Tsirub		
Black-backed jackal and springbok	0.75	29
Black-backed jackal and oryx	0.89	156
Brown hyena and springbok	0.43	-3
Brown hyena and oryx	0.60	124
Leopard and springbok	0.56	-8
Leopard and oryx	0.75	119
KAV		
Black-backed jackal and horse	0.68	487
Black-backed jackal and springbok	0.66	29
Black-backed jackal and oryx	0.99	156
Black-backed jackal and cattle	0.71	627
Brown hyena and horse	0.21	455

Brown hyena and springbok	0.22	-3
Brown hyena and oryx	0.72	124
Brown hyena and cattle	0.28	595
Leopard and horse	0.38	450
Leopard and springbok	0.37	-8
Leopard and oryx	0.88	119
Leopard and cattle	0.48	590
NBR		
Black-backed jackal and horse	0.59	487
Black-backed jackal and springbok	0.53	29
Black-backed jackal and oryx	0.82	156
Black-backed jackal and cattle	0.64	627
Spotted hyena and horse	0.25	432.5
Spotted hyena and springbok	0.07	-25.5
Spotted hyena and oryx	0.58	101.5
Spotted hyena and cow	0.13	572.5
Leopard and horse	0.30	450
Leopard and springbok	0.05	-8
Leopard and oryx	0.54	119
Leopard and cattle	0.09	590

Correlation analysis between difference in body mass and Pianka's index for carnivores, game and domestic livestock showed no significant association ($r_s = -0.17$, $P = 0.36$), however a significant, positive association was seen between difference in body mass and Pianka's index for carnivores and game ($r_s = 0.83$, $p = 0.00$) and for springbok ($r_s = 0.63$, $P = 0.05$) and oryx ($r_s = 0.72$, $P = 0.02$) separately. No significant association was seen for carnivores and domestic livestock ($r_s = 0.32$, $P = 0.37$) together but a significant, positive association was seen for cattle ($r_s = 0.74$, $P = 0.05$), but not for horse ($r_s = 0.35$, $P = 0.55$) (Figure 4.16).

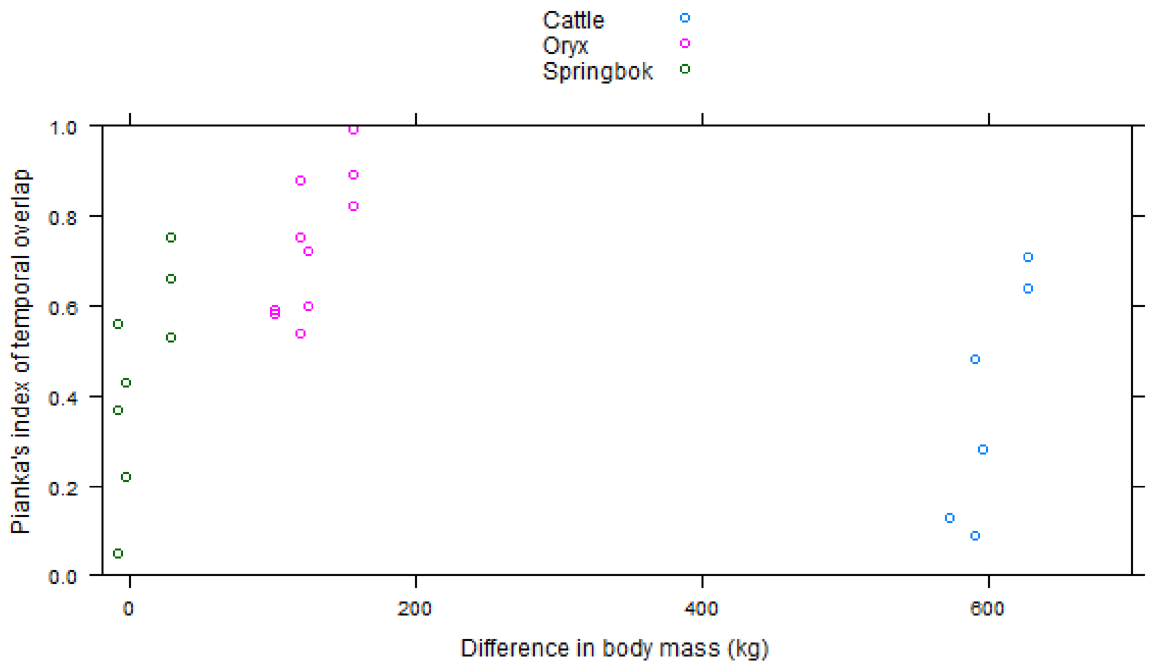


Figure 4.16: Association between difference in body mass and Pianka's index for temporal overlap for carnivores and springbok, oryx and cattle

4.4.4. Spatial resource partitioning between carnivores and game

Game species had a more uniform distribution across water points than carnivores as shown by Figures 4.17 and 4.18. On both farms oryx were recorded at every water point with the number of independent events ranging from 163 to 313 on Tsirub and from 85 to 239 on KAV (Table 4.8). Springbok were also recorded at every water point on Tsirub, with the number of independent events ranging from 88 to 289, whilst on KAV springbok were recorded at all but one water point (Spring) with the number of independent events ranging from 87 to 295 (Table 4.8).

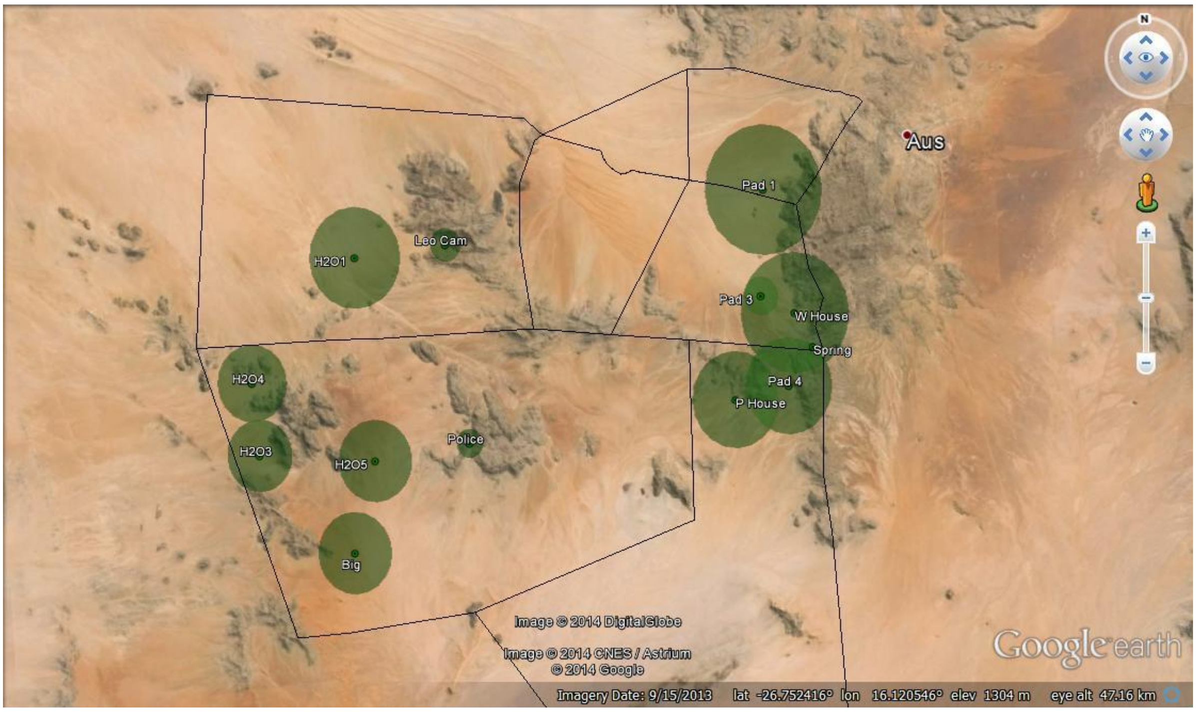


Figure 4.17: Buffer map showing proportion of independent events of springbok at water points on Tsirub and KAV

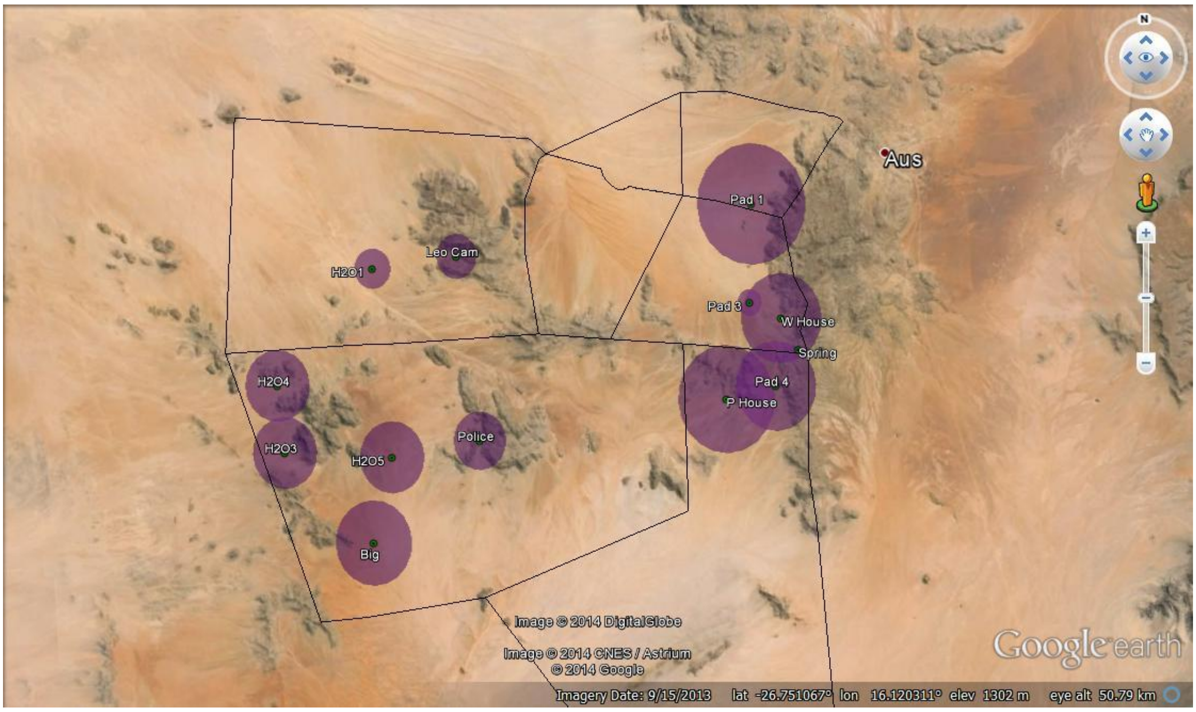


Figure 4.18: Buffer map showing proportion of independent events of oryx at water points on Tsirub and KAV

Table 4.8: Number of independent events (24 hours) recorded at each water point camera trap for focal carnivores and wild game on the northern study sites; Tsirub and KAV

Location	Black-backed jackal	Brown hyena	Leopard	Springbok	Oryx
Tsirub					
H2O1	240	57	1	289	163
H2O3	258	45	0	216	266
H2O4	131	24	4	226	270
H2O5	188	14	1	248	259
Big	241	1	0	236	313
Police station	68	18	24	88	223
Leo cam	63	48	13	90	171
Total	**1,189**	**207**	**43**	**1,393**	**1,665**
KAV					
Pad 1	310	0	6	271	239
Pad 3	63	4	0	87	63
Pad 4	232	46	23	197	232
P House	275	36	5	195	75
W House	233	12	27	295	233
Spring	25	16	27	0	25
Total	**1,138**	**114**	**88**	**1,045**	**867**

Pianka's index showed the highest levels of overlap occuring between black-backed jackal and springbok on Tsirub and between black-backed jackal and oryx on KAV. Spatial overlap was lowest on both study sites for leopard and springbok, however no significant associations were seen. Spearman's rank correlation analysis showed no significant association between Pianka's index for spatial overlap and difference in body mass for carnivores and game ($r_s = 0.52$, $P = 0.08$), yet showed significant, positive associations between difference in body mass and Pianka's index for spatial overlap for springbok ($r_s = 0.96$, $P = 0.003$) and oryx ($r_s = 0.91$, $P = 0.01$) when tested separately.

Table 4.9: Pianka's index of spatial overlap, differences in body mass and Spearman's rank correlation results for spatial resource partitioning between focal carnivores and game for Tsirub and KAV. Significant Spearman's rank correlation result shown in bold

Species	Pianka's index		Difference in body mass/kg	Spearman's rank correlation
	Tsirub	KAV		r_s
Black-backed jackal & springbok	0.89	0.79	29	-0.36
Black-backed jackal & oryx	0.81	0.85	156	0.45
Brown hyena & springbok	0.75	0.67	-3	-0.08
Brown hyena & oryx	0.69	0.73	124	-0.08
Leopard & springbok	0.31	0.61	-8	-0.3
Leopard & oryx	0.51	0.69	119	0.22

4.5 Discussion

4.5.1. Resource partitioning between carnivores

Carnivores showed either temporal or spatial resource partitioning at water points, with a significant, negative association between spatial overlap and difference in body mass between species pairs. Only black-backed jackal and leopard showed both temporal and spatial resource partitioning. Only species pairings involving cheetah and African wild cat showed no resource partitioning. Partitioning between carnivores has been documented for a number of species, either through the temporal (Di Bitetti et al. 2009; Di Bitetti et al. 2010; Romero-Muñoz et al. 2010; Ramesh et al. 2012), spatial (Ralls and White 1995; Fedriani et al. 2000; Tannerfeldt et al. 2002; Thompson and Gese 2007; Schwartz et al. 2010; Mills and Gorman 1997; Vanak et al. 2013) axes, or occasionally through both (Atwood et al. 2011; Kamler et al. 2012; Steinmetz et al. 2013). Most previous studies have focused on two or three species or multiple species of the same family, this study is the first to focus on partitioning within a sympatric guild of nine carnivore species representing the Canidae, Felidae, Hyaenidae and Mustelidae families.

Temporal resource partitioning, either in the form of differences in activity patterns, or avoidance of water points on a daily basis was more common than spatial resource partitioning, as initially hypothesised. For example, of the 28 species pairings observed on Tsirub and KAV 19 showed temporal partitioning, compared to seven pairs showing spatial partitioning. This result agrees with Hayward and Slotow's (2009) prediction of temporal resource partitioning being the main mechanism for the coexistence of large African carnivores, and contradicts Schoener (1974) who stated temporal partitioning to be less common than spatial. However, partitioning at spatially fixed resources may represent a special case; Atwood et al. (2011) also recorded temporal partitioning between a subordinate species, gray fox *Urocyon cinereoargentus*, two dominant carnivore species coyotes *Canis lutrans* and bobcats *Felis rufus* at artificial water points in an arid environment. As coyotes were seen at all of the water points and bobcats seen at 26 out of 31 water points, Atwood et al. (2011) argued there was little opportunity for obligate spatial partitioning by gray fox, thus explaining the temporal segregation. As carnivore species occurred at 46 % - 100 % of all water points monitored, limited opportunity for spatial resource partitioning also existed in this study, meaning carnivores must use another mechanism to avoid direct carnivore encounters at waters.

Spatial rarity of water points means carnivores may have few alternatives but to use those also used by dominant species. Water points on farms are rare, with Tsirub having 7.25 water points/ 100km^2 and KAV having 3.92/100 km^2. Such a low density could mean smaller species with small home range sizes could have just one water point within their home range, further limiting opportunities for spatial partitioning. Romero-Muñoz et al. (2010) found wide spatial overlap between puma *Puma concolor* and jaguar *Panthera onca* on roads and trails, suggesting the scarcity of such travels routes within the area may not allow spatial segregation between the two species. Therefore despite the rarity and necessity of using water sources, a relatively large number of carnivore species are able to coexist through the use of temporal partitioning.

Associations between certain species pairings showed positive associations between relative abundance indices across locations (Fig. 4.12). However, such associations may be due to extreme values in the data sets, for example when one species was not present at a particular water point, giving a relative abundance of 0. Similarly, the negative associations seen between leopard and black-backed jackal, cheetah and brown hyena, and between leopard and cheetah, may have been simply driven by extreme values. Reasons for a certain species not being present at a water point could include habitat preference, not having that water point included within a home range, or avoidance of a dominant competitor. Therefore, for associations in spatial partitioning where extreme are present, the reasoning for an association cannot be determined, and spatial partitioning cannot be assumed.

Temporal partitioning occurred on a finer scale than simple nocturnal, crepuscular and diurnal partitioning recorded in other studies (Crooks and Vuren 1995; Hon and Shibata 2003). All carnivores showed night time mean vector lengths with the majority of activity at water points occurring at night for all species, with the exception of black-backed jackal and honey badger which showed activity throughout both day and night. Harrington et al. (2009) recorded American mink *Neovision vision* to switch from primarily nocturnal to primarily diurnal behaviour with increasing abundance of two competitors, the otter *Lutra lutra* and polecat *Mustela putorius*. Whilst it may aid temporal partitioning for some species to show diurnal activity at water points, Daan (1981) argued diurnal and nocturnal activity require very different evolutionary adaptations and that many recorded shifts in activity patterns are usually seen within the normal diel cycle of the species. Furthermore, increased daytime activity may result in increased contact and conflict with humans; carnivores have been shown to shift activity patterns in order to avoid human activity, for example brown bears *Ursus arctos* were seen to decrease daytime activity in areas with higher road density (Ordiz et al. 2014), and leopards showed significantly less daytime activity in logged areas as compared to unlogged areas in Gabon (Henschel and Ray 2003). Whilst it is possible prior experience with humans may alter activity patterns of carnivores, on the study sites persecution often involves shooting on site, and therefore it is unlikely any carnivores having experienced persecution would still be alive.

Temporal partitioning in the form of significant differences in activity patterns at water points was seen more often than complete avoidance of a water point on the same day another carnivore species was present. Seventeen species pairings showed significant differences in activity at water, whilst four species pairings showed avoidance of joint occurrence on a daily basis. Data pertaining to the water requirements of carnivores is scarce, with Bothma (2005) recording Kalahari leopards drinking, or having access to water in the form of kills, at intervals of 2.5, 2.2 and 1.6 days for males, females without cubs and females with cubs respectively. Metabolic water requirements may halt avoidance of water points on the same day as competitors, alternatively fine scale shifts in temporal activity at water points may be sufficient to minimise risk of intraguild predation.

No partitioning at either scale was seen for cheetah between Cape fox and between African wild cat and bat-eared fox, leopard and cheetah. Abundance of competitors has been cited as the most important factor influencing competition between interacting species (Creel 2001). Romero-Muñoz et al. (2010) recorded no temporal partitioning between jaguar and puma at a site with low jaguar density, suggesting the low density of the dominant competitor decreased probability of encounter, making separation unnecessary. Cheetah only occurred on Tsirub where individual spot pattern showed repeated visits from one, or possibly two individuals, whilst African wild cat had a mean photographic rate of just 3.05 events per 100 trap nights. Low densities of cheetah and African wild cat may simply mean chances of direct encounters with other species are simply too low to make partitioning necessary. The possibility of these species not posing a threat to each other is not supported; Begg et al. (2003) recorded African wild cat in the diet of honey badger, although the possibility of scavenging cannot be ruled out, and leopard was recorded killing African wild cat (Mills 1990).

Temporal activity patterns seen from carnivores were mainly as expected, with the expecion of cheetah, which showed nocturnal activity. Cheetahs are usually documented as showing mainly diurnal activity, believed to be a response to avoid encounters with larger nocturnal predators such as spotted hyena (Cozzi et al. 2012). The nocturnal activity recorded in this study, from both Tsirub and NBR may represent cheetah showing nocturnal activity as a response to persecution from humans. Such a response has been recorded in serval *Leptailurus serval*, on farmlands, where individuals showed significantly higher degrees of nocturnal activity, than those individuals residing in a protected area with no human activity (Ramesh and Downs 2013). Cozzi et al. (2012) noted nocturnal activity of cheetah in the presence of both spotted hyena and lion in Botswana, noting such activity coincided with full moon. The authors suggest cheetah are hunting at night during those nights when moon illumination is brightest, and that such individuals are 'starvation driven' to hunt at such times (Cozzi et al. 2012). Given the low productivity of the study sites, it is possible cheetah are also active at night to try and hunt in the moonlight, however, the low population density of spotted hyena, their dominent competitor, may also mean chances of direct encounter are low enough to allow such behaviour.

It is possible other factors, besides avoidance of dominant competitors, or predators, may affect timing of the species visits at water holes. It is not known the distance at which carnivores are able to detect each other, however given their keen since of smell, especially the hyena species which reply on smell for detecting carcasses (Estes 1992; Mills 1990), it is possible they rely on scent to detect and avoid each other. A carnivore at a water point may leave its scent in the area long after it has left the locale, especially if hyena species are performing paste marking behaviour whilst in the area. An experimental approach to try and answer such a question may be useful, for example, leaving a paste mark, or other carnivore scent such as urine at a water point and timing how long it takes a different carnivore species to approach. Alternatively examining if the addition such a carnivore scent, causes a change in the usual timings of visits to water points by other species, could be useful. However, the human scent of the person adding the scent to the water point may also have an effect.

The length of time species can go without water may also play a role in species timings at the water points. For example, a species able to go longer without water may show more temporal partitioning within the guild, than species needing to drink regularly, which may be obliged to visit the water point within a certain time period. As mentioned, little information is available regarding the water requirements of African carnivores, however, it is believed aardwolves are able to obtain their water requirements from their termite prey (Sliwa 1996). Aardwolves were seen infrequently at water points, with sample sizes for this species being too low for statistical analysis. Therefore, it is possible this species has no need to visit water points, and thus minimises the risk of direct encounters with larger competitors. An important factor which may influence species timings to water points is day time temperatures, for example, brown hyena, given their thick coat, showed strictly nocturnal behaviours at water point, however this species is commonly observed active throughout the day on the Namibian coasts, where day time temperatures are cooler (Wiesel 2010). Therefore, high day time temperatures may be one reason carnivores show nocturnal behaviour at water points and must therefore risk direct encounters with other, larger carnivore species.

Another factor which may influence the timings of species visiting a water point, is the social behaviour of the species, in particular differences between solitary and social species. Social species may be more likely to risk visiting a water point during a peak time for a dominant competitor, as the risk of being predated upon may be diluted between each individual, to so called 'Dilution effect' (Pulliam 1973). Alternatively, social species may benefit from enhanced predator detection, given that there are more individuals listening, smelling and looking for predators (Hamilton 1971). Within the study area, although black-backed jackal and brown hyena are known to be social species, they were usually recorded at water points alone, which may reflect individuals within a social group foraging alone, which has been documented for brown hyena (Mills 1990). Spotted hyena and bat-eared fox are both known social species, and were recorded regularly at water points in groups, however neither species was recorded as not showing temporal partitioning. Such a result may suggest the small group sizes recorded (maximum of 3 for species), may not be large enough to overcome the risk of predation through dilution or enhanced predator detection. Such an idea may be investigated further in areas where larger social groups are seen within the carnivore guild.

A significant, negative association between spatial, but not temporal, overlap and difference in body mass between carnivore species pairs was recorded. Intraguild predation is largely asymmetrical, with relative body mass being cited as one of the most important factors influencing its frequency and distribution; most intraguild predation is by larger carnivores predating upon smaller intraguild prey (Polis et al. 1989). Palomares and Caro (1999) found on average victims were just 0.47 times the mass of the killer species in African carnivores. In contrast, Di Bitetti et al. (2010) found temporal partitioning between species more similar in body mass for neotropical felids, stating this pattern may explain the lack of morphological community-wide character displacement within the ecosystem. Whilst closely related species are prime candidates for competition (Daan 1981), carnivores with relatively large differences in body size are prime candidates for intraguild predation. As the main risk to carnivores visiting water points is intraguild predation, it is not surprising to see such a negative association between spatial partitioning and difference in body mass. Such a result would suggest carnivores are able to partition themselves in a way that incorporates risk of intraguild predation in relation to body mass.

The result that carnivores are using temporal partitioning to avoid direct and potentially lethal encounters at water points is encouraging from a conservation aspect. Given the aridity of the environment, water points are areas which must be visited by carnivores in order to forfill their water requirements. Given the frequency of such visits, it is possible that dominent members of the guild could predate smaller carnivore species at these areas to the extent that these smaller species become locally extinct. Larger carnivores causing the local extinction of smaller species on farmlands could have big consequences for carnivore conservation, given the importance of farmlands to Namibian carnivores. A total of 13.2 % of Namibia's total land mass has been designated as protected area (Barnard et al. 1998), which has resulted in over 90 % of the country's wildlife living outside of protected areas, mainly on farmlands (Krugmann 2001). Therefore farmlands can be seen as important areas for the continued survival of wildlife, yet due to human-wildlife conflict potentially dangerous areas for carnivores. This study has shown, even farmlands in arid environments, where access to water is limited, can support a relatively high diversity of carnivore species, a guild in which intraguild predation is known to be common (Palomares and Caro 1999), through the use of temporal, and more rarely spatial resource partitioning.

4.5.2 Resource partitioning between carnivores, domestic livestock and game

Temporal resource partitioning at water points was seen between domestic livestock and springbok and focal carnivore species, as evidenced by domestic livestock and springbok having diurnal peak activity times at water points, in contrast to the nocturnal activity peaks shown by carnivores. Temporal partitioning between potential predators and natural prey has been recorded previously; Hayward and Hayward (2012) found herbivores to show mainly diurnal, and predators mainly nocturnal behaviour at waterholes, and Valeix et al. (2009a) found herbivores to avoid water holes at peak times of lion activity. Such a result is not surprising given that water holes can be viewed as high risk areas for herbivores, with a higher probability of encountering prey at water sources (Valeix et al. 2009b). Additionally, on NBR a leopard was twice captured dragging a springbok past a camera trap positioned at a water source (Fig. 4.19) and several farmers noted water points as a location of carnivore predation (pers. comm.). No previous studies have examined partitioning between this range of carnivore species and domestic livestock at water sources.

Figure 4.19: Leopard with springbok kill at NBR water source as an example of carnivores using water points as areas for hunting

Oryx at Tsirub and KAV, but not NBR showed nocturnal peak activity times. Due to their large size, (males 176 kg, female 162 kg) (Estes 1992) oryx are not within the preferred prey range of leopards; 10 - 40 kg with a preferred mass of 25 kg (Hayward et al. 2006), the top resident carnivore species on both Tsirub and KAV. Oryx do however, fall within the preferred prey mass (56 - 182 kg) of spotted hyena (Hayward 2006), and have been recorded as a preferred prey species of spotted hyena in Etosha National Park (Trinkel 2010b). Spotted hyenas were regularly recorded on NBR only, and thus the reasoning for a diurnal peak activity time at water by oryx at NBR only may be explained by the presence of a major predator.

A significant, positive relationship between Pianka's index for temporal overlap and difference in body mass was seen for focal carnivores and cattle, springbok and oryx. Therefore larger, positive differences in body mass (where herbivore has the greater body mass) correspond to the largest levels of temporal overlap, and negative body mass differences (where carnivore has the greater body mass) correspond to the least amount of temporal overlap. Spatial partitioning between predators and prey has been described in previous studies; wolves *Canis lupus* and elk *Cervus elaphus* (Atwood et al. 2009), the long-term risk of predation by lion influencing the distribution of herbivores (Valeix et al. 2009c), and spatial avoidance of risky water holes by lions' preferred prey (Valeix et al. 2009a). However, as discussed for carnivores, as water points are spatially fixed and occur at low density, spatial partitioning may not be possible in this environment.

As body-mass is known to be a key factor in predator-prey associations (Lundvall et al. 1999) and the risk of predation for smaller species is higher than for larger species (Sinclair et al. 2003), such results are expected. Differences in anti-predator behaviour related to prey body mass have been described previously. For example Matsika et al. (2007) found the decision to drink when at a water hole was influenced by perceived risk of predation for smaller herbivore species, whilst decision to drink for larger species was influenced more by interference competition from African elephants *Loxodonta africana* and other large herbivores.

Given the largely diurnal activity patterns shown by herbivores at water points, it is perhaps interesting to ask why carnivores do not change their behaviour, to take advantage of these spatial and temporal peaks of herbivore presence at water points when hunting. As discussed previously in the case of cheetah, activity patterns are not rigid, however, due to differences in levels of light betwen day and night, requiring anatomical, physiological and behavioural adaptations for species, changing from nocturnal to diurnal behaviour is rare (Kron-feld and Dayan 2003). Therefore, the role of vision, may limit an animal's ability to change to diurnal hunting. Furthermore, given the lack of vegetation and openess of the study sites, it is possible the lack of cover for concealing predators from prey, may be an important factor. Species like leopard, which rely on approaching prey undetected to within four meters (Stander 2007), may not be able to acheive such distances in the day, and may therefore forced to hunt at night to increase chances of success.

Anti-predator behaviour shown by domestic livestock could have important implications for carnivore conservation in areas where human-wildlife conflict is a problem (Muhly et al. 2010). Domestic animals may be expected to react differently to predators than wild prey in a number of ways. Muhly et al. (2010) showed cattle have been recorded to show variable anti-predator behaviour towards wolves (Laporte et al. 2010), and Muhly et al. (2010) observed lagged responses to wolves by cattle. As the focal carnivore species here were chosen due to their frequent involvement in human-wildlife conflict with domestic livestock in Namibia, the anti-predator behaviour shown by both cattle and horses is encouraging. Domestic livestock were able to decrease predation risk at water points by avoiding visiting water points at peak times of carnivore activity. Additionally, cattle showed lower levels of temporal overlap with large carnivores which represent a greater predation risk, than with smaller carnivores.

The results of this study show temporal resource partitioning to be the main driver for coexistence of a relatively large number of carnivore species, and as an anti-predator strategy used by both wild game and domestic livestock. Such results would suggest commercial farmlands have the potential to accommodate a good diversity of carnivores species, even with limited water resources available. Additionally, due to both domestic livestock and wild game showing some degree of anti-predator behaviour through avoiding peak activity times of carnivores at water points, such water sources are not necessarily hotspots for predation. Further studies to investigate partitioning of home ranges both within and between species would be of interest as home range size variations have been related to water availability (Bowers et al. 1990; de Beer and van Aarde 1998). As a result density and positioning of artificial water points may influence spatial ecology of species and ultimately the carrying capacity of an area.

5.0 Leopard density estimates from commercial farmlands in southern Namibia; a comparison to farmer estimates

N.B. This chapter has been adapted for publication and has been published as a Notes and Record article in African Journal of Ecology, see Appendix two for a full copy

5.1 Abstract

Leopard *Panthera pardus* is currently listed by the IUCN as Near Threatened, being subject to lethal removal following real or perceived conflict and trophy hunting across southern Africa. Sustainable trophy hunting quotas are essential for ensuring the practice is not detrimental to the long term survival of the species, and are usually based at 2 - 5 % of the adult male population. Such quotas are therefore reliant upon accurate national population estimates. However, in Namibia, most of the leopard density map and subsequent national population estimate is based on farmer questionnaires, rather than ecological data. This study aimed to produce the first leopard density estimates for southern Namibia across five study farms, and to compare farmer estimates of leopards on their property to those recorded by camera traps. The study area straddled medium and high density contours, as based purely on questionnaire data, however, due to the arid nature of the environment, it was hypothesised a low density population existed. Standard camera trapping methodology developed and used by the Namibian National Leopard Survey were used. Individual detection histories were constructed and used with the programme CAPTURE to produce abundance estimates, using capture-recapture methods. The half mean maximum distance moved by individuals was then placed as a buffer around camera trap stations to give the total area covered by traps and hence density estimates produced. As predicted, density estimates fell into the low category as defined by the National Leopard Survey, being 0.9 leopards/100 km^2 for the northern sites and 0.59 leopards/100 km^2 for the southern sites. Variation was seen in the accuracy of farmer estimates of leopard numbers, with one farmer estimating five times the number recorded by camera trap on his property. Such results show the need for field surveys for accurately determining local density and national population estimates. Additionally, due to the variation in farmer accuracy, it is not recommended that questionnaire data is used for producing population estimates, especially for those species used for trophy hunting.

5.2 Introduction

Leopards *Panthera pardus* are the most geographically widespread of all felids, ranging from sub-Saharan Africa to the middle East and into tropical and temperate Asia (Nowell and Jackson 1996). The ability of leopards to live in a wide variety of habitats, from rainforest to desert (Henschel et al. 2008), has been largely attributed to their adaptable hunting strategy and extremely catholic diet (Balme et al. 2007); 92 prey species have been recorded for sub-Saharan Africa alone (Bailey 1993). The species is currently listed by the IUCN as Near Threatened (Henschel et al. 2008), having been eradicated from 13.6 % of their historical range (Ray et al. 2005), although no current global or even African population estimates exist (Henschel et al. 2008). In 1998 the sub-Saharan population was estimated at 714,000 adult individuals (Martin and Meulenaer 1988), however this has been widely regarded as an overestimate (Nowell and Jackson 1996). The current Namibian population estimate stands at 14,154 adults (range 13,356 - 22,706) (Stein et al. 2011a), which is over double the 2004 estimate of 5,469 - 10,610 produced by the Namibia Large Carnivore Atlas (Hanssen and Stander 2004).

The IUCN lists habitat conversion and intense persecution as threats to the survival of the leopard throughout its range (Henschel et al. 2008). Within Namibia, farmer conflict with leopards regarding livestock predation is common, with 770 animals reported as killed as problem animals to the Ministry of Environment and Tourism between 1997 and 2003 (CITES Resolution Conf. 10.14 (Rev. CoP13)). In a recent questionnaire of 250 Namibian farmers, leopards were recorded as the third largest cause of financial loss, after lion and cheetah, with 15 % of respondents shooting leopard on sight and 60 % shooting following livestock depredation. However, compared to responses to other carnivores, they were the most tolerated carnivore species across respondents (Lindsey et al. 2013). In the actual study area, four leopards were allegedly trapped and subsequently shot on a neighbouring farm in December 2012 as part of routine farming practices (i.e. not following livestock predation) (W. Theile, *pers. comm*).

Leopards in Namibia and other African countries are also killed for sport in the trophy hunting industry where paying tourists visit the country with the main purpose of shooting an animal. In the case of leopards, individuals with exceptional attributes such as large males, are targeted under the guidance of a professional hunter. Trophy hunting in Namibia generates a mean gross annual revenue of US$ 28.5 million from an annual average of 22,462 animals shot, with 5,363 foreign hunters visiting the country in 2004 alone (Lindsey et al. 2007). The annual quota for leopard trophy hunting is 250 adult males, which was increased from 100 in 2004 (CITES Resolution Conf. 10.14 (Rev. CoP13)). The trophy permit for a leopard currently costs US$ 5,000 from the Ministry of Environment and Tourism, with an internet search showing a number of professional hunting safari companies offering 14 day leopard hunting packages at US$ 16,000 (Ozondjahe Hunting Safaris Namibia, 2015).

Although controversial, the practice of trophy hunting is regarded by many as a much needed revenue for wildlife conservation outside of protected areas which can be used to complement that revenue generated from ecotourism (Lindsey et al. 2006). For example, the primary motivation for the development over 70,000 km^2 of communally owned and managed conservancies across Namibia has been revenues from trophy hunting (Weaver and Skyer 2003). However, for trophy hunting to aid conservation, it must be done sustainably and pose a low risk to wildlife communities. An annual off-take rate of 2 - 5 % of the adult male population is usually quoted as sustainable (Bond et al. 2004), with Namibia using 3 - 4 % of the adult male population as a guide for calculating the number of annual hunting quotas for leopard. The annual quota of 250 adult male leopards for Namibia is based on a national population estimate of 14,154 adults at a presumed sex ratio of 1:1 (Stein et al. 2011a). This population estimate is based on the National Leopard Survey (Stein et al. 2011a), the results of which were used to produce the leopard density map in the Namibia Large Carnivore Atlas (Fig. 5.1) (Stein et al. 2012). The survey only used camera traps to estimate density in three sites across Namibia, for other areas density contours were extrapolated from questionnaire data from landowners and farmers.

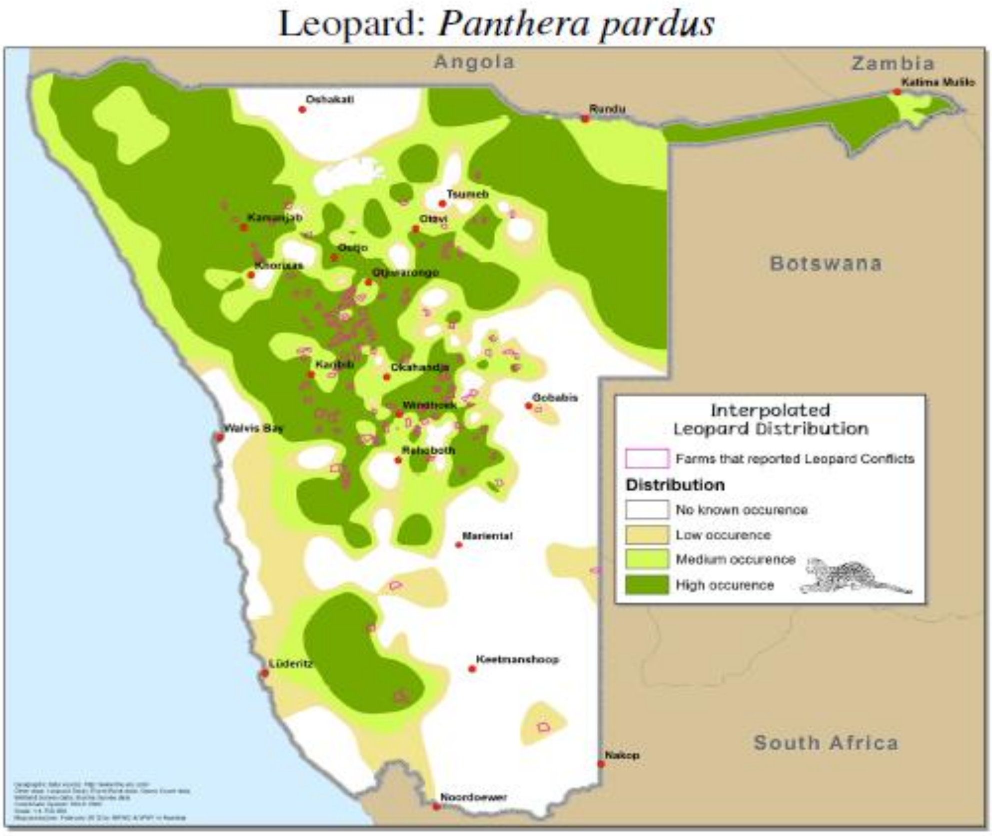


Figure 5.1: Leopard density map for Namibia from the 2012 Namibian Large Carnivore Atlas (Stein et al. 2012)

The actual study area falls under medium/high occurrence contours (densities of 2.0 and 3.1 leopards/100 km^2 respectively) on the leopard density map (Fig. 5.1) (Stein et al. 2012). However the authors of the National Leopard Survey (Stein et al. 2011a) note the subjective nature of the questionnaire, i.e. asking farmers if they saw leopards/tracks rarely or frequently, and that farmers might deliberately inflate leopard numbers to increase hunting quotas. Additionally, they recommend surveying the southern area of the country to confirm these high density contours. A high density in such an arid area is not expected, as in sub-Saharan Africa leopard density is positively correlated with rainfall (Martin and de Meulanaer 1988). Confirming the density within the south should therefore be seen a priority for producing a more accurate population estimate. If the trophy hunting quota is over the recommended sustainable level, the conservation value of trophy hunting leopard and the viability of the leopard population will likely be compromised.

Whilst the current trophy hunting quota, based on the current Namibian population size, may be sustainable if current population estimates are correct, the number of animals removed following involvement in livestock predation, albeit real or perceived, does not seem to be taken into account. Table 5.1 (taken from CITES Resolution Conf. 10.14 (Rev. CoP13)), shows the number of leopards reported to the MET as removed by farmers due to being problem animals annually compared to the number taken as trophy animals. It can be seen the number removed as problem animals is often more than the annual quota for trophy hunting, meaning the total number of leopards removed annually is unlikely to be sustainable. Additionally the assumption of sustainable take-off rests with only males being taken from the population. In a genetic study by Spong et al. (2000) 29 % of 77 trophy leopards tagged as males were females in Tanzania. It is also mainly assumed males are responsible for livestock production, however in a genetic study of 53 leopards removed as problem animals in Botswana, 39.6 % were females (Kerth et al. 2013). Therefore total numbers and sexes of leopards removed annually from Namibia may be unsustainable for the long term viability of the population.

Table 5.1: Numbers of leopards removed as problem animals (as reported to MET) compared to number of trophies from 1997 to 2003

Year	Number shot as problem animal	Number trophy hunted	Total
1997	52	57	109
1998	93	33	126
1999	89	56	145
2000	138	59	197
2001	131	66	197
2002	122	98	220
2003	145	106	251
Total	**770**	**475**	**1,245**

This chapter aims to estimate leopard density across the two study sites and compare farmer estimations of leopard numbers on their land, to the number estimated to be present by camera traps. The objectives linked to this chapter are; to use the program CAPTURE with camera trap data to estimate leopard abundance on both the northern and southern study sites. To then use the half mean maximum distance used by individual leopards between camera traps to estimate the total area covered by the camera traps, and convert the abundance estimate into a density estimate. Finally, to gain estimates from study farm owners concerning the number of leopards present on their land, and to make comparisons between these estimates and the number of leopards recorded on camera trap on each property. It is hypothesised, due to the arid conditions, that leopard density will be low, as defined by the National Leopard Survey. Additionally, due to the secretive nature of leopards, farmers will be unable to accurately determine the number of leopards on their property.

5.3 Methodology

5.3.1 Camera traps

A total of 42 camera traps were set up across the northern and southern study sites, as detailed in sections 2.3.1 and 2.3.2. Due to the closure assumption, discussed below, two survey periods were used, winter (29th May - 28th July 2013) and summer (11th December 2013 - 4th March 2014). Due to the removal of MET camera traps from the southern site in August 2013, only a winter period is available for the south.

5.3.2 Farmer estimates

During the course of the study, each farmer was asked to estimate the number of leopards present on their property as part of a larger questionnaire (see Chapter seven).

5.3.3 Data analysis

Individual leopards were identified using unique pelage patterns, any unclear photographs (*n* = 2 north winter period, *n* = 1 north summer period and *n* = 3 south winter period) were disregarded. Sex was determined by the presence of a dewlap and visible testes for males (Fig. 5.2). All photograph captures were identified by one observer. Capture histories were then developed for each individual in a standard X-matrix format, where rows represented capture histories of each individual. A '1' was scored if an individual was detected in that sampling period, and a '0' scored if the individual was not detected. As the main objective of the collaboration between the project and the MET on the National Leopard Survey was to produce comparable density estimates from other study areas across Namibia, the standard 60 day period was used, with 24 hour sampling occasions. Population sizes were then estimated using programme CAPTURE, where comparison of probabilistic model was used to generate estimates for the number of individuals present. CAPTURE was also used to check population closure.

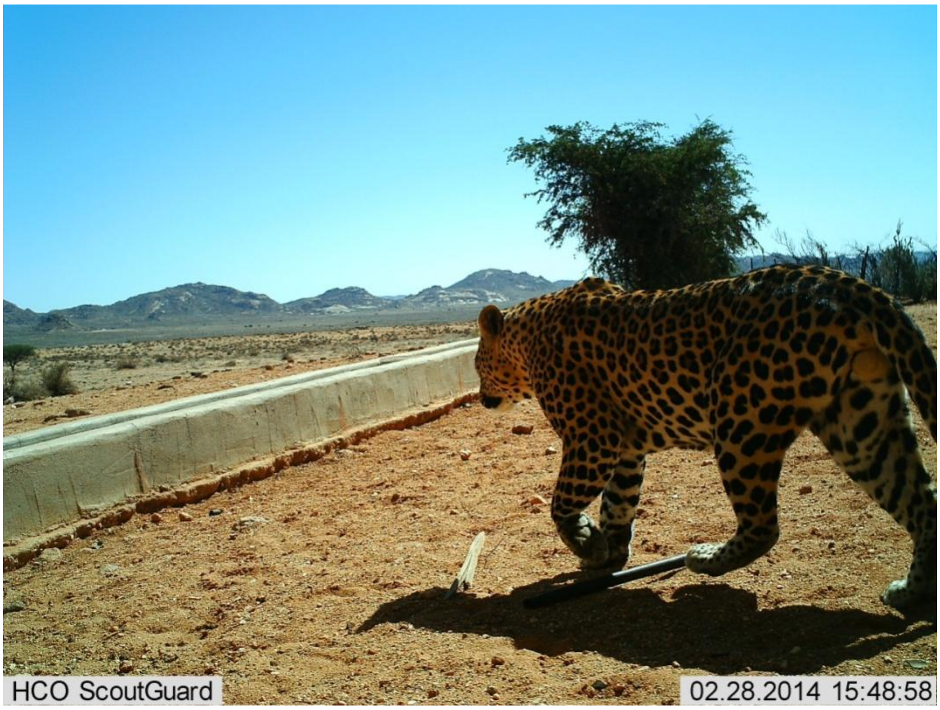


Figure 5.2: Male leopard with testes clearly visible, Klein Aus Vista

5.4 Results

5.4.1 Leopard density

During the winter period in the northern sites, leopards were only recorded on Namtib, where three individuals, a male and two females, were captured. The mean capture frequency, i.e. number of camera trap nights needed to produce a single independent event, was 29 ranging from 15 days for a female and 60 days for the male. Programme CAPTURE showed the model Mh (Jack-knife), which shows heterogeneity between individuals for capture probability, to be the best fit for the data. This model suggested an abundance of four individuals (S.E. = 1.15) with 95 % confidence intervals of 4 - 11 individuals (Table 6.2). Population closure was confirmed by CAPTURE ($z = -0.88$, $P = 0.19$). The half 1/2MMDM was 4.3 km, which when placed as a buffer around each camera trap gave a total area covered of 428.92 km^2 (Figure 5.3). This gives a leopard density estimate of 0.93 leopards/100 km^2.

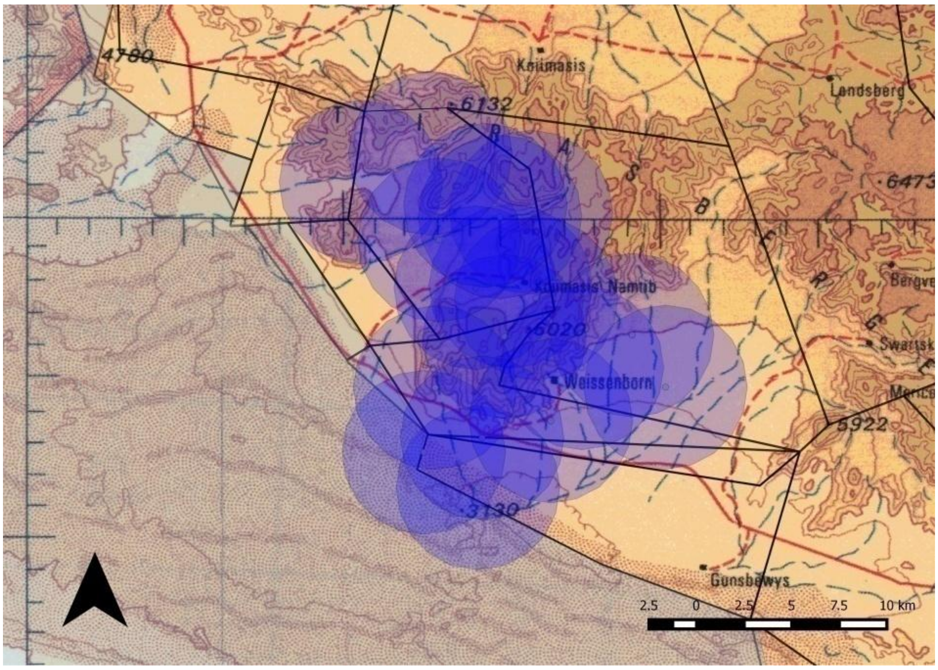


Figure 5.3: Total area covered during summer period in northern sites. Buffer of 4.3 km placed around each camera trap, showing the total 428.95 km^2 believed to be covered by camera traps and thus used to convert the abundance estimate into a density estimate.

In the summer period a total of five individual leopards were captured, the same three individuals captured during the winter period on Namtib, and a new female and male captured on Weissenborn. One of the females recorded on Namtib during the winter period was captured on Weissenborn with three 8 - 10 week old cubs in December 2013 (Fig. 5.4). No leopards were captured on Gunsbewys during the period. The mean capture frequency ranged from 20 for one of the females to 60 for both males and some of the females. Again, like for winter, the model Mh (Jack-knife) was shown to be the best fit for the data and gave an abundance estimate of 7 individuals (S.E. = 2.12) with 95 % confidence intervals of 2 - 12 individuals. Population closure was again confirmed by CAPTURE (z = - 0.30, *P* = 0.23). During the summer period the 1/2MMDM increased to 6.69 km (Fig 5.5), giving a total area covered of 665.45 km^2, and a density estimate of 1.05 leopards/100 km^2 (Table 5.2).

Figure 5.4: Female leopard with 8 - 10 week old cub Weissenborn (cub under bush in left hand corner)

Table 5.2: Leopard density estimation parameters calculated from camera trap data, along with the best fitting models as chosen by program CAPTURE, and the half mean maximum distance moved between camera traps by individual leopards which was used to calculated the total area covered by camera traps and thus the figure used to convert the abundance estimate to a density estimate

Site	**Season**	**# leopards captured**	**# recaptures**	**Mean capture freq.***	**Range capture freq.***	**Model**	**Abundance (S.E)**	**95 % CI**	**1/2MMDM (km)**	**Total Area/km^2**	**Density (# adults/100 km^2)**
North	Winter	3	7	29	12 - 60	Mh	4 (1.15)	4-11	4.3	428.92	0.9
North	Summer	5	3	46	20 - 60	Mh	7 (2.12)	6-15	6.69	665.45	1.05
South	Winter	5	13	31.11	8.57 - 60	Mo	5 (0.41)	5-5	6.88	852.01	0.59

**freq. of capture refers to the average number of camera traps nights for per event*

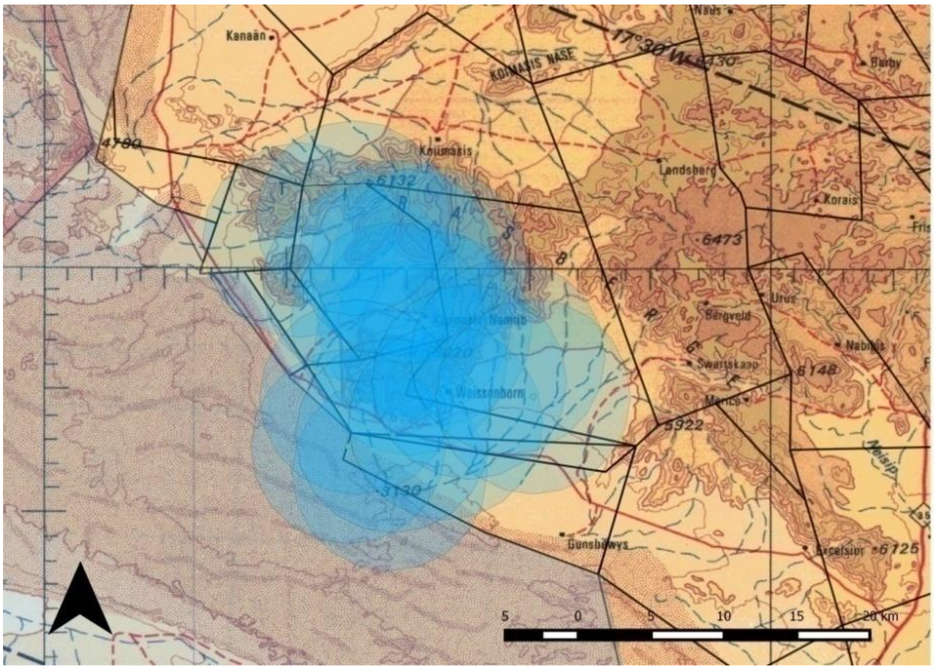


Figure 5.5: Total area covered during summer period in northern sites. Buffer of 6.69 km placed around each camera trap showing the 665.45 km^2 believed to be covered by the camera traps, and used to convert the abundance estimate into a density estimate

In the southern sites in winter, five leopards were captured across both Tsirub and Klein Aus Vista. Three females and two males were captured, one female being seen with cubs estimated to be 4 - 7 months old in July 2013. Capture frequency ranged from 8.57 to 60 camera trap nights, with a mean of 31.11 nights (Table 5.2). CAPTURE showed the best model to be Mo (homogeneous capture probability between individuals) to be the best fit for the data, this gave an abundance estimate of 5 individuals (S.E. = 0.41) with 95% confidence intervals of 5 - 5. Population closure was confirmed (z = -0.52, *P* = 0.16). The 1/2MMDM was 6.88 km, resulting in a total area covered of 852.01 km^2 (Fig. 5.6)and a density estimate of 0.59 leopards/100 km^2.

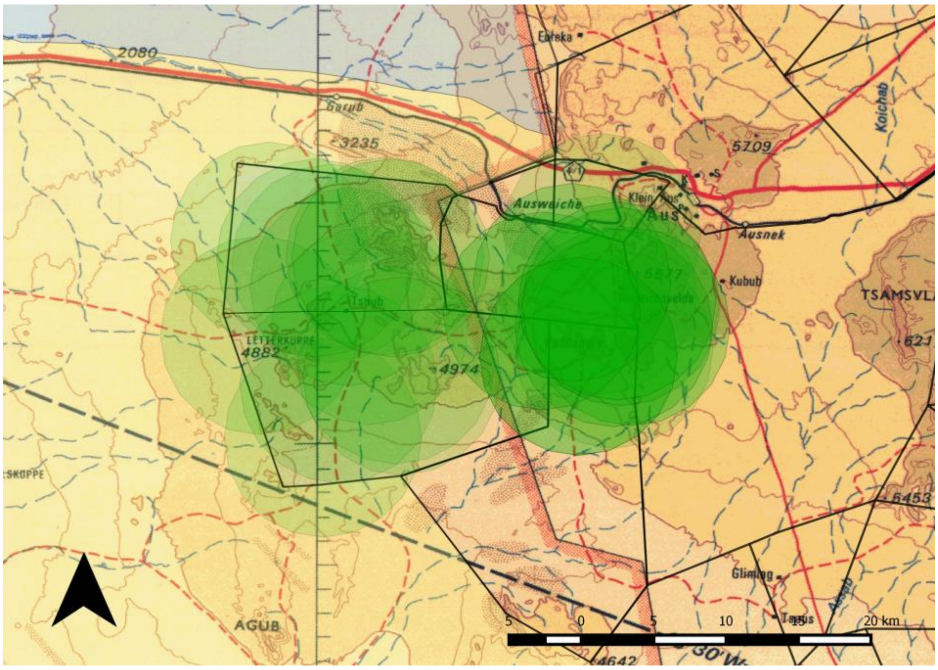


Figure 5.6: Total area covered during winter period in the southern sites. Buffer of 6.88 km placed around each camera trap

Little difference in leopard density was seen across the northern sites between the seasons; 0.9 and 1.05 leopards/100 km^2 for winter and summer respectively (Table 5.3). However, constant occupancy was around twice as high in summer than winter, whilst mean RAI was lower in summer. Naive occupancy changed from 0.21 in winter to 0.09 in summer. Comparing between the sites density was much lower in the southern sites, however RAI, constant occupancy and probability of detection were highest in the south.

Table 5.3: A comparison of leopard statistics derived from camera trap data across sites and seasons, with constant occupancy (ψ) and constant probability (*p*), estimated using program CAPTURE, and the resulting density estimates.

Site	**Season**	**RAI**	**Naive *ψ***	**1/2MMDM/ km**	**Constant *ψ* ± 1 S.E.**	**Constant *p* ± 1 S.E**	**Density (# leopards/100 km^2)**
North	Winter	2.02	0.24	4.3	0.41 - 0.67	0.27 - 0.41	0.9
North	Summer	0.95	0.09	6.69	0.13 - 0.35	0.24 - 0.46	1.05
South	Winter	2.67	0.31	6.88	0.74 - 0.74	0.50 - 0.74	0.59

5.4.2 Farmer estimates

The number of leopards detected by camera trap on each farm was compared to the number predicted to be on the farm by farmers. Figure 5.7 shows the differences between the number of leopards determined by camera trap and that estimated by farmer varied between sites, with Tsirub being the most accurate and Namtib Biosphere being the least accurate. Gunsbewys stated no leopards were present on the property whilst one was detected on camera trap (although not during the camera trapping period used here for density estimation), however leopard was only detected once and most likely represented a transient individual coming through or a neighbouring resident expanding their home range. The farmer from Klein Aus Vista was unable to estimate the number of leopards on the farm, however he did acknowledge they were present.

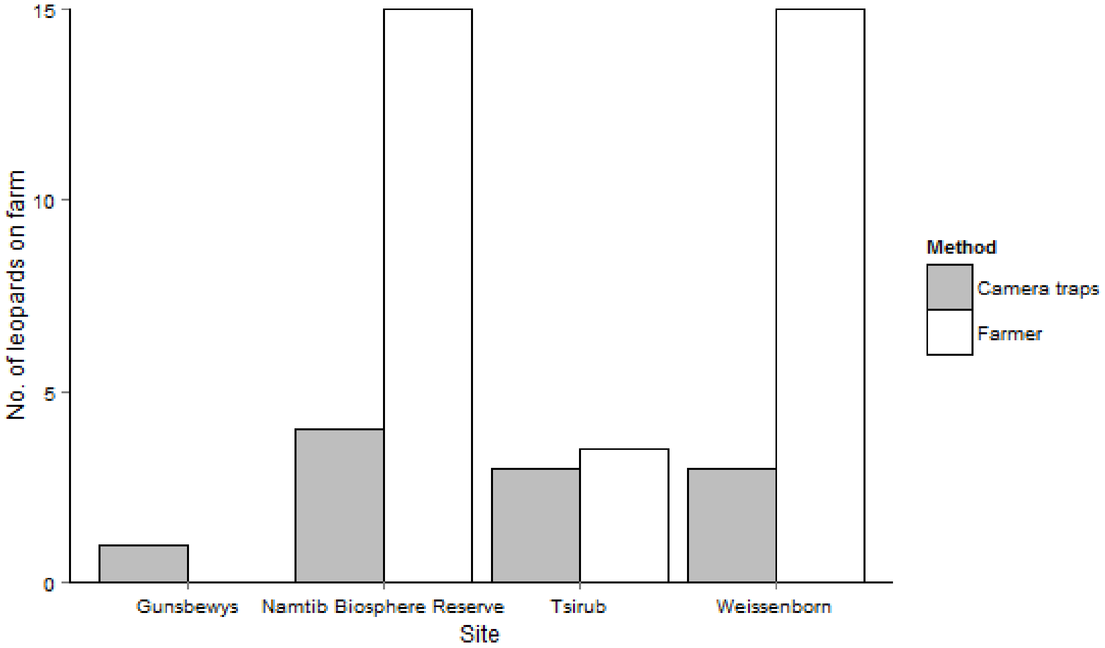


Figure 5.7: Visual comparison of number of leopards on each study farm, compared to the number estimated by farmers, it should be noted that the owner of Klein Aus Vista could not estimate the number of leopards on his property, although he did acknowledge their presence.

5.5 Discussion

Across southern Africa leopard density (number of adult leopards per 100 km^2) is highly variable; 1.3 in the Kalahari (Bothma and Le Riche 1984), 1.5 in northeast Namibia (Stander et al. 1997), 2.64 in Zululand Rhino Reserve, KwaZulu Natal South Africa (Chapman and Balme 2010), 10.73 in the Soutpansberg Mountains, South Africa (Chase et al. 2013) and up to 30.3 in the Kruger National Park, South Africa (Bailey 2005, cited by Chase et al. 2013). Leopard density estimates (0.9 and 1.05 for the northern sites in winter and summer respectively, and 0.59 in the southern sites) from this study were the lowest recorded for the Namibian National Leopard Survey (Stein et al. 2011a), and lower than estimated for the Waterberg Plateau Park in north-central at 1.0 leopards/100 km^2 (Stein et al. 2011b). The 1/2MMDM were also the largest recorded for the NLS.

In general, leopard density in sub-Saharan Africa is positively correlated with rainfall (Martin and de Meulanaer 1988), with Marker and Dickman (2005a) finding rainfall influencing leopard abundance, but not home range size on Namibian farmlands. As arid conditions are likely to give rise to low density leopard populations, with large home ranges (Mizutani and Jewell 1998), such comparatively low density estimates for this study are hardly surprising, especially given the lack of surface water and low mean annual rainfall for the study area. Additionally, female leopards are believed to base home ranges around microhabitat features such as water points (Mizutani and Jewell 1998). As water is sparsely distributed on Namibian farmlands, females could have larger home ranges (Marker and Dickman 2005a) and due to the lack of overlap between individuals (Stander et al. 1997) a correspondingly low density. Indeed Marker and Dickman (2005a) recorded the largest home ranges reported in the literature for Namibian farmland leopards.

The 1/2MMDM, used to define the total area surveyed, was the largest recorded for the entire National Leopard Survey, which showed increasing distances with decreasing average rainfall (Stein et al. 2011a). Sollmann et al. (2011) found male jaguars moved larger distances than females, which also resulted in males encountering more camera traps than females. Although sample sizes were too small for statistical analysis, the largest 1/2MMDM moved across each site came from males, with one male moving 25.1 km between traps in the southern sites. Such large distances moved could also explain the relatively long time periods between recapture of individuals seen for all leopards in the survey, especially if part of the home range is in areas not covered by camera traps. The use of the 1/2MMDM ad hoc method of determining the area covered by the camera traps has been criticised previously for having little theoretical justification (Williams et al. 2002), However, for leopards Balme et al. (2009) found this method to give the best density estimations, in comparison to a reference density, after the mean maximum distance moved outside sampling area (MMDMOSA), which was determined using radiotagged leopards.

Farmer estimates showed variation in accuracy when compared to the number of leopards detected by camera traps. Two of the farmers overestimated the number of leopards; Weissenborn by 12 animals and NBR by 11 animals, whilst Tsirub was very accurate estimating between three and four animals compared to three individuals detected by camera trap. Gunsbewys believed they did not have leopards present on the farm and data suggested indeed no resident animals were present, only one individual was detected during the entire study period which was most likely a transient animal. Stein et al (2011a) noted in the National Leopard Survey that farmers may deliberately over-inflate leopard numbers in order to obtain more trophy hunting permits, however, none of the study farms currently practice trophy hunting or showed any intention to start. Other studies have discussed problems with the use of questionnaires, for example, with deliberately inflating livestock losses (Hermann and Funston 2001; MET 2005), or locals not being aware of the presence of certain species (Can and Togan 2009). These results show that two of the four farmers overestimated the number of leopards by 3.75 to 5 times the actual numbers. Such results across the country could mean the national leopard population estimate could potentially be highly overestimated and therefore the current trophy animal quota combined with the number of animals removed as problem animals could mean the current level of take off is actually unsustainable.

The trophy hunting quota is currently set at 250 adult males, which is set using an assumed sex ratio of 1 : 1 (Stein et al. 2011a). However the results of this study showed a ratio of 1 : 2 males to females for the northern sites in both winter and summer, and a ratio of 2 : 3 males to females in the south. Studies of leopards from other areas in southern Africa have shown sex ratios closer to the assumed 1 : 1 used by Stein et al. (2011a) for example across Namibia Stander et al. (1997) recorded a ratio of 1 : 0.7 males to females and (Balme et al. 2009) recorded 1 : 1.11 males to females in Phinda Private Game Reserve, South Africa. The results here contrast with those from other large cat surveys which found sex ratios to be skewed towards males, for example pumas (Kelly et al. 2008, Negroes et al. 2010), tigers (Karanth and Nichols 1998; O'Brien et al. 2003) and jaguars (Silver et al. 2004). Salom-Perez et al. (2007) found female jaguars to avoid forest trails which could explain such skewed ratios. However in this study, the ratio was skewed towards females and placed cameras both at trails and in the presence of water. Balme et al. (2010) believed that most leopards dying as a result of human-wildlife conflict were males, which could explain the skewed ratio in their study area. However in a genetic study of stock-raiding leopards, 39.6 % of 59 individuals shot in conflict situations in Botswana were female (Kerth et al. 2013). Whatever the reason, the sex ratios seen in this study could mean there are less males in the population than predicted from the population estimate, further making the quota unsustainable.

Trophy hunting rountinely comes under fire from animal rights groups given the ethical issues it raises. However, from a biological standpoint, the practice may be detrimental to the population, given its secondary effects on wildlife. Trophy hunting is often thought to improve population persistence, through increases in female reproductive success, survival and population growth following the removal of old, territory holding males within the population (Wielgus et al. 2013). However, for some species, the opposite effect has been found to be true. Packer et al. (2009) found excessive trophy hunting of male leopards under seven years of age, caused a decrease in population persistence as females were unable to raise sufficient numbers of cubs owing to a constant cycle of infanticide, a behaviour common to leopards (Balme and Hunter 2013). Similar effects have also been noted in European brown bears (Swenson et al. 1997), pumas (Ruth et al. 2011) and North American grizzly bears (Wielgus et al. 2011). A somewhat more surprising effect was noted in African elephant following the removal of older bulls from the population following a cull. Slotow et al. (2011) found in the absence of older males, young bulls entered musth, a state of heightened sexual activity and aggressive behaviour, around the age of 18, compared to 25 to 30 years in natural populations. One result of this in Pilaneberg National Park, South Africa, was the killing of over 40 white rhino *Ceratotherium simum*, which stopped following the addition of mature bulls into the environment.

Whilst capture-recapture methods for modelling population have been widely used previously, concerns have been raised regarding the ad hoc methods of determining size of the sampling grid and thus the conversion of the abundance estimate to density. Efford and

Fewster (2013) argued there to be no adequate theory for defining the area sampled (A) in the equation D = N/A, where D = density and N = number of individuals, independently of the equation, nor is there a reliable estimator. Additionally Parmenter et al. (2003) reported that in respect to the sampling area, survey plot abundance is likely to be an overestimation, as individual animals with just part of their home range on the grid are still available for capture. Obbard et al. (2010) also suggested the assumption of geographical closure during the survey period to be rarely achieved in large carnivores. In response to such problems, a class of spatially explicit capture-recapture models (SECR) have been developed, combining capture-recapture with distance sampling, estimating each animal's range and centre of activity and producing a probability density functions of animals based on distance from activity centres (Borchers and Efford 2008). SECR models presume that individual activity centres follow a Poisson point process, i.e. that individuals are uniformly and independently distributed across the area of interest (Borchers and Efford 2008). However, due to the presence of territoriality in species, this assumption is unlikely to hold true (Reich and Gardner 2014), and recently Reich and Gardner (2014) have developed a new statistical spatial model allowing for dependence between locations, and have already shown this to improve population size estimates.

SECR have been widely accepted as a robust method for estimating population size, and have been used in a number of studies with a range of species; leopard (Gray and Prum 2012), Asian bears (Ngoprasert et al. 2012), Scottish wild cat *Felis silvestris sivestris* (Kilshaw et al. 2014) and sympatric leopard, aardwolf, spotted and striped hyena (O'Brien and Kinnaird 2011). In a comparison of density estimation methods for leopard in Cambodia, Gray and Prum (2012) found SECR and traditional capture-recapture models gave similar results. In contrast Obbard et al. (2010) found SECR density estimates of American black bear *Ursus americanus*, were 20 - 200 % lower than those derived from traditional capture-recapture methods. The authors suggested methods relying on the conversion of abundance to density estimates are positively biased towards edge effects and therefore violate the geographical closure assumption. Whilst there is a large body evidence suggesting SECR to be advantageous, the safe minimum number of recaptures recommended is 20, with studies using less than this number resulting in wide confidence intervals (Efford 2012). Therefore, such an approach would not be possible for the data from this study. Sample sizes could be potentially increased by using more camera traps to create a bigger trapping grid and therefore including more individuals, however survey length could not be increased without potentially violating the demographic closure assumption. As some individuals were not recaptured once during the sampling period, it is difficult to say if adding more camera traps would actually result in higher numbers of recaptures.

Differences between the sexes of large felids have been shown previously in behaviour and ranging patterns (Gray and Prum 2012), and therefore modelling sex specific factors into various models may be appropriate. Conde et al. (2010) found short forest habitat and roads to be significantly avoided by female jaguars in South America, and showed incorporation of such differences increased the precision of habitat models. Leopards are known to show sex differences in home range sizes; Stein et al (2011b) found male home range size to be twice that of females in northcentral Namibia, whilst Stander et al. (1997) calculated male home ranges to be 210 - 1.164 km^2, compared to 183 - 194 km^2 of females in northeastern Namibia. Such differences in movements and home range sizes may be expected to result in sex differences in detection rates of camera traps (Sollmann et al. 2011), as males may be exposed to more camera traps (Sollmann et al. 2011). Although SECR models allowing the inclusion of sex-specific differences to be modelled, they were not suitable for the data from this study, for reasons explained above. An alternative could be to calculate the 1/2MMDM, and therefore density estimates for males and females separately. However, in this study small sample sizes would hinder such an approach, for example in the north, winter period, only a single male was captured.

The results of this study show the difficulty in accurately assessing cryptic carnivore populations, especially when interview/questionnaire data is used in lieu of on the ground surveying. When the focal carnivore species is also used for trophy hunting, it is essential that a population estimate is produced as accurately as possible to ensure annual trophy quotas are set at a sustainable level. National leopard population estimates produced by Stein et al. (2011a) are likely to be inaccurate given the medium to high density contours of this study area were actually low density, and this new data should be taken into account when setting the new annual hunting quota. It is also recommended, following the study by Spong et al. (2000) who found 29 % of 77 trophy leopards tagged as male proving to be female, that a similar study be conducted within Namibia. Hunters mistakenly or knowingly taking females as trophies will make the take-off rate unsustainable, therefore ensuring only males are taken should be a priority for wildlife managers and the Ministry of Environment and Tourism.

6.0 Examination of diet of carnivores on commercial farmlands, using stable isotopes and camera trapping

6.1 Abstract

Anthropogenic food resources have the potential to influence various aspects of carnivore ecology, including home range size and foraging behaviours, as well as carnivore population density within the local area. Establishing the long term use of such resources by carnivores is of key importance when those carnivores are also involved in real or perceived human-wildlife conflict situations. Whilst traditional methods used in dietary studies, such as scat and stomach content analysis, have several disadvantages such as only representing a single meal, stable isotope analysis offers a solution to such problems. The relatively new technology of stable isotope, allows a examination of the long term diet of consumers, with different tissue types representing diet from different time periods. This study used stable isotope analysis to examine the diet of carnivores living on commercial farmlands in southern Namibia. Specifically, it asked if the diet of carnivores was influenced by the presence of an anthropogenic food resource, by comparing diet of carnivores with access to this resource, to carnivores without. Additionally, the offal pit and two cattle carcasses were monitored by camera traps to document their use by carnivores. Results showed the offal pit was extensively used by both brown hyena and black-backed jackal, and that the diet of these species showed a greater overlap in the south, where the offal pit was located, than in the north. Within species comparisons showed no dietary overlap for brown hyena between the north and south, and little overlap between black-backed jackal from the north and south, suggesting differences in diet. Monitoring of the cattle carcasses showed species not traditionally seen as scavengers, such as aardwolf and bat-eared fox were present, as well as the species known to scavenge such as spotted hyena and black-backed jackal. Whilst sample sizes were small, the results of the study suggest diet of scavenging species in the south to be influenced by the presence of the offal pit, which may in turn have influence on various aspects of their ecology, which could affect human-wildlife conflict in a number of ways.

6.2 Introduction

Human-carnivore conflict is largely centred around the actual or alleged predation of livestock species by carnivores (Treves and Karanth 2003; Graham et al. 2005), and has been the topic of a vast number of studies globally, for example Li et al. (2013) examined livestock predation by large carnivores in China, and Dickman (2005) investigated the patterns of carnivore predation of livestock in Tanzania. Understanding the long-term diet of carnivores potentially involved within human-wildlife conflict is of key importance, especially in areas where anthropogenic influences have the potential to affect diet. Anthropogenic influences affecting diet may include the addition of domestic livestock into an area, which may in turn be associated with a reduction in abundance of native prey species (Saberwal et al. 1994), or the presence of refuse pits used to dispose a variety of waste including offal from animal slaughter.

Whilst studies have examined the effect of refuse pits, pits used for the sole purpose of dumping human household waste, on carnivore densities and spatial ecology, few have examined the influence of such pits on actual carnivore diet. Many studies have shown the presence of refuse pits can result in higher densities of carnivores in the area (Bino et al. 2010), which can lead to increased levels of conflict (Woodroffe and Ginsberg 1998; Beckman and Burger 2003; Baruch-Mordo et al. 2013). Furthermore, in line with optimal foraging theory (Stephens and Krebs 1986), home ranges of carnivores within the presence of such resources are smaller than those in more natural habitats, due to increases in food resources resulting in decreases in foraging related behaviours and movements. Yirga et al. (2012) found spotted hyena to predominantly scavenge on anthropogenic waste in northern Ethiopia. However, during the religious fasting period of Abye Tsome, when there is a sharp decline in offal available from slaughter, hyenas switched to actively hunting donkey, bringing them into conflict with humans. Bino et al. (2010) found red foxes to be so reliant on anthropogenic resources from villages near poultry farms in Israel, experimental removal of such food sources resulted in a drastic decrease in survival rate, reaching 100 % mortality in one village.

The presence of offal pits on Namibian commercial farmlands and their effect on carnivore diet has not yet been examined, but should be considered given their potential influence on carnivore abundance, diet and spatial ecology. Any studies examining the diet of carnivores potentially involved in conflict situations should have an understanding of the utilisation of anthropogenic food resources, especially those containing animal products from species which are of value to the farmer. In order to gain a better understanding of their use in carnivore diet, the long-term diet must be considered, rather than single meals.

Traditionally, studies of carnivore diets have been limited to stomach content analysis, faecal analysis or, where possible, direct observations of foraging activities (Jones et al. 2006). Whilst such methods provide a direct assessment of diet, they have the potential to vastly underestimate the consumption of highly digestible material (Stapp 2000). Furthermore, due to the fact that such methods only represent a very short time frame, they are unlikely to reflect the complexity of, and spatio-temporal variation in carnivore diets (Codron et al. 2006). Such methods can also be unethical, for example destructive sampling of endangered species to access stomach contents, impractical or prohibitively expensive (Boecklen et al. 2011). The relatively new technology of stable isotope analysis (SIA) overcomes the problems of traditional dietary methodologies as it reflects assimilated diet (Jones et al. 2006, Meckstroth et al. 2007). Tissues, such as hair can be used, which can be collected non-invasively and therefore negate the need for direct contact with the animal (Jones et al. 2006).

Stable isotope analysis in ecology is based on the fact that several elements exist in multiple forms, known as isotopes. Different isotopes of the same element differ from each other by having different numbers of neutrons in the nucleus, producing different atomic masses. For example, carbon has two stable forms; ^{12}C which has six protons and six neutrons in the nucleus, and ^{13}C which has six protons and seven neutrons (Ben-David and Flaherty 2012a). Such differences in the physical properties of isotopes leads to natural variation in the ratios of heavy to light isotopes in organic compounds (Crawford et al. 2008; Ben-David and Flaherty 2012a). Such natural variation in ratios is useful to ecologists as consumer tissues are synthesised from dietary nutrients and reflect the composition of their diet in a predictable manner (Crawford et al. 2008), and therefore, it is a useful tool for reconstructing diets (Boecklen et al. 2011). The isotopic composition of an animal's tissues reflects and integrates their diet from a period of time ranging from a few hours to several years, depending on the tissue type (Stapp 2000; Wang et al. 2004).

The use of stable isotope technology in ecology has dramatically increased in recent decades (Boecklen et al. 2011, Ben-David and Flaherty 2012b). Dietary studies using stable isotope analysis have included defining diets of wolves *Canis lupus* in British Columbia, Canada using tissue and blood samples collected during collaring activities (Milakovic and Parker 2011). Meanwhile Voigt et al. (2013) developed a breath test for cheetah to determine if the individual predominantly fed on browsers or grazers. Some studies using stable isotopes have highlighted where the approach can add new information to a previously studied situation, for example Newsome et al. (2010) used SIA to examine the diet of San Joaquin kit fox *Vulpes macrotis mutica*, and found that in sharp contrast to scat analysis, the species fed extensively on anthropogenic food sources.

Within southern Africa, plants are known to vary in their isotopic ratios due to variations in their carbon dioxide photosynthetic pathways (Bender 1971). Grasses and sedges use the C4 photosynthetic pathway, whilst trees, bushes, forbs and shrubs use the C3 photosynthetic pathway. C3 plants discriminate more strongly against the heavier ^{13}C isotope than the C4 plants, therefore C3 plants have lower ratios of ^{13}C : ^{12}C than C4 plants (Vogel et al. 1978). Herbivores feeding on grasses have a significantly different isotope ratio to herbivores feeding on browse (Sponheimer et al. 2003). In a study of farmland cheetah diet in Namibia, Voigt et al. (2014) were able to divide potential prey items into three isotopically distinct categories; a C4 food web with high δ^{15}N values (oryx, cattle, springhare *Pedetes capensis* and guinea fowl *Numida meleagris*), a C4 food web with low δ15N values (hartebeest *Alcelaphus buselaphus* and warthog *Phacochoerus africanus*), and a C3 food web (eland *Taurotragus oryx*, kudu, springbok, steenbok and scrub hare *Lepus saxatilis*). Due to cattle not having a distinct signature from other prey items, the relative contribution of cattle to the diet could not be identified (Voigt et al. 2014).

This study aimed to investigate the diet of carnivores occurring on Namibian farmlands using stable isotope analysis as a means of representing a longer term diet than the more traditional methods of scat analysis and direct observation. Originally, the study had aimed to estimate the relative contribution of domestic livestock to the diet through the use of mixing models. Statistical mixing models are commonly used in isotopic studies of diet, allowing an estimation of the relative contribution of food sources to the isotopic composition the tissues of the consumer (Phillips 2002). Such mixing models are a relatively new technique of analysing stable isotope data, offering a practical solution to when there are multiple potential sources of food (Phillips et al. 2005). Therefore, the use of mixing models would have allowed the estimation of the relative contribution of domestic livestock to the diet of carnivores, but only if the isotopic signatures of domestic livestock were significantly different to other potential prey items (Crawford et al. 2008), which in north central Namibia was not the case, the isotopic signature of cattle was not isotopically distinct from oryx and other ungulate species, and thus these species were aggregated together into one prey category (Voigt et al. 2014).

Small sample sizes of both potential prey and items and carnivore hair samples meant mixing models could not be used. Additionally, the two species with the highest sample sizes, brown hyena and black-backed jackal, were both scavengers and therefore it would not be certain if any domestic livestock in their diet was from predation or scavenging. Therefore stable isotope data was used to examine the dietary niches of carnivores, comparing niches between species and site. Additionally two offal pits on Tsirub and NBR were monitored by camera trap to examine their use by carnivores in the area. Two cattle carcasses were also opportunistically monitored on NBR to record which species utilised these resources.

This chapter aims to use stable isotope analysis of hair samples, to examine and compare the diet of scavenging species, specifically brown hyena and black-backed jackal, at the northern site, where an offal pit is not used, and the southern sites where an offal pit is active. It also aims to document the species utilising cattle carcasses, which were opportunistically found on NBR. The specific objectives for this chapter are, firstly, to analyse carnivore hair samples, and prey tissue samples, to obtain a carbon and nitrogen value for each species, using stable isotope analysis. Secondly, to make statistical comparisons between the carbon and nitrogen values, as well as the isotopic niche space occupied by black-backed jackal and brown hyena from the northern and southern study sites. Thirdly, to produce a species inventory of species visiting the offal pit, as well as calculating relative abundance indices, as a measure of activity, for each species, using camera traps. Finally, to use camera traps to compile an inventory of those species utilising two cattle carcasses on NBR.

Due to the presence of an offal pit on Tsirub, it is hypothesised black-backed jackal and brown hyena, will have similar isotopic signatures in the southern sites, and show a greater overlap of isotopic niche space between the two species, than in the north. In the north, due to the lack of an active offal pit, it is hypothesised that black-backed jackal will occupy the largest isotopic niche space and have the highest carbon value, indicative of a width of dietary items within the diet, due to its opportunistic nature. As aardwolf are known to specialise in termites which have a lower nitrogen value than herbivores, it is hypothesised aardwolf will have the lowest nitrogen value of all carnivores. Due to their known behaviours as scavengers, it is hypothesised brown hyena and black-backed jackal will be the only species visiting the offal pit at Tsirub. Lastly, as spotted hyena and black-backed jackal are the resident scavenging species in the north, it is hypothesised they will be the only species utilising the cattle carcasses on NBR.

6.3 Methods

6.3.1 Sample collection

6.3.1.1 Carnivore hair samples

Carnivore hair samples were collected mainly by non-invasive hair snares and rub stations (as described in section 2.3.3). In addition to these, hair samples were also collected from animals killed on the road (*n* = 4; black-backed jackal, bat-eared fox and spotted hyena), killed by a farmer as a result of human-wildlife conflict (*n* = 4; spotted hyena, black-backed jackal), and one black-backed jackal hair sample from an individual found dead by a water point at NBR, with no obvious signs of injury or cause of death.

6.3.1.2. Prey item tissue samples

Potential prey item tissue samples were collected by a variety of methods. Game species, oryx (*n* = 3) and springbok (*n* = 3), were collected during routine slaughter for human meat consumption, whilst one cow sample was collected when a sub-adult individual was shot due to a broken leg, another cow sample was collected when an individual died of unknown causes and a further two samples came from cows killed for human meat consumption. All three sheep samples were collected during routine slaughter on NBR. Other tissue samples were taken when potential prey items were found dead in the field or at the road side and the carcass was fresh enough to give a good quality sample.

Invertebrate samples were collected in April and November 2013, over a total of 420 trap nights using a grid of 15 pitfalls, 500 ml in size, set out in a 10 x 20 m grid with 5 m between traps, on NBR (-26.01703/16.24784). Traps were originally filled with water to ensure any invertebrates falling into the trap would drown, or at least not be able to climb back out, however, this resulted in all traps being pulled out of the ground overnight by unknown species. Therefore the traps were filled with a small amount of sand and dug level to the ground to encourage invertebrates to fall in. Invertebrates were identified to order and stored in 90 % ethanol until stable isotope analysis was undertaken. Stable isotope analysis was performed on the internal soft tissue, as the exoskeleton is not digested by carnivores and therefore would not be assimilated into the tissue.

Small mammal samples were limited to non-lethal ear clippings of individuals captured during April, August and November 2013 and February 2014, although no individuals were captured in November 2014 during the 630 trap night trapping period. A total of 20 Sherman type traps were set out in a grid of 30 x 40 m, with traps being set 10 m apart. Traps were baited with a mixture of oats and peanut butter and opened just before sun set and checked an hour after sun rise. In the winter trapping period (August 2013), a small ball of cotton wool was added to each trap to provide bedding and warmth for the animal. When an individual was captured, it was transferred into a clear plastic bag where it was identified to species and sexed. It was then handled to take a small ear clipping and a section of fur clipped to allow capture-recapture analysis. Sharp, small scissors were used and sterilised between each use with 90 % ethanol to reduce the risk of infection. All handling and sampling procedures were cleared by the Royal Holloway Ethics Committee prior to trapping. All individuals were released at the site of capture. All ear clippings were stored in 90 % ethanol until stable isotope analysis was performed.

6.3.2 Offal pit monitoring

The only offal pit on Tsirub where oryx and springbok offal, skin and bones were dumped approximately 2 - 3 times a week was monitored by a single Bushnell (Overland Park, Kansas, USA) X8 camera trap from 14th January 2014 to 3rd June 2014, after signs of brown hyena and black-backed jackal were observed here. The offal pit represents a reliable source of food for scavenging animals and has the potential to influence their diet. The camera trap was focused on a hole under the main gate into the fenced offal pit, which was believed to be the main access point for animals wishing to access the offal within the fenced off pit. A hair snare was also placed under the same hole.

The offal and waste pit at NBR where general waste as well as offal, skin and bones were dumped, was monitored by a single Bushnell X8 camera trap from 10th January 2014 to 20th March 2014, when it started to malfunction. The camera was mounted on a pole and focused on the entire pit area. Both camera traps were set to take one photo per trigger, with a minute delay between triggers on medium sensitivity. Carnivore photos were classified into independent events and mean relative abundance indices calculated using the criteria detailed in section 4.3.1.1.

6.3.3 Carcass monitoring

Two adult cattle carcasses, which died of unknown reasons in 2014 were monitored by camera trap to document the species scavenging from them. Both carcasses were found opportunistically on NBR. The first was found near the main water point (-25.98036/16.18402) on 19th February 2014 and monitored until 28th April 2014. A second carcass was found close to the first (-25.98689/16.19812) on the 28th April 2014 and monitored until 1st June 2014. Both carcasses were not yet opened by carnivores at the start of monitoring. A single Bushnell X8 camera trap was used for both carcasses, mounted on a metal pole and set to take three photos per trigger, with a minute delay between triggers and set to medium sensitivity. Carnivore photos were classified into independent events and mean relative abundance indices calculated using the criteria detailed in section 4.3.1.1.

6.3.4 Stable isotope analysis

When conducting stable isotope analysis, the measurements taken are the ratio of heavy to light isotopes within a sample, for example the ratio of C^{13}:C^{12}. These measurements are taken using a thermal ionization mass spectrometer, which is able to measure the mass of gaseous inorganic compounds. Organic compounds, for example tissue samples, are combusted at high temperatures into gaseous compounds, using oxygen and metal catalysts, such as tin. Once in a gaseous form, the now inorganic molecules are injected into the source of the thermal ionization mass spectrometer (Ben-David and Flaherty 2012).

The gaseous compound, once injected into the mass spectrometer, is accelerated at high speed into an evacuated flight tube, with a strong magnet. The magnet has the result of deflecting the molecules passing through the tube, based on their mass. These beams are then collected at the end of the flight tunnel in Faraday cups. The collection of these molecules results in a slight electrical current, which is then measured by a connected, controlling computer (Ben-David and Flahery 2012). The process is summaried below in a flow diagram (Figure 6.1).

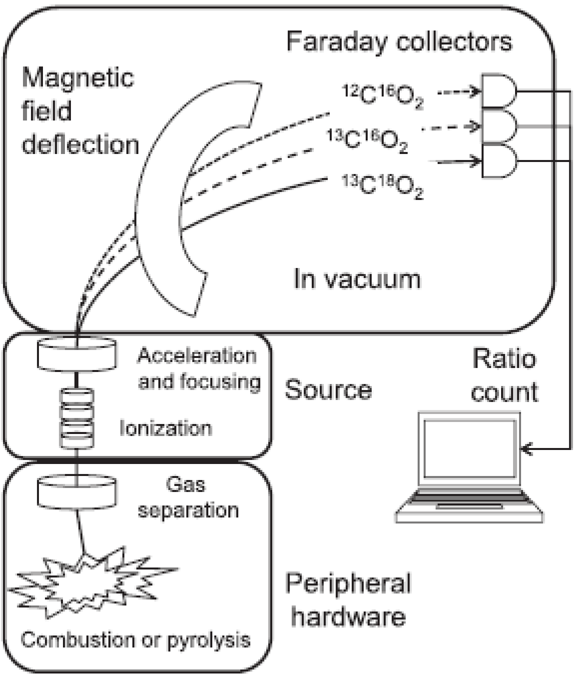


Figure 6.1: Schematic diagram of a continuous-flow isotope-ratio, taken from Ben-David and Flaherty (2012). Mass spectrometer coupled to an elemental analyzer. Organic samples are homogenized and weighed into tin or silver cups. The samples are injected into the analyzer where organic compounds are converted to gaseous inorganic compounds such as N2,CO2,H2O, or SO2 via combustion or pyrolysis. The gases are separated and then injected into the source of the mass spectrometer. There they are ionized and accelerated into the flight tube where a strong magnet deflects them and separates them based on mass. The resulting beams of ionized, gaseous molecules are collected at the end of the flight tube in Faraday cups; their collection creates a weak electrical current measured by the controlling computer.

Stable isotope analysis was performed at the Leibniz Institute for Zoo and Wildlife (Berlin). Samples were dried over 24 hours at 50 ^{o}C, before being combusted and analysed using an elemental analyser (CE 1110 EA, Thermo Finnigan, Berman, Germany), coupled to a Delta Plus isotope mass spectrometer (Thermo Finnigan), as detailed in Voigt et al. (2014). Precision of measurements was always better than 0.05 ‰ (one standard deviation; SD).

6.3.5 Data analysis

One of the difficulties in interpreting stable isotope data in diet construction of mixed diets is the fact that the consumer metabolic processes may discriminate between different isotopes, meaning the consumer's tissue isotopic ratio may not exactly correspond to the isotopic ratios of the food resource. The difference between the tissue of an animal and its diet is known as a discrimination factor (Caut et al. 2008). It is generally believed a consumer tissue to be enriched by around 3 - 4 ‰ for nitrogen, whilst carbon changes little (Post 2012). However a dietary study by Roth and Hobson (2000) with red fox *Vulpes vulpes* showed for hair consumer tissues were enriched by 2.6 ‰ for carbon and 3.3 ‰ for nitrogen. These figures are the only values available for mammalian carnivores and thus have been used by a number of studies, and were used as the discrimination factor in this study. Therefore discrimination factors were applied to δ13C and δ15N values of carnivore hair samples when examining their relation to prey samples.

Both δ13C and δ15N data were tested for normality using Shapiro-Wilks tests, due to sample sizes being less than 30 (Zar 1999). Differences between site (north and south) and species were tested for δ13C and δ15N separately. Isotopic niche space and trophic relations between species were described using Stable isotope Bayesian ellipses (SIBER) in the SIAR package (Parnell et al. 2008) in R 3.1.1. Five metrics proposed by Layman et al. (2007) were calculated; nitrogen range (NR), which provides information on the trophic length of the species, carbon range (CR) which provides an estimate of the diversity of basal resources, mean nearest neighbour distance (MNND) which is a measure of diversity and clustering of the species within isotopic space, and the standard deviation of the nearest neighbour (SDNND) which provides a measure of evenness of spatial density and packing.

A standard ellipse area (SEA) approach to calculating isotopic niche space was chosen over the Layman's convex hull area, as a standard ellipse contains 40 % of the data regardless of the sample size, whilst the convex hull is highly sensitive to sample size, with its value increasing with sample size. Additionally, a small sample size correction to the SEA provides a highly satisfactory estimate for all sample sizes (Jackson et al. 2011). SIBER was used to estimate the degree of overlap between standard ellipse areas between species, and sites, and Bayesian inference was used to calculate the probability of a significant difference in standard ellipse area size between species and sites.

6.4 Results

6.4.1 Potential prey items

Potential prey item δ13C ranged from -27.44 ‰ for tsamma melon to -13.03 ‰ for cow, whilst δ15N ranged from 4.41 ‰ for the gerbil species *Gerbillurus vallinus* to 13.65 ‰ for slender mongoose (Table 6.1). Potential prey item isotopic signatures in relation to those of carnivores are presented in the bi-plot below (Fig 6.2). Potential prey item isotopic signatures were adjusted according to the fractionation values presented by Roth and Hobson (2000) for red fox *Vulpes vulpes* fur; 2.6 ‰ for carbon and 3.3 ‰ for nitrogen. The plot shows all carnivore isotopic signatures fell well within the range of potential prey item tissue sample signatures, with the exception of aardwolf and one brown hyena sample which fall below the nitrogen range of any prey items sampled.

Table 6.1: Stable carbon and nitrogen isotope data for the potential prey items sampled on Namibian commercial farmlands and used to visually inspect the diet of carnivores, i.e. these values were not able to be used in mixing models, given the low sample sizes.

Source	***n***	**Mean δ13C (‰) (±S.D.)**	**Mean δ15N(‰) (±S.D.)**
Centipede	1	-24.82	11.63
Grasshopper	1	-21.06	8.11
Giant armoured ground cricket (*Aconthoplus discoidalis)*	1	-20.39	5.15
Baboon (*Papio ursinus*)	1	-19.85	10.48
Namaqua rock mouse (*Aethomys namaquensis*)	1	-19.49	8.54
Amphibian	1	-18.94	9.53

Slender mongoose (*Galerella sanguinea*)	1	-18.6	13.65
Araneae	1	-16.5	11.4
Cow (*Bos taurus*)	4	-13.03 (0.62)	10.14 (1.04)
Oryx (*Oryx gazella*)	3	-13.48 (0.20)	11.62 (0.68)
Sheep (*Ovis aries*)	3	-15.72 (0.15)	9.29 (0.11)
Termite	5	-16.49 (0.79)	8.22 (0.13)
Scorpion	2	-16.65 (2.64)	12.43 (1.22)
Gerbil - *Desmodillus auricularis*	2	-16.74 (5.49)	10.28(1.17)
Coleoptera	4	-17.25 (3.79)	12.56 (1.3)
Ants	5	-17.92 (2.77)	12.08 (0.85)
Springbok (*Antidorcas marsupialis*)	3	-18.09 (1.14)	12.98 (0.31)
Gerbil - *Gerbillurus vallinus*	2	-22.22 (6.02)	4.41 (1.38)
Tsamma melon (*Citrullus eeirrhosus*)	2	-27.44 (0.05)	8.03 (0.06)

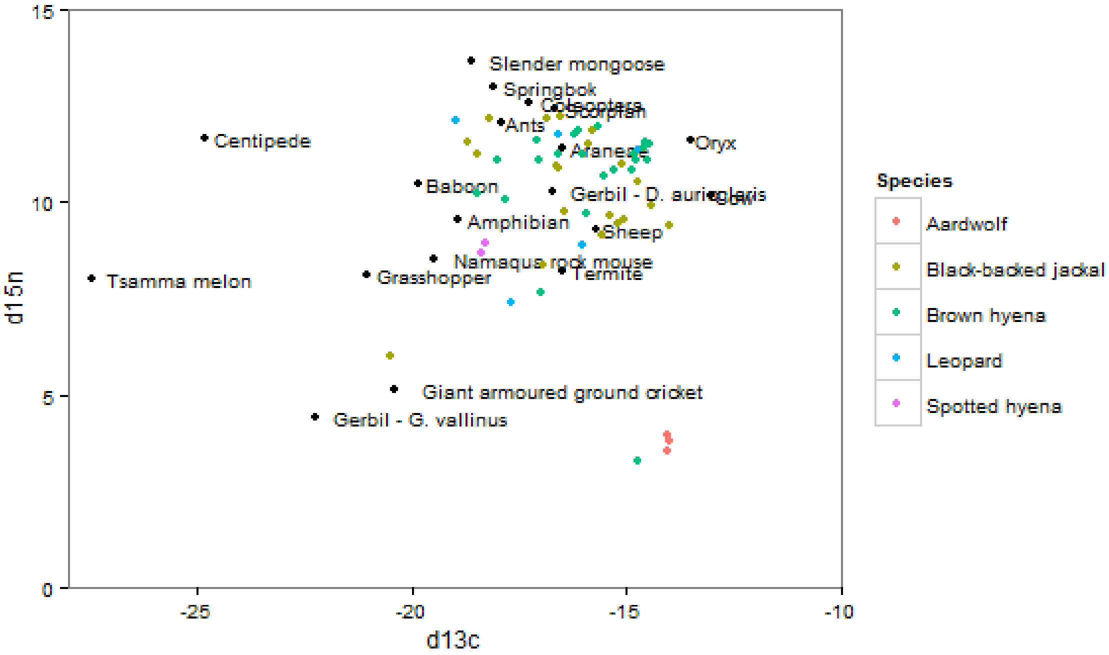


Figure 6.2: δ13C- δ15N bi-plot of sampled potential prey items and carnivore samples, with carnivore sample values adjusted for discrimination factors presented by Roth and Hobson (2000) for red fox hair. Carnivore carbon-nitrogen values shown by the coloured point (see

legend on the right hand side), and potential prey item carbon-nitrogen values shown as black point, with species name placed to the left of the corresponding point.

A bi-plot showing just the scavenger (brown hyena and black-backed jackal) isotopic data, adjusted for discrimination factors from Roth and Hobson (2000) for red fox hair, in comparison to springbok and oryx, the main food items in the Tsirub offal pit, signatures is given in Figure 6.3. It can be seen in comparison to scavengers from the northern sites, black-backed jackal and brown hyena from the south showing isotopic signatures closers to springbok and oryx.

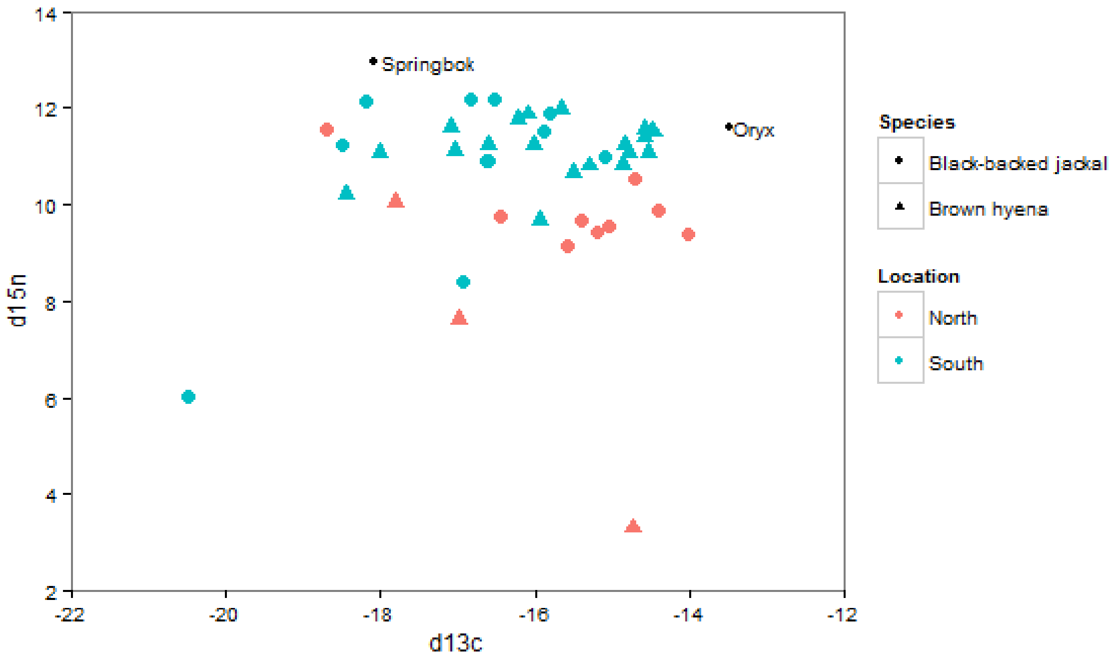


Figure 6.3: δ13C- δ15N bi-plot of mean oryx and springbok values, the main food items within the Tsirub offal pit. Brown hyena and black-backed jackal carbon-nitrogen values shown in relation to the oryx and springbok values, with carnivore sample values adjusted for discrimination factors presented by Roth and Hobson (2000) for red fox hair. Brown hyena and black-backed jackal carbon-nitrogen values are shown for both the northern and southern study sites, as referenced in the legend to the right hand side of the plot.

6.4.2 Carnivores

Due to small sample sizes of aardwolf (*n* = 3), spotted hyena (*n* = 2) and leopard (*n* = 5), statistical analysis could not be conducted for these species. Mean δ13C values ranged from -15.74 ‰ for spotted hyena to -11.42 ‰ for aardwolf (Table 6.2). Mean δ15n values ranges from 7.08 ‰ for aardwolf to 13.89 ‰ for brown hyena (Table 6.2), showing aardwolf occupied the lowest trophic position, as demonstrated by the lowest mean δ15N, whilst brown hyena occupied the highest position. Black-backed jackal, leopard and brown hyena had a wide range of basal resources in their diet, as demonstrated by the range of δ13C values for these species. Aardwolf and spotted hyena showed a much narrower carbon width, however this may simply be a reflection of the small sample sizes. A δ13C- δ15N bi-plot of data for all species is shown in Figure 6.4.

Table 6.2: Mean values of δ13C and δ15N for all sampled carnivore species on commercial farmlands derived from hair samples. The number of samples the mean values are taken from is given.

Species	***n***	**Mean δ13C (‰) (±S.D.)**	**Mean δ15N (‰) (±S.D.)**
Aardwolf	3	-11.42 (0.04)	7.08 (0.21)
Black-backed jackal	20	-13.75 (1.62)	13.67 (1.53)
Brown hyena	22	-13.31 (1.23)	13.89 (1.88)
Leopard	5	-14.02 (1.61)	13.61 (2.06)
Spotted hyena	2	-15.74 (0.07)	12.12 (0.19)

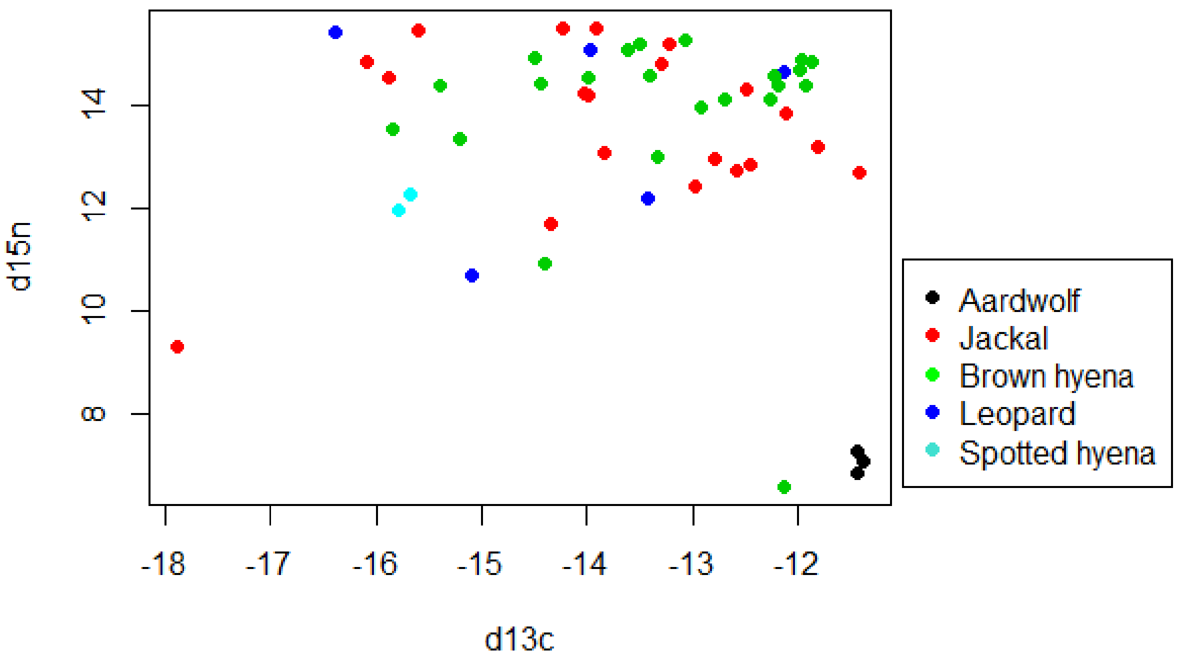


Figure 6.4: δ13C- δ15N bi-plot for sampled carnivore species, with each species represented as a different coloured point within the plot, as referenced in the legend to the right hand side of the plot.

6.4.2.1 δ13C

A Mann-Whitney U test showed no significant difference between brown hyena and black-backed jackal populations from all sites ($W = 191$, $P = 0.48$). As aardwolf, leopard and spotted hyena samples sizes were too small for statistical analysis, a visual representation of the data in comparison to all other species is shown below (Fig. 6.5).

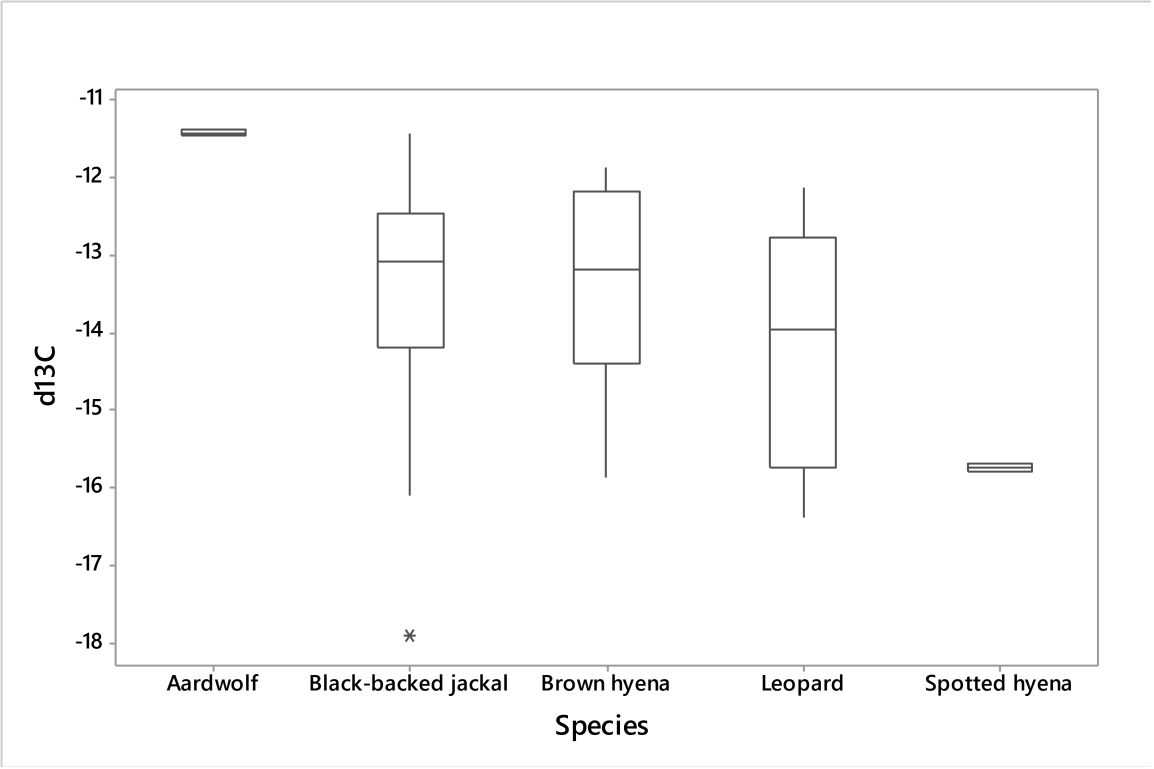


Figure 6.5: Visual representation of δ13C (‰) (minimum, quartiles, median, maximum) for each sampled carnivore species; aardwolf (*n* = 3), black-backed jackal (*n* = 20), brown hyena (*n* = 22), leopard (*n* = 5) and spotted hyena (*n* = 2). Data is visually represented to allow comparison of the δ13C (‰) values, as sample sizes of aardwolf, leopard and spotted hyena were too small for statistical analysis.

Mann-Whitney U tests showed a significant difference in δ13C between the northern and the southern study sites for black-backed jackal (*W* = 83, *P* = 0.01) with the northern sites being significantly higher than the south (Fig. 6.6), indicating black-backed jackal in the south have a larger range of basal resources in their diet. No significant difference was detected for brown hyena (*W* = 21, *P* = 0.52), suggesting brown hyena from both sites use a similar range of basal resources in their diet. Only one leopard sample came from the northern sites, statistical and a visual inspection of the data showed no evidence towards there being a difference in δ13C between the two sites, additionally no evidence of a difference between the sites existed for spotted hyena, and both aardwolf samples came from the north. No significant differences in δ13C by season were shown for black-backed jackal (Mann-Whitney U: *W* = 44, *P* = 0.94), brown hyena (Mann-Whitney U: *W* = 57, *P* = 0.95), indicating their basal resources in the diet did not change significantly with season, nor was there any evidence for a difference in leopard, aardwolf or spotted hyena δ13C between seasons on a visual inspection of the data.

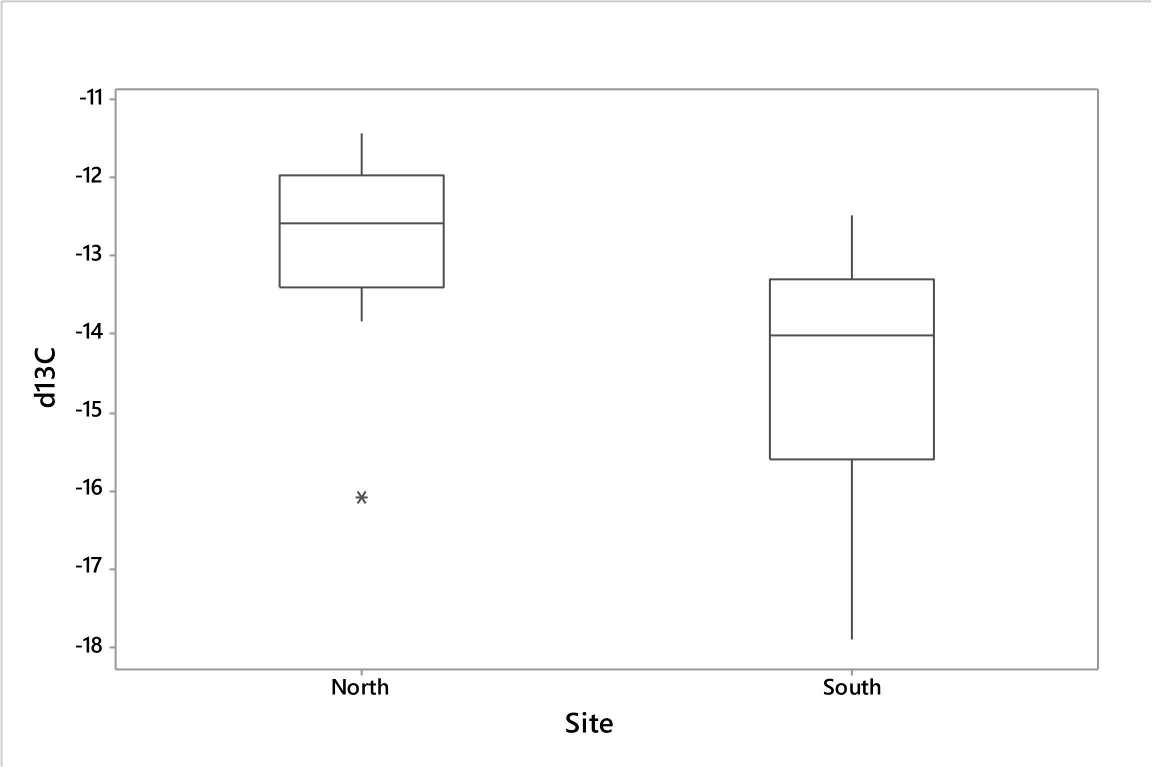


Figure 6.6: Comparison of black-backed jackal δ13C (‰) (minimum, quartiles, median, maximum) by study sites; north (*n* = 8) and south (*n* = 12), showing δ13C (‰) to be significantly higher in the northern sites (Mann-Whitney U: *W* = 83, *P* = 0.01).

6.4.2.2 δ15N

No significant difference was seen in δ15N between brown hyena and black-backed jackal samples from all sites (Mann-Whitney U: *W* = 180, *P* = 0.32). As aardwolf, leopard and spotted hyena samples sizes were too small for statistical analysis, a visual representation of the data in comparison to all other species is shown below (Fig. 6.7).

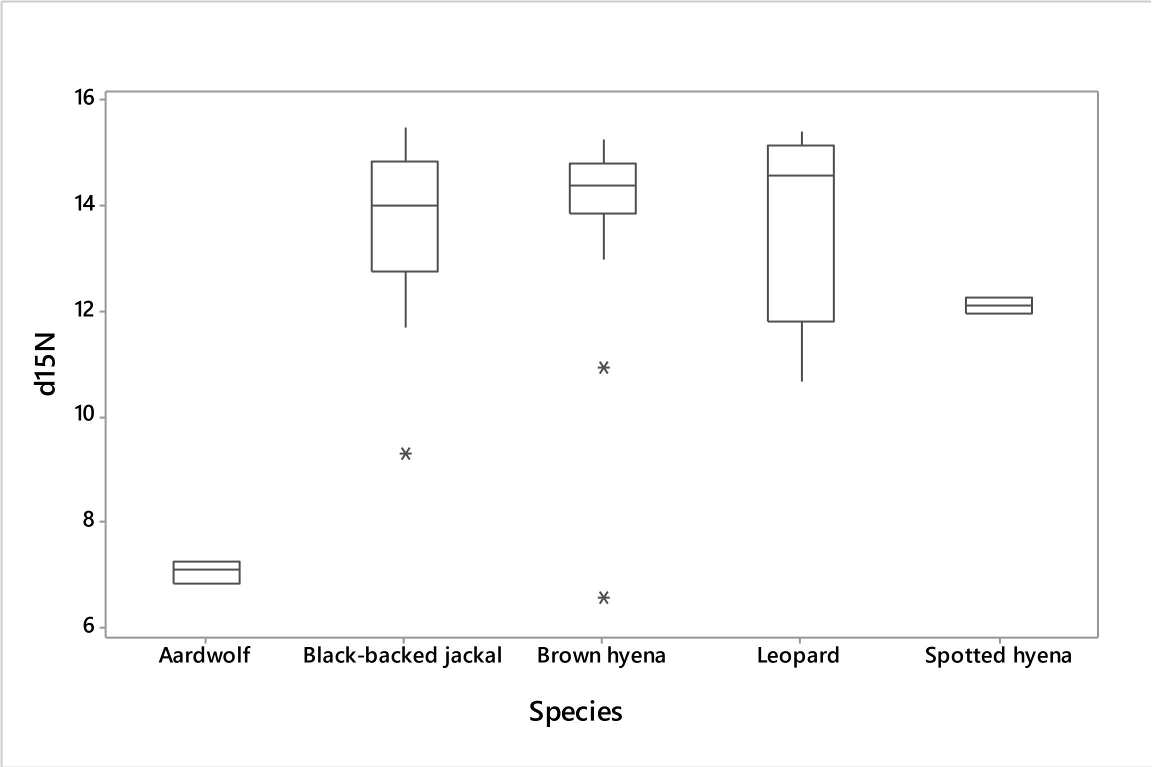


Figure 6.7: Comparison of δ15N (‰) (minimum, quartiles, median, maximum) for each sampled carnivore species; aardwolf (*n* = 3), black-backed jackal (*n* = 20), brown hyena (*n* = 22), leopard (*n* = 5) and spotted hyena (*n* = 2). Data is visually represented to allow comparison of the δ13C (‰) values, as sample sizes of aardwolf, leopard and spotted hyena were too small for statistical analysis.

A significant difference was seen in δ15N between the northern and southern study sites for brown hyena (Mann-Whitney U: *W* = 1, *P* = 0.01), as shown in Figure 6.8, with the δ15N being significantly higher in the south, indicating brown hyena in the south to occupy a higher trophic position than those in the north. No significant differences was seen between the sites for black-backed jackal, however the result was close to significance (Mann-Whitney U: *W* = 23, *P* = 0.0046), with the southern sites having higher δ15N. Only one leopard sample came from the north, and a visual inspection of the data did not suggest the δ15N value of this sample to be significantly different from the southern samples. There was no evidence to suggest a significant difference in spotted hyena δ15N values between the two sites, and both aardwolf samples came from the north. Mann-Whitney U tests showed there to be no significant differences in δ15N between the seasons for brown hyena (*W* = 59.5, *P* = 0.97), or black-backed jackal (*W* = 37, *P* = 0.54) suggesting the trophic positions on these species remains constant throughout the year. A visual inspection of the data did not show evidence to suggest a seasonal effect on δ15N for aardwolf, leopard or spotted hyena.

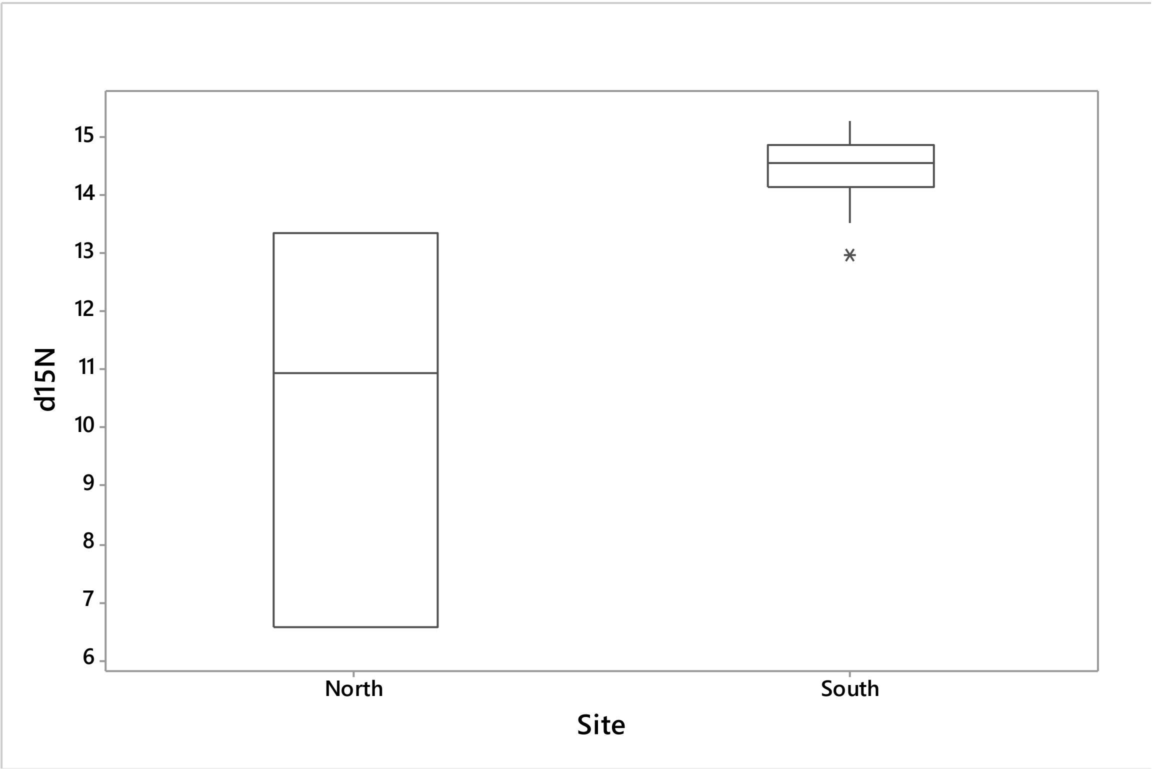


Figure 6.8: Comparison of brown hyena δ15N (‰) (minimum, quartiles, median, maximum) by site; north (*n* = 3) and south (*n* = 19). δ15N (‰) is significantly higher in the south (Mann-Whitney U: *W* = 1, *P* = 0.01).

6.4.2.3 Isotopic space

Estimation of Layman's metrics (Layman et al. 2007), as shown in Table 6.3 (below), revealed brown hyena to occupy the widest niche width (NR = 8.66), whilst black-backed jackal occupied the lowest (NR = 6.17). Black-backed jackal had the greatest diversity of basal resources in its diet, as shown by the highest CR value. Niche width, as estimates by mean distance to centroid, was highest for black-backed jackal and lowest for brown hyena. The mean nearest neighbour distance, which is a measure of spatial density and clustering was highest for black-backed jackal and lowest for brown hyena, whilst the standard deviation of this (SDNND), which estimates evenness in spatial density and packing was highest for black-backed jackal and lowest for brown hyena.

Table 6.3: Population metrics of trophic structure for the species with adequate sample sizes, black-backed jackal and brown hyena acroos all study sites. Explanations of the abbreviations used for metrics given below the table.

Species	**NR (‰)**	**CR (‰)**	**CD (‰)**	**MNND (‰)**	**SDNND (‰)**	**SEAc (‰^{2})**
Black-backed jackal	6.17	6.47	1.86	0.67	0.91	8.16
Brown hyena	8.66	4.23	1.79	0.61	0.74	7.63

NR = δ15N (‰) range, CR = δ13C (‰) range, CD = mean distance to centroid, MNND = mean nearest neighbour distance, SDNND = standard deviation of MNND, SEAc = standard ellipse area.

Standard ellipse areas were calculated using the small sample size correction and are shown in Figure 6.9 (below), the degree of niche overlap between black-backed jackal and brown hyena was estimated at 6.08 ‰^{2}, which equated to a proportion of 38.51 % of brown hyena and black-backed jackal overlap. Two clear outliers can be seen at the lower end of the δ15N scale, which are not believed to effect the ellipse size or shape given that the ellipses contain ~40 % of the data only (Jackson et al. 2011) Bayesian inference was then used to estimate the probability of the brown hyena standard ellipse area being larger than the black-backed jackal ellipse, and estimated a probability of 0.57. The result indicates black-backed jackal and brown hyena occupy similar isotopic niche spaces.

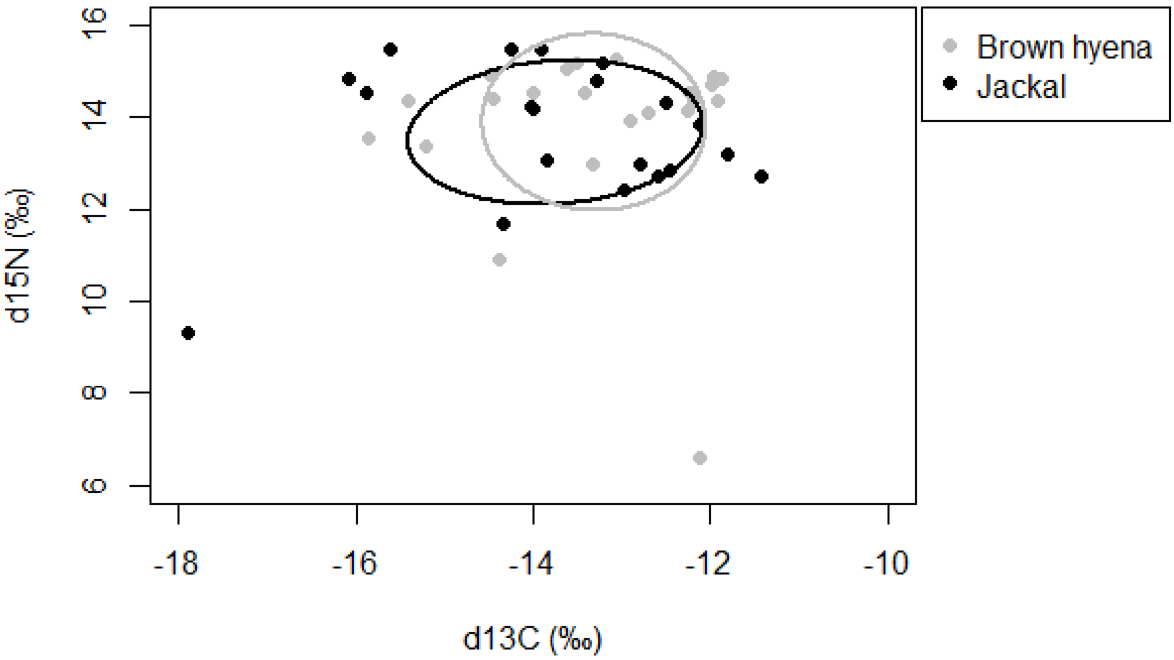


Figure 6.9: δ13C- δ15N bi-plot for black-backed jackal and brown hyena across all study farms with standard ellipses (SEAc), representing the isotopic/dietary niche space occupied by each species, shown as ovals around the data points. Species are differentiated based on the colour of the data points, as referenced by the legend to the right hand side of the plot.

6.4.2.3.1 Comparisons by site

6.4.2.3.1.1 North

In the northern sites, brown hyena nitrogen range was almost three times that of black-backed jackals (Table 6.4), suggesting individuals within the population occupy a larger range of trophic positions than black-backed jackal. However, such a result could be due to the potential outlier for brown hyena, seen as the data point with the lowest δ15N. No overlap was seen between the ellipses for the two species (Fig. 6.10), indicating different diets and Bayesian inference gave a 0.94 probability of the brown hyena standard ellipse being significantly larger than that of black-backed jackal, suggesting no difference in size of isotopic niche space occupied by the two species.

Table 6.4: Population metrics of trophic structure for brown hyena and black-backed jackal in the northern sites. Explanations of the abbreviations used for metrics given below the table.

Species	***n***	**Mean δ15N (‰) (±SD)**	**Mean δ13C (‰) (±SD)**	**NR (‰)**	**CR (‰)**	**CD (‰)**	**MNND (‰)**	**SDNND (‰)**	**SEAc (‰^{2})**
Brown hyena	3	10.29 (3.42)	-14.09 (1.70)	6.76	3.08	2.74	3.34	1.34	3.62
Black-backed jackal	8	13.18 (0.74)	-12.90 (1.39)	2.4	4.6	1.1	0.78	0.83	2.6

NR = δ15N (‰) range, CR = δ13C (‰) range, CD = mean distance to centroid, MNND = mean nearest neighbour distance, SDNND = standard deviation of MNND, SEAc = standard ellipse area

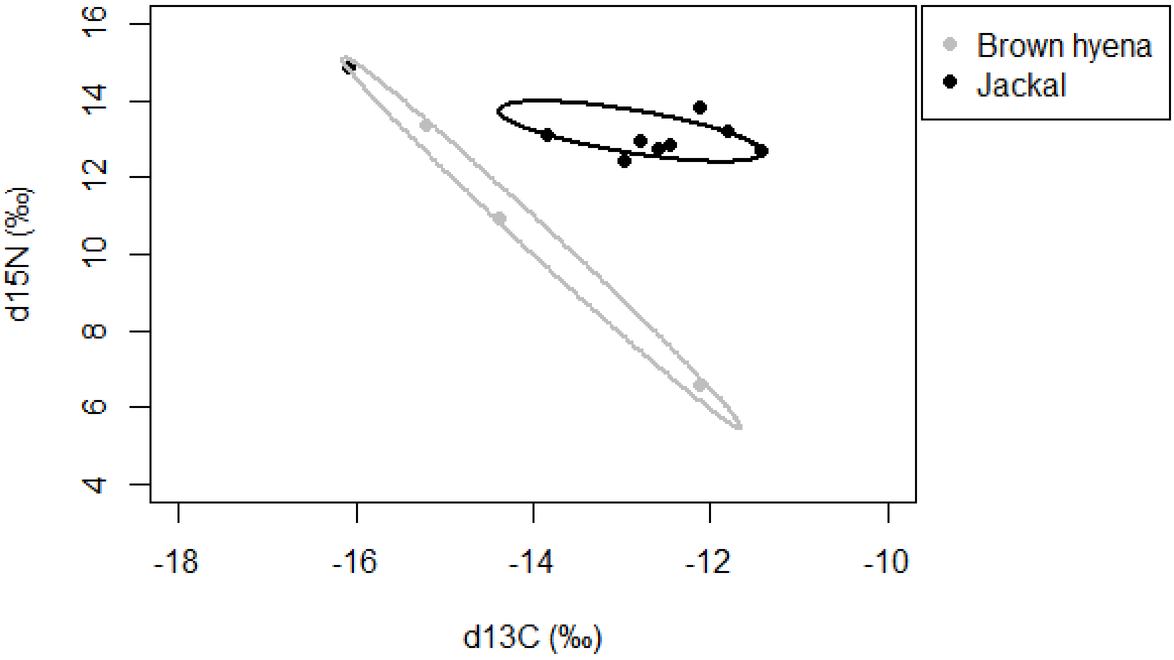


Figure 6.10: δ13C- δ15N bi-plot for black-backed jackal and brown hyena from the northern sites with standard ellipses (SEAc), representing the isotopic niche/dietary space occupied by each species, shown by ovals. Species are differentiated by the data point colour, as referenced in the legend to the right hand side of the plot.

6.4.2.3.1.2 South

Black-backed jackal from the southern sites showed a nitrogen range over twice as large as brown hyena (Table 6.5), suggesting individuals within the population to occupy a large range of trophic positions than brown hyena. The standard ellipse area of black-backed jackal was estimated to have a 0.99 probability of being larger than that of brown hyena, indicating black-backed jackal diet occupies a significantly larger isotopic niche space than brown hyena, and is more of a generalist consumer than brown hyena in the south. The two ellipses overlapped by a total of 1.29 ‰^{2}, which is 12.84 % overlap (Fig. 6.11).

Table 6.5: Population metrics of trophic structure for brown hyena and black-backed jackal in the northern sites. Explanations of abbreviations used for population metrics given beneath the table.

Species	***N***	**Mean δ15N (‰) (±SD)**	**Mean δ13C (‰) (±SD)**	**NR (‰)**	**CR (‰)**	**CD (‰)**	**MNND (‰)**	**SDNND (‰)**	**SEAc (‰^{2})**
Brown hyena	19	14.46 (0.56)	-13.22 (1.19)	2.28	3.99	1.15	0.4	0.3	2.18
Black-backed jackal	12	14.06 (1.90)	-14.44 (1.51)	6.17	5.4	1.86	1.02	1.29	7.86

NR = δ15N (‰) range, CR = δ1C (‰) range, CD = mean distance to centroid, MNND = mean nearest neighbour distance, SDNND = standard deviation of MNND, SEAc = standard ellipse area

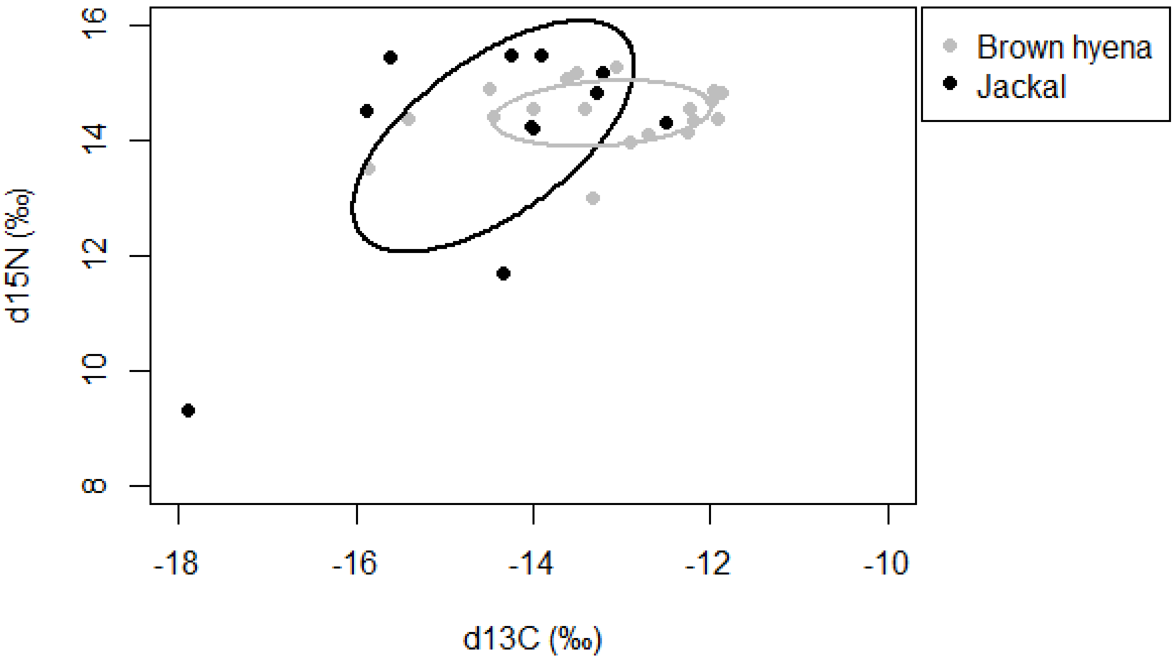


Figure 6.11: δ13C- δ15N bi-plot for black-backed jackal and brown hyena from the southern sites with standard ellipses (SEAc), representing the isotopic/dietary niche space, shown by ovals. The two species are differentiated by the colour of the data point, as referenced in the legend to the right hand side of the plot.

6.4.2.3.2 Within species comparisons

6.4.2.3.2.1 Brown hyena

Brown hyena hair samples from the north showed a nitrogen range of nearly three times that of brown hyena hair samples from the southern sites (Table 6.6), with a lower mean δ15N value. Brown hyena from the north showed a larger standard ellipse area, although Bayesian inference suggested estimated a probability of 0.63, that this ellipse was bigger. There was no overlap between standard area ellipses of the northern and southern samples (Fig. 6.12).

Table 6.6: Population metrics of trophic structure for brown hyena at the northern and southern study sites. Explanations of abbreviations used for metrics given below the table.

Site	*n*	Mean δ15N (‰) (±SD)	Mean δ13C (‰) (±SD)	NR (‰)	CR (‰)	CD (‰)	MNND (‰)	SDNND (‰)	SEAc (‰)
North	3	10.29 (3.42)	-14.09 (1.70)	6.76	3.08	2.74	3.34	1.34	3.62
South	19	14.46 (0.56)	-13.22 (1.19)	2.28	3.99	1.15	0.4	0.3	2.18

NR = δ15N (‰) range, CR = δ13C (‰) range, CD = mean distance to centroid, MNND = mean nearest neighbour distance, SDNND = standard deviation of MNND, SEAc = standard ellipse area

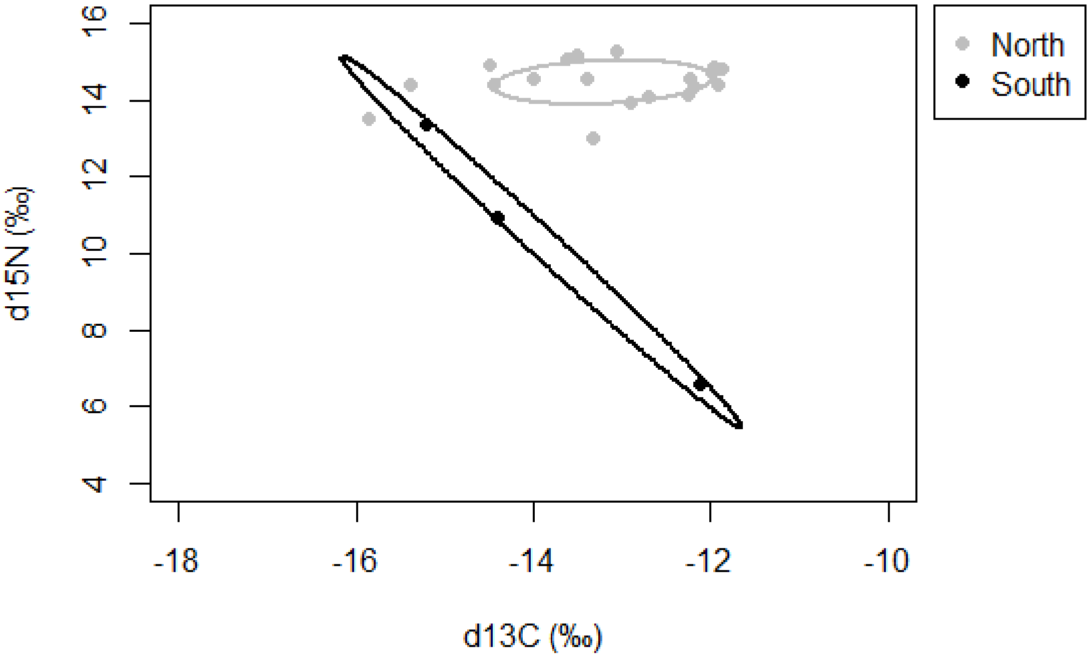


Figure 6.12: δ13C- δ15N bi-plot for brown hyena from the northern and southern study sites with standard ellipses (SEAc) representing the isotopic/dietary niche space occupied by each species, shown by the ovals surrounding the data points. The two species are differentiated by the colour of data points, as referenced in the legend to the right hand side of the plot.

6.4.2.3.2.2 Black-backed jackal

A comparison of population metrics for black-backed jackal between the northern and southern sites showed the δ15N range from the south was over twice as large as the north (Table 6.7). The standard ellipse area of the southern data was nearly three times larger than the northern standard area ellipses, with Bayesian inference estimating a 0.97 probability that southern SEA was significantly larger than the north SEAc, indicating black-backed jackals in the south were more generalist consumers than those in the north. The two ellipses overlapped by 0.59 ‰^{2}, which is 5.62 % of the two standard ellipse areas (Fig. 6.13).

Table 6.7: Population metrics of trophic structure for black-backed jackal for the northern and southern sites. Explanations of the abbreviations used for each metric given below the table.

Site	***n***	**Mean δ15N (‰) (±SD)**	**Mean δ13C (‰) (±SD)**	**NR (‰)**	**CR (‰)**	**CD (‰)**	**MNND (‰)**	**SDNND (‰)**	**SEAc (‰^{2})**
North	8	13.18 (0.74)	-12.90 (1.39)	2.41	4.6	1.14	0.78	0.83	2.64
South	12	14.06 (1.90)	-14.44 (1.51)	6.17	5.4	1.86	1.02	1.29	7.86

NR = δ15N (‰) range, CR = δ13C (‰) range, CD = mean distance to centroid, MNND = mean nearest neighbour distance, SDNND = standard deviation of MNND, SEAc = standard ellipse area

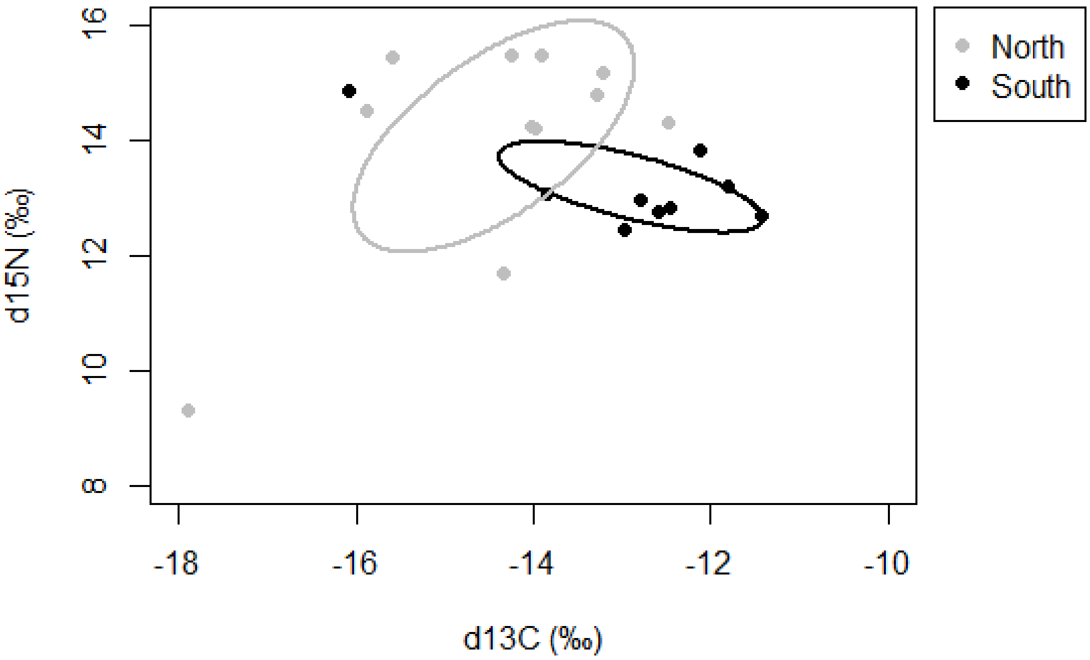


Figure 6.13: δ13C- δ15N bi-plot for black-backed jackal for the northern and southern sites with standard ellipses (SEAc), representing the isotopic/dietary niche space occupied by each sub-group, shown by the ovals surrounding the data points. The north and south sub-groups are differentiated by the colour of the data point, as referenced in the legend to the right hand side of the plot.

6.4.3 Offal pit monitoring

A total of four carnivore species were recorded at the Tsirub offal pit; brown hyena, black-backed jackal, Cape fox and African wild cat. Black-backed jackal were the most frequently recorded species, having a mean RAI of 434.78 events per 100 trap nights. Brown hyena were the second most frequently recorded species, with a mean RAI of 108.70 events per 100 trap nights. Examination of front leg stripe pattern showed a total of four individual animals visiting the pit, with the same individual visiting the site one than once a night on several occasion. Relative abundance indices from camera trap are in contrast to the numbers of black-backed jackal and brown hyena hair samples gained from the hair snare set up there, where brown hyena was the more frequently detected species. Cape fox had a mean RAI of 12.34 events per 100 trap nights whilst African wild cat was only detected once. At NBR offal pit black-backed jackal was the only carnivore to be detected, and was only detected once in 69 trap nights.

6.4.4 Carcass monitoring

Five carnivore species were recorded at carcass one over 67 trap nights; Cape fox, bat-eared fox, black-backed jackal, aardwolf and spotted hyena. Spotted hyena was the most frequently detected species, followed by black-backed jackal (Table 6.8). Bat-eared fox was recorded nine times giving a mean RAI of 13.44 events/100 trap nights, whilst aardwolf was only detected once. The second carcass was monitored over 34 trap nights, in which four species were detected; Cape fox, black-backed jackal, aardwolf and spotted hyena. Black-backed jackal was the most frequently detected species, followed by spotted hyena , whilst Cape fox was only detected twice, whilst aardwolf was detected once (Table 6.8). More detail regarding carnivore attendance at the carcasses, including timings of species visits can be found as a Roan journal article in Appendix three.

Table 6.8: Relative abundance indices of carnivore species detected at two cattle carcasses, where cause of death was not believed to be due to carnivores, on NBR.

	Carcass 1	**Carcass 2**
Species	**Relative abundance**	
Cape fox	37.31	2.94
Bat-eared fox	13.44	NA
Black-backed jackal	176	272.27
Aardwolf	1.49	2.94
Spotted hyena	476.21	108.7

6.5 Discussion

Stable isotope analysis of diet has several advantages over the more traditional methods such as scat analysis and direct observation, and as a result is becoming an increasingly used tool in ecology. This study represents the first stable isotope approach to examining diet of carnivores occurring on commercial farmlands in southern Namibia. Previous studies of carnivore diet in sub-Saharan Africa have been limited to a study on numerous carnivores species from Kruger National Park, South Africa (Codron et al. 2006), brown hyena in the Waterberg, South Africa (Codron et al. 2005), and a more recent study by Voigt et al. (2014) examining cheetah diet on commercial farmlands in central Namibia. Sample sizes from carnivore species other than the scavenging species black-backed jackal and brown hyena were too low to allow reliable examination of diet, and therefore the original aim of investigating the relative contribution of domestic livestock to the diet of carnivores could not be met. However, the presence of an offal pit in the south allowed stable isotope data to be used to examine its affect on the two scavenging species, being an accessible and reliable food source.

Carnivore δ13C values from this study showed all species were clustered around the C4 end of the carbon spectrum, suggesting they form part of the C4 food web. C4 plants are grasses and have δ13C values between -10 ‰ and -20 ‰, whilst C3 plants are usually trees and shrubs with δ13C values between -22 ‰ and -33 ‰. Therefore grazing species usually form the C4 food web, whilst the C3 web is represented by browsing species (Bender 1971). That carnivores should form part of the C4 food web was mostly expected given the study sites are largely characterised by vast open grassy plains with relatively few trees and shrubs. Codron et al. (2006) also found carnivore species to cluster at the C4 end of the spectrum in the Kruger National Park, suggesting carnivores are predominantly hunting in areas they are likely to encounter a C4 prey base, i.e. open savannah grasslands. Similarly, Codron et al. (2005) showed brown hyena scats to have a mean δ13C of -15.9 (± 2.3) ‰, in South Africa's Waterberg. Voigt et al. (2014) showed male cheetah to feed mainly on grazers, whilst females feed predominantly on browsing species, such as springbok and steenbok, which may represent easier prey to catch for female cheetahs which are smaller than males. As hair samples were collected for the most part non-invasively it is not possible to comment on differences in prey types between male and female carnivores in this study, and would warrant further investigation.

Springbok are usually categorised as browsers (Estes 1992), with Voigt et al (2014) recording the species of having a mean δ13C of -23.8 (± 1.1) ‰ in central Namibia. However, springbok samples from the study area had a mean of -18.09 (± 1.14) ‰, placing them within the C4 food web. Lehmann et al. (2013) found springbok in northern Namibia to be dietary generalists, feeding on both C3 and C4 plants, albeit with a higher proportion of C3 plants, irrespective of environmental conditions. The relative scarcity of trees within the study area may therefore explain why springbok from this study show a more C4 isotopic signature. Other browsing species from the study sites would potentially include kudu, steenbok and klipspringer (Estes 1992). As all carnivore samples showed δ13C values within the C4 range of the carbon spectrum, it is unlikely any of the carnivores were specialising in these species. However, as springbok isotopic data from the study area were not within their expected range it is possible these browsers would not be within the C4 food web either. Further research into the isotopic signatures of these browsing species within the study area would be useful for future research.

Examination of the δ15N values of carnivore samples when adjusted for fractionation, shows all carnivores to fall well within the range of δ15N values for herbivore muscle tissue samples, with the exception of aardwolf. Aardwolf δ15N values were below those of other carnivore species, suggesting they occupy a lower trophic level than other carnivores, which is expected given their specialised diet of termites (Estes 1992). However, Figure 8.1 shows aardwolf to occupy a lower trophic position than the termites sampled from the study site, with mean aardwolf δ15N of 7.08 (± 0.21) ‰, and termites 8.22 (± 0.13) ‰. Termites from a South African study by Sponheimer et al. (2005) showed highly variable δ15N values, ranging from 3.8 (± 1.2) ‰ for C3 feeding species to 4.4 (± 3.2) ‰ for C3/C4 mixed feeding species. It is possible aardwolf in the study sites were feeding on different termite species than those sampled, with those species having similar δ15N values to those recorded by Sponheimer et al. (2005).

Camera trap data from the offal pits showed the Tsirub pit was extensively used by brown hyena and black-backed jackal, with Cape fox visiting the pit on a much less frequent basis, and African wild cat being recorded once. In comparison, the offal pit at NBR was only visited on one occasion by a single black-backed jackal. Such a difference in offal pit use between the two sites may be attributed to a number of reasons. Firstly, the offal at the Tsirub pit was dumped into the pit on a much more regular basis than on NBR, and may have represented a much more reliable food source. Secondly, the contents of the offal pit at NBR also included general household waste and was regularly burnt to prevent build up of pit contents. Lastly, NBR were culling animals when needed, in comparison to Tsirub, where oryx and springbok were killed twice a week for commercial sale, which again may result in the Tsirub offal pit being a more reliable food source than NBR. Camera trap data from the Tsirub offal pit suggested both black-backed jackal and brown hyena were eating at the pit as well as taking pieces out of the pit (Fig. 6.14), presumably to take back to dens or to cache.

When examining the effects of a vulture restaurant, a supplementary feeding site, on brown hyena and black-backed jackal abundance in the local area, Yarnell et al. (2014), stated the sites led to an increase in abundance of both species. However, the study looked only at relative abundance indices before, during and after establishment of the vulture restaurant. This study has shown, for brown hyena, high relative abundance indices rather indicated higher activity at the offal pit, with a total of just four individual brown hyenas being recorded. As brown hyena presence was only detected by hair snares in the north, it is not possible to comment on the group size in comparison to that in the north. Brown hyena group size has been shown to vary with a number of factors including availability of food resources in the environment (Mills 1990), therefore whilst it is possible the presence of the offal pit could influence clan size of brown hyena in the local area, this study cannot comment on this. Furthermore, the results here suggest that the high relative abundance indices recorded by Yarnell et al. (2014), may have been related to increased activity in the area of the restaurant rather than strict increases in abundance.

Figure 6.14: Brown hyena with oryx skin in mouth at Tsirub offal pit, a location where brown hyenas were detected regularly and a total of 19 hair samples were obtained from a single hair snare

The proportions of hair samples from black-backed jackal and brown hyena from the offal pit camera trap differ to those expected from camera trap data. A total of 71.4 % of hair samples came from brown hyena, making up the majority of samples. In comparison, black-backed jackal comprised 77.99 % of all carnivore independent events from the offal pit camera trap, whilst 19.64 % were brown hyena. Additionally neither Cape fox or African wild cat, which were detected by camera trap, were not detected by the hair snare. It is possible that the hair snare was simply too high from the ground to snare hair from Cape fox and African wild cat, and some of the individual black-backed jackal passing through. The hair snare was set up along a hole underneath the main access gate to the offal pit, which seemed from a visual inspection of the perimeter of the fence enclosing the pit to be the main access point for carnivores. Camera trap data showed all individuals entering and leaving the pit via this hole. As the gate was regularly used by farm staff to enter the pit to dump offal, no modifications could be made to the height of the snare.

Extensive use of the offal pit by brown hyena and black-backed has the potential to affect diet of these scavengers so that it is different to those individuals not having regular access to such quantities of this resource. This study showed in comparison to scavengers from the northern study sites, southern scavengers had more similar diets, as shown by an overlap of 12.84 % isotopic niche space in the south, compared to zero overlap in the north. Furthermore, brown hyena from the north and south showed zero overlap in isotopic niche space, indicating very different diets between the two sites, although it should be noted only four brown hyena samples from the north were collected. Black-backed jackal from the north and the south showed just 5.67 % overlap. Both brown hyena and black-backed jackal in the south had higher mean δ15N values than their counterparts in the north, significantly so for brown hyena, suggesting scavengers in the south occupy higher trophic positions than those in the north. A visual inspection of scavenger isotopic data in comparison to springbok and oryx signatures, as shown in Figure 6.2, also shows scavengers in the south had signatures closer to springbok and oryx than scavengers from the north. Such results suggest the presence of the offal pit could be having a significant effect on the diet of scavengers within in the area, and it is hypothesised springbok and oryx from the offal pit make up a significant part of brown hyena and black-backed jackal diet in the south.

It was hypothesised both black-backed jackal and brown hyena in the south would be more specialist consumers than those in the north, due to the presence of the offal pit. However, black-backed jackal in the south occupied a significantly larger isotopic niche space than those the south, suggesting them to be more generalist consumers. Brown hyena followed the same pattern, although the standard ellipse sizes were not found to be significantly different. It is possible not all individual black-backed jackal from the south had access to the offal pit, due to territory placement in relation to the pit. Therefore samples from the south may have represented individuals from with and without offal pit access. As only two black-backed jackal samples came from the offal pit snare hair, it is not possible to compare the isotopic signature of those hair samples from the offal pit to those from elsewhere, with any confidence.

The effect of anthropogenic food sources on carnivores has been the subject of numerous studies, with most studies showing carnivores living within areas containing such resources to have smaller home range sizes than those in more natural environments

(Prange et al. 2004; Kolowski and Holekamp 2007; Rotem et al. 2011). Whilst it is beyond the scope of this study to examine the effect of the offal pit on spatial movements of brown hyena and black-backed jackal, the frequency of visits to the offal pit, higher than the frequency of visits to any water point, suggests it is a highly attractive area and has the potential to effect the spatial movements of scavengers using it.

The use of anthropogenic resources on carnivores in the context of human-wildlife conflict has been discussed previously within the literature, with some authors suggesting areas with such resources to contain higher densities of carnivores, which in turn could result in increases in human-wildlife conflict situations (Bino et al. 2010). However, it has also been suggested that a de-coupling of the predator prey relationship can occur when predators are heavily subsidised with anthropogenic resources (Rodewald et al. 2011). Therefore in the study site, the presence of a well-used, reliable food source for brown hyena and black-backed jackal may result in a reduction in predatory killings by these species, on both domestic and wild prey species. However, it should be noted inland brown hyenas are known to scavenge, rather than hunt, the vast majority of their food (Mills 1990). Further research is suggested into this possibility, although it is unlikely to be a practical conflict resolution method and the addition of an offal pit into a new area may simply attract scavengers into the locale that were not previously present.

Data from the carcass monitoring showed scavenging species such as black-backed jackal and spotted hyena made extensive use of the carcasses as hypothesised. However, the presence of aardwolf, bat-eared fox and Cape fox at the carcasses was not expected and deserves some discussion, especially given that Cape fox was also detected at the Tsirub offal pit. Given their usual diets specialising in small mammals, invertebrates and termites (Estes 1992), these species are not usually regarded as scavengers of carrion. However, Nel and Mass (2004) suggested bat-eared fox may be sometimes mistaken as livestock predators when seen consuming fly larvae at carcasses. Such an explanation may provide an answer to why these three species were seen at the carcasses. However, in the case of aardwolf, the species was only detected once at each carcass, which might suggest the species was simply passing by rather than foraging from the carcass.

Diet studies of carnivores potentially involved in human-wildlife conflict situations usually aim to document the presence of occurrence of domestic livestock in the diet. However, data from this study has shown the presence of domestic livestock in the diet of those species recorded scavenging from the cattle carcasses cannot be used as evidence of livestock predation. Ogara et al. (2010) used scat analysis of lion, leopard, wild dog and both spotted and striped hyena faeces from communal ranches in Kenya. They stated that hairs in the scats from wild and domestic ungulate species were "depredated" by spotted hyena. Such a statement is likely to be particularly damaging, given that the spotted hyena population in the study was already subject to retaliatory killings followed alleged livestock predation (Ogara et al. 2010). Similarly a recent study of black-backed jackal diet in South Africa (Humpries et al. 2015) recorded the presence of domestic livestock in scats, stating that mean occurrences of 19.7 % in winter and 16.3 % in summer suggested that domestic livestock was an important food source. However the authors did state that the exact percentage of livestock killed, rather than scavenged, cannot be determined via scat analysis.

Despite the small sample sizes involved in this study, the data collected are of interest, representing the first stable isotope analysis of carnivore diet on commercial farmlands in southern Namibia. Furthermore, the data suggest the offal pit on Tsirub having a potential effect on the diet on scavenging species from the southern sites. That both black-backed jackal and brown hyena visit the offal pit so frequently suggests it would be of further interest to investigate the effect on this food resource on the spatial movements on these species, and the potential of this food resource leading to a decoupling of the predator-prey relationship in the context of human-wildlife conflict. This study has also demonstrated that species not traditionally known to scavenge; Cape fox, bat-eared fox and aardwolf may still be present at domestic livestock carcasses. Therefore any studies finding domestic livestock in their diet should consider the possibility of them having scavenged it rather than predated it.

7.0 Assessing the human perspective of human-wildlife conflict on commercial farmlands in southern Namibia

7.1 Abstract

The successful mitigation of human-wildlife conflict situations is reliant on a thorough understanding of the human perspective of the problem. However, this is often difficult given that tolerance of problem-causing species is known to be affected by a range of factors including social group and financial impact of predation. Where previous studies have examined the human-carnivore conflict within Africa, few patterns within the data exist, making generalised mitigation solutions difficult. This study used a questionnaire approach to examine the human perspective of conflict on commercial farmlands up to 150 km east of the Namib-Naukluft and Sperrgebiet National Parks borders in southern Namibia. The questionnaire covered a range of topics detailing physical farm characteristics, perceived risk scores of carnivore species present, livestock management techniques and problems pertaining to water pipe damage and baboons. Results showed few associations to exist within the data; only water point density and livestock density were associated with carnivore risk scores, and not for all species. The percentage of the farm covered by mountain was positively associated with livestock losses. Such results show the complexities of human-wildlife conflict, and make recommendations regarding the mitigation of such conflict difficult. Results suggested within southern Namibia water pipe damage by a number of wildlife species to be common, as were problems caused by baboons. This suggests further research into such problems would be warranted, and that these problems are included in future studies of human-wildlife conflict within southern Africa.

7.2 Introduction

By its very nature, human-wildlife conflict involves, and is largely driven by, humans (Teel et al. 2010; Kansky and Knight 2014). Therefore, addressing and understanding the human perspective of, or attitudes towards, a conflict situation is an essential component of any effective mitigation strategy (Ogra 2009; Teel et al. 2010; McLennan and Hill 2012; Kansky and Knight 2014; Thorn et al. 2015). Any attempts to improve the conservation status of any conflict causing species should be based on a thorough understanding of conflict patterns (Dar et al. 2009). This, however may be difficult given the complexities of human attitudes towards wildlife, which may vary significantly to the same situation (Dickman 2010). Attitudes towards problem causing species have been shown to vary according to a number factors such as financial impacts of conflict, or from misconceptions and prejudices (Lindsey et al. 2013). Social factors have also been shown to affect tolerance levels, for example Selebatso et al. (2008) found that the tribe to which the farmer belonged had a significant effect on perception towards cheetah conservation in Botswana, whilst Ogra (2009) found responses to carnivore conflict resolution differed between gender, literacy level and relative wealth in Uttarakhand, India.

A number of studies have aimed to gain an understanding of the human perspective of conflict situations across the globe. For example, Soto-Shoende and Main (2013) assessed differences in stakeholder perceptions of, and problems with, jaguar *Panthera onca* and puma *Puma concolor*, two species frequently perceived to cause conflict in Guatemala. Similarly Inskip et al. (2014) used interviews to gather data on the motivations for human killings of tiger *Panthera tigris* in Bangladesh. Some studies focusing on conflict have used questionnaires to quantify the numbers and value of livestock taken by carnivores, for example Gusset et al. (2009) recorded 958 predation events across 77 cattle posts and farms in northern Botswana. Furthermore, Lindsey et al. (2013) issued a questionnaire to farmers throughout Namibia and estimated the average financial cost of leopard predation on Namibian commercial farms at US$ 2,644 per farm.

Within Africa, a relatively small number of studies have aimed to examine the human perspective of human-wildlife conflict, and as such information is still relatively scarce (Thorn et al. 2015), with few patterns existing between or within the published studies. For example Hermann et al. (2001) found conflict with carnivores around the borders of the Kgalagadi Transfrontier Park was diverse, resulting in varying attitudes of livestock farmers towards carnivores from Namibia, South Africa and Botswana. Within Namibia, both Lindsey et al. (2013) and Schumann et al. (2008) found members of conservancies were more likely to be tolerant towards large carnivores. However, Marker et al. (2003b) found game farmers to be more likely to perceive cheetah as a problem, whereas in contrast Lindsey et al. (2013) recorded carnivores to be more likely to be tolerated where income from wildlife was higher and income from domestic livestock was lower.

Evidence has suggested that social factors, rather than actual losses of livestock, can be the most important drivers of human-wildlife conflict (Dickman 2010). Most studies of conflict assume wildlife damage is accurately assessed and the treatment of problem-causing species is directly linked to reported conflict levels (Dickman 2010). It is, therefore often assumed that a reduction in levels of livestock losses will result in a reduction in the number of lethal removals of carnivores. However, Marker et al. (2003b) found that 60 % of Namibian farmers who were experiencing no problems with cheetahs, to still lethally remove them, whilst Thorn et al. (2012) recorded 16 % of interviewees reporting carnivore conflict in South Africa had no evidence of livestock loss being caused by carnivores. Rasmussen (1999) suggested livestock losses in Zimbabwe were blamed on wild dogs as a plausible excuse for cattle theft by the herdsmen employed to protect them. Such situations add to the complexity of gaining a thorough understanding of conflict situations and in identifying effective mitigation methods which will both reduce the level of livestock losses and the number of carnivores being killed in a particular conflict situation.

Questionnaires are often used in ecology when information is needed from human populations, or when there is a need to quantify human opinion, and are becoming an increasingly used approach (Li et al. 2010; White et al. 2012). White et al. (2012) found the number of papers using questionnaires in journals with an impact factor of 0.3 or more, increased fivefold from 1991 to 2003. A number of studies examining wildlife populations and conservation management have used questionnaires previously for a variety of purposes from gaining simple presence-absence data about specific species to quantifying complex human attitudes regarding conflict or reintroductions. Questionnaires used to assess the status of specific species have included mountain hares *Lepus timidus* in Scotland (Patton et al. 2010), polecats *Mustela putorius* in Luxembourg (Baghi and Verhagen 2003) and mountain lions *Puma concolor* in Oklahoma (Pike et al. 1999). A study by Larivière (2000) even used results of hunter questionnaires to estimate wolf *Canus lupus* densities in wildlife reserves in Québec, Canada. Other studies have used questionnaires to assess local people's attitudes and awareness of species, for example Ghimire et al. (2014) conducted structured questionnaire interviews with local inhabitants of the lowlands of Nepal on yellow monitor *Varanus flavescens*.

This chapter aims to use a questionnaire approach to examine the human perspective of the human-wildlife conflict situation in southern Namibia. The specific objectives for this chapter are, to use a questionnaire to collect data regarding various physical aspects of each respondents farm, as well as data regarding the livestock management and current conflict mitigation methods used by each respondent. Secondly, for each respondent to gain a perceived risk score for each focal carnivore species, incorporating a measure of perceived risk towards each livestock type on the farm, and the farmers attitude towards the carnivore, i.e. if they tolerate the species, or should shoot on site. To then produce a list of significant associations between those variables described in the first objective and carnivore risk scores. To also calculate the number of respondents experiencing conflict with baboons, a problem noted by study farm owners, and to produce a list of the problems caused by baboons. Finally, to produce an inventory of those species identified by respondents as causing water pipe damage, a problem also noted by study farm owners.

Given the complex nature of conflict, found in previous studies, and the variety of respondents, there will be no significant associations between farm physical characteristics or management practices and the perceived risk scores of carnivores. It is hypothesised baboon conflict will be a common problem across respondents, affecting the majority of respondents who have baboons present on their property. Finally, it is hypothesised that water pipe damage will be mainly caused by porcupine, a species known to cause damage with their teeth

7.3 Methods

Data were obtained using a questionnaire that was initially conducted with farmers face to face, however due to problems regarding farmers being available for such appointments, the same questionnaire was then sent in the post (Appendix four) to 72 farmers living up to 150 km east of the Sperrgebiet or Namib-Naukluft National Park borders in the Luderitz and Helmeringhausen districts from January 2014 to March 2015, along with a self addressed envelope to try and encourage replies. Additionally, questionnaires were emailed to all Helmeringhausen Farmers Association members and handed out at the Helmeringhausen Farmers Association meeting in March 2015. The questionnaire focused on human-wildlife conflict and farmer attitudes towards all carnivore species potentially present on farms, as well as any conflict experienced due to water pipe damage and from baboons. The questionnaire consisted of twenty questions broken into eight sections covering physical farm characteristics such as size, habitat, as well as water point, livestock and game numbers, carnivore presence and abundance, problems with carnivores, other causes of livestock loss, problems with water pipe damage, livestock management, problems with baboons and the importance of carnivore conservation.

7.3.1 Data collected through the questionnaire

7.3.1.1 General farm characteristics

The first section of the questionnaire was concerned with the physical characteristics of the farm, focusing on size, main agricultural activity (i.e. smallstock, cattle etc), habitat, water point density and domestic livestock and game densities. Definitions of each characteristic addressed are detailed in Table 7.1.

Table 7.1: Physical characteristics of the farm, which farmers were asked about within section one of the questionnaire, it was believed these characteristics had the potential to affect human-wildlife conflict

Characteristic	**Definition**	**Unit**
Size	Total size of the farm	km^2
Type	Cattle, smallstock (sheep and goats), mixed cattle and smallstock and game, where no domestic livestock were present	NA
Mountain	% of the total farm consisting of mountainous habitat	%
Water points	Density of artificial water points on the farm	#/100 km^2
Cattle	Stocking density of cattle	#/100 km^2
Smallstock	Total stocking density of sheep and goats combined	#/100 km^2
Total livestock	Total stocking density of smallstock and cattle combined	#/100 km^2
Large game	Total density of large game species, defined as oryx, springbok, kudu and mountain zebra, as estimated by farmer	#/100 km^2
Small game	Total density of small game species, defined as steenbok and klipspringer, as estimated by farmer	#/100 km^2

7.3.1.2 Carnivore presence

The second section of the questionnaire focused on the presence, abundance and population status of 11 carnivore species potentially occurring in the area; Cape fox, bat-eared fox, black-backed jackal, honey badger, aardwolf, spotted hyena, brown hyena, leopard, cheetah, caracal and African wild cat. Respondents were asked if each species were present, and if so how many were present on the farm, and if the population status of each species present had been increasing, decreasing or had remained stable in the last 12 months.

7.3.1.3 Problems with carnivores

The third section asked farmers to detail problems with each of the focal species (black-backed jackal, spotted and brown hyena, leopard, cheetah and caracal), including type and number of livestock killed, time of the year, location on the farm and their response to the problem. A second question asked farmers to detail any problem with the five remaining, smaller non-focal carnivore species. Respondents were asked to state which species they perceived to be no, high, medium and low risks to each livestock type on the farm, and their attitude towards the carnivore; tolerate, tolerate until causes a problem and shoot on sight.

7.3.1.4 Other causes of livestock loss

This section asked respondents to show in a table which other causes of livestock, out of a list of seven possible options (Table 7.2), they had experienced previously and which type of livestock they had lost.

Table 7.2: Possible causes of livestock loss and definitions, farmers were asked within the questionnaire which type of livestock losses they had experienced

Cause	Definition
Stock theft	Livestock stolen by humans
Poisonous plants	Death from ingestion of poisonous plants present on the farm
Disease	Death of livestock following contraction of a disease
Domestic dogs	Livestock killed by domestic dogs
Veld injuries	Injuries sustained whilst livestock grazing in the field (*veld*) such as broken legs
Birthing problems	Mother dying during labour

7.3.1.5 Livestock management

This section asked which, if any, non-lethal mitigation methods (i.e. methods which did not involve lethal removal of the carnivore) were used to try and protect livestock from predation by carnivores, how often they checked livestock and lastly what percentage of their livestock they would find acceptable to lose to carnivores annually. Table 7.3 details definitions of the data obtained from this section. It should be noted, despite Potgieter et al. (2014) recently challenged the status Anatolian livestock guarding dogs as non-lethal, they are classed here as non-lethal within the questionnaire.

Table 7.3: Definitions of variables focusing on livestock management and loss, farmers were asked about these variables within the questionnaire as it is possible they could influence perceptions of conflict

Variable	Definition
Mitigation	Number of non-lethal mitigation methods practiced to reduce conflict
Acceptable loss	The total % of livestock the respondent would find acceptable to lose to carnivores annually
Actual loss	The total % of livestock the respondent loses to carnivores annually
No. of checks	The average number of days between checks on livestock

7.3.1.6 Water pipe damage

Personal communication with study farm owners suggested damage to the plastic water piping used to connect the water supply from boreholes to artificial water points around the farm could be a problem in the area. Therefore a section of the questionnaire regarding this particular type of conflict was added. In this section respondents were asked if they experienced damage to water pipes, which species were responsible and the mitigation methods used to prevent such damage, if any.

7.3.1.7 Problems with baboons

The seventh section of the questionnaire asked respondents to detail any problems with baboons they experienced. Respondents were provided with a comments box to detail any problems. Baboons are not considered a typical carnivore, yet discussions with study farm owners suggested they are a potential cause of human-wildlife conflict for farmers in the area and thus were included in the questionnaire.

7.3.1.8 Importance of carnivore conservation

The last section of the questionnaire asked respondents to rank on a scale of one to five, how important carnivore conservation was to them. Here, ‘one’ indicated not important at all with ’five ’ being the most important.

7.3.2. Statistical analysis

All statistics were conducted using R 3.1.1 (R Development Core Team, 2014), with specific analyses detailed below.

7.3.2.1 Carnivore presence

Fisher's exact tests, which are specifically recommended as a more robust alternative to chi-square tests when expected values are less than five (Zar 1999), were used to test if focal carnivore presence was significantly associated with the presence of other focal carnivore species and farm type.

7.3.2.2 Risk scores

Risk scores for each focal species were calculated for each farm and consisted of two parts; the first, a proportion, representing the perceived risk presented by that carnivore species to each livestock type. Farmers were asked to score each carnivore species as either no, low, medium or high risk to each livestock type (smallstock, cattle or game), which were equated to zero, one, two and three points respectively. If a farmer had both smallstock and cattle for example, and scored leopard as high risk for smallstock and low risk for cattle, there would be a score of four out of a possible six points, giving a proportion of 0.67. A farmer having just one livestock type would be scored out of a possible three points. The second part of the risk score reflected attitude towards each particular carnivore species. Three options were possible; tolerate; which scored one point, tolerate until causing problem; scoring two points, and shoot on sight; which scored three points. The attitude score was added to the perceived risk score and therefore the total risk score was out of a potential four points in total. Therefore high combined risk scores would represent species viewed as higher risk and more likely to be lethally removed from the farm.

Risk scores were calculated each for focal species present for each farm as well as a combined tolerance score for all focal carnivores present for each farm. Combined risk scores were proportions, calculated by summing all individual carnivore risk scores and dividing them by the number of focal carnivore species present, to account for farms where not all focal species were present. For example a farm having three focal carnivore species would have had the individual species tolerance scores summed and divided by three.

A Kruskal-Wallis test was used to test for significant differences in tolerance scores between each focal carnivore species, and Fisher's exact tests were used to test if tolerance was significantly associated with farm type, by categorising tolerance into three categories, low = 1 - 1.99, medium = 2 - 2.99, and high 3 - 4. Individual species and combined tolerance scores were then tested for associations with each physical farm characteristic, as well as each livestock management variables and importance of conservation, using Mann-Whitney U tests in R. As the data was non-parametric and often had ties, the Kendall tau-b correlation test was used as this is the non-parametric correlation tests recommended for dealing with ties (Zar 1999). Kendall tau-b was also used to test for a significant association between attitude and risk scores.

7.3.2.3 Livestock management

Kendall tau-b correlations were also used to test for significant correlations between the livestock management variables themselves, farm characteristics and importance of conservation.

7.4 Results

A total of 24 responses were collected; 14 replies from postal questionnaires, six from face to face interviews and four from the Helmeringhausen Farmer's Association meeting. Postal questionnaires returned a response rate of 22.58 %. The 24 responses totalled 33 farms in the area covering a total area of 4,881.40 km^2, and consisted of 18 mixed cattle and smallstock farms from 15 farmers, 11 pure cattle farms from 6 owners, 3 game farms from two owners and one pure smallstock farm. Figure 7.1 gives a map of respondents.

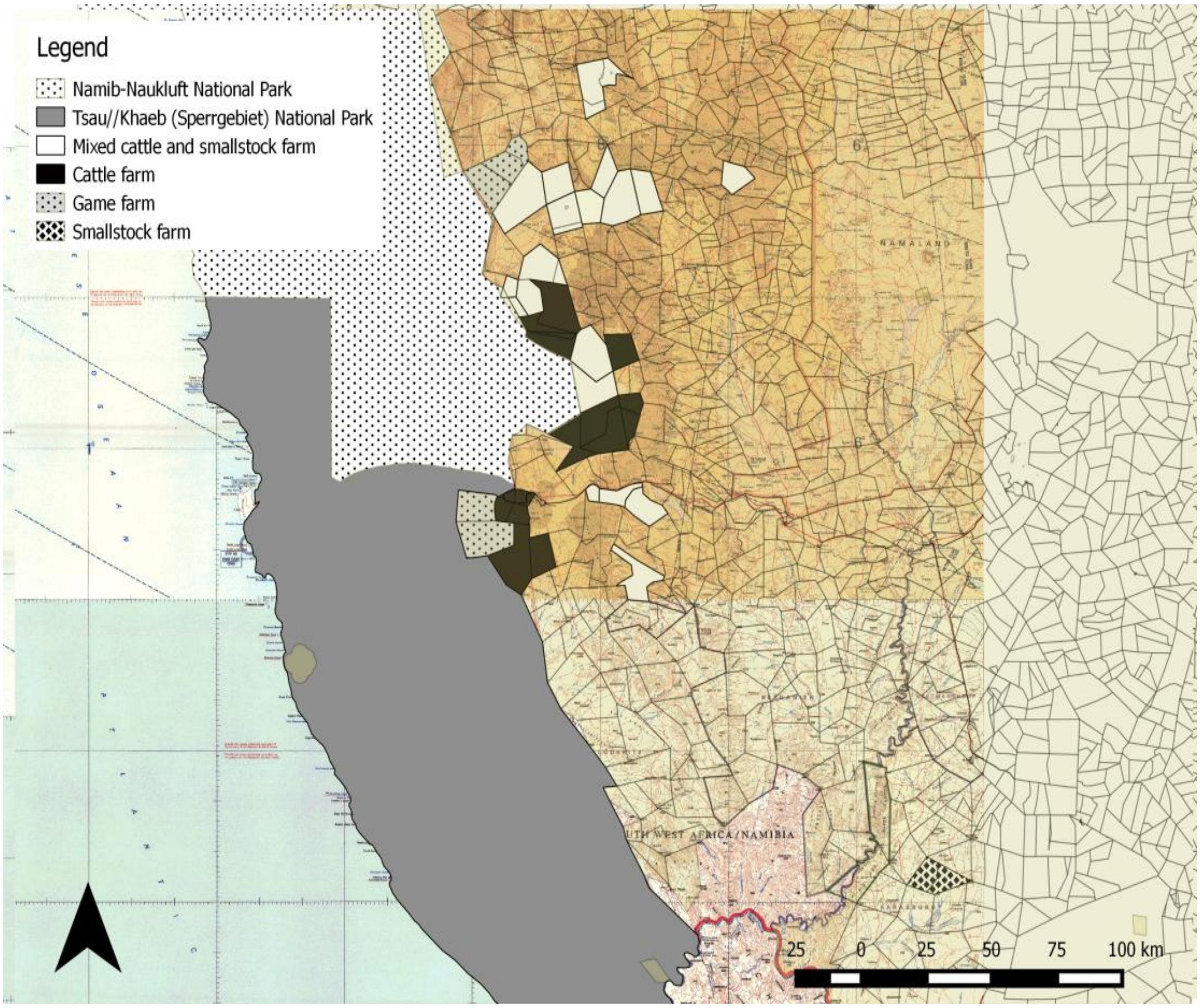


Figure 7.1: Map the locations of the farms of the 24 farmers who responded to the questionnaire, in relation to the Sperrgebiet and Namib-Naukluft National Parks. Farm types, as defined by the main agricultural activity, are shown by colour and pattern of the farm on the map, and referenced within the legend in the top left hand corner.

7.4.1 Carnivore presence

Carnivore diversity on farms ranged between one and 11 species, with a mean of 8.17 (± S.E. 0.49). Bat-eared fox and black-backed jackal were the most widely distributed carnivore species, occurring on 97.06 % of all farms each, whilst spotted hyena was the least frequently recorded species, occurring on just 41.18 % of all farms (Table 7.4). Due to low sample sizes of both game and pure smallstock farms (*n* = 2, *n* = 1 respectively), these farm types were not included when testing for associations between carnivore presence and farm type. Fisher's exact tests showed carnivore presence was not significantly associated with farm type for any species, and Mann-Whitney U test showed no significant differences in carnivore diversity between farm type (*W* = 44, *P* = 0.98). Fisher's exact tests showed leopard and spotted hyena presence were significantly and positively associated (*P* = 0.04), as were cheetah and spotted hyena presence (*P* = 0.02) and leopard and cheetah presence (*P* = 0.003).

Table 7.4: Carnivore presence across different type of farms as indicated by the 24 farmers which responded to the questionnaire.

	% occurrence				
Species	**All farms**	**Cattle**	**Smallstock**	**Cattle and Smallstock**	**Game**
n	**24**	**6**	**1**	**15**	**2**
Cape fox	76.47	66.67	100	68.75	100
Bat-eared fox	97.06	83.33	100	100	100
Black-backed jackal	97.06	83.33	100	93.75	100
Honey badger	52.94	33.33	100	50	50
Aardwolf	88.24	66.67	100	100	100
Spotted hyena	41.18	50	0	37.5	100
Brown hyena	58.82	83.33	100	31.25	100
Leopard	82.35	83.33	0	68.75	100
Cheetah	79.41	66.67	0	68.75	100
Caracal	70.59	50	100	81.25	100
African wild cat	99.18	83.33	100	81.25	100

7.4.2 Physical farm characteristics

Farm size was highly variable, ranging in size from 55 km^2 to 500 km^2, with a mean of 203.39 km^2 (Table 7.5). No significant difference in size was detected between pure cattle farms and mixed smallstock and cattle farms (Mann-Whitney U: *W* = 4.85, *P* = 0.18). Percentage of farm covered by mountainous habitat ranged from 0 % to 90 %, with a mean of 37.83 %. A Mann-Whitney U test showed a significant difference in percentage of mountain by farm type (*W* = 10, *P* = 0.006), with mixed smallstock and cattle farms having significantly higher mountain cover than pure cattle farms (Fig 7.2).

Table 7.5: Summary of physical farm characteristics of those 24 farms whose owners responded to the questionnaire

Characteristic	**Mean (S.E)**	**Range**
Size (km^2)	203.39 (24.96)	55 - 500
Mountain (%)	37.83 (5.58)	0 - 90
Water point s (/100km^2)	12.07 (2.56)	1.51 - 57.36
Cattle (/100km^2)	147.31 (23.81)	12.19 - 389.94
Smallstock (/100km^2)	572.54 (123.99)	23.80 - 1550.39
Total livestock (/100km^2)	520.16 (107.48)	44.69 - 1674.42
Large game (/100km^2)	282.95 (58.26)	21.82 - 1250.00
Small game (/100km^2)	30.6 (6.52)	0 - 122.99

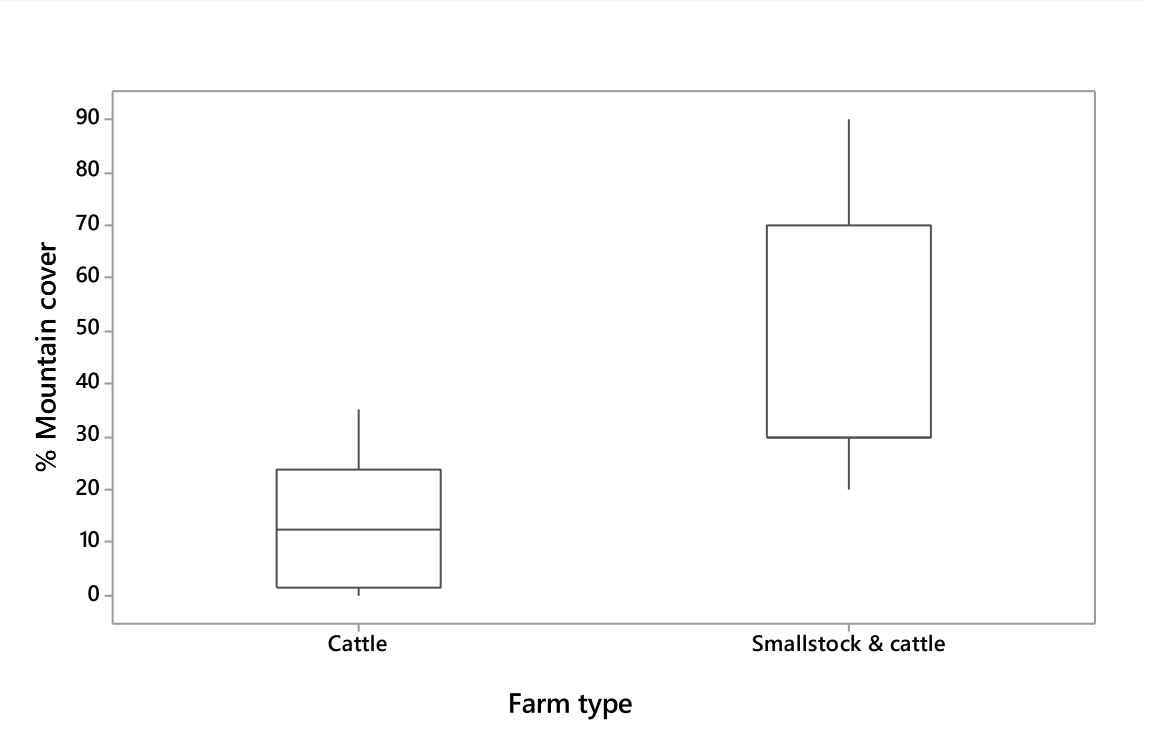


Figure 7.2: Comparison of percentage (minimum, quartiles, median, maximum) mountain cover by cattle farms (*n* = 6) and mixed smallstock and cattle (*n* = 15), with significantly higher percentage cover seen on mixed smallstock and cattle farms (Mann-Whitney U: *W* = 10, *P* = 0.006).

Water point density ranged between 1.51 - 57.36 points/100 km^2, with a mean of 12.07 points/100 km^2, with no significant difference in water point density between farm type (Mann-Whitney U: *W* = 20, *P* = 0.08). Mean smallstock density was nearly four times higher than mean cattle stocking density (572.54/100km^2 compared to 147.31/100 km^2 respectively), however as livestock density was expected to vary with farm type, significant differences between farm type were not tested for. Large game density had a mean of 282.95/100 km^2, with a range of 21.81 - 1250/100 km^2, with no significant difference detected between farm type (Mann-Whitney U: *W* = 32, *P* = 0.86). Small game density ranged between 0 and 122.99/100 km^2, with a mean of 30.6/100 km^2, a Mann-Whitney U test showed no significant difference in small game density by farm type (*W* = 36, *P* = 0.07).

Within the physical farm characteristics, farm size and large game density were significantly associated, with Spearman's rank correlation showing a postive, significant association (r_s=0.51, *P* = 0.02). Water point density and livestock density were positively associated (Spearman's rank: r_s = 0.64, *P* = 0.001), as were mountain cover and livestock density (Spearman's rank: r_s = 0.32, *P* = 0.04).

7.4.3 Risk score and physical farm characteristics

7.4.3.1 Focal carnivore risk scores

Black-backed jackal ranked the highest mean risk to livestock score at 2.65, followed by leopard with a mean of 2.34 (Table 7.6), spotted hyena (2.33), caracal (2.28) and brown hyena (1.93). Cheetah had the lowest mean risk score at 1.81. No significant differences were seen in risk to livestock scores between species (Kruskal-Wallis: *H* = 8.41, *P* = 0.13).

Table 7.6: Summary of risk scores given to focal carnivores by farmers, combining a measure of risk to livestock and degree of tolerance towards them by farmers

Species	Mean (S.E.)	Range
Black-backed jackal	2.65 (0.22)	1 - 3.83
Spotted hyena	2.33 (0.26)	1 - 3.33
Brown hyena	1.93 (0.27)	1 - 4
Leopard	2.34 (0.22)	1 - 3.67
Cheetah	1.81 (0.23)	1 - 3.67
Caracal	2.28 (0.27)	1 - 3.67

When tested against farm characteristics, focal species risk scores showed few significant associations; water point density was positively associated with both black-backed jackal (Kendall tau-b: *tau* = 0.39, *P* = 0.01) and caracal risk scores (Kendall tau-b: *tau*

= 0.41, *P* = 0.03). Cheetah risk score was positively associated with livestock density (Kendal tau-b: *tau* = 0.46, *P* = 0.02). It should be noted, due to the relatively high proportion of respondents not able to answer questions regarding carnivore abundance and recent population trends (38 %), carnivore abundance and population status was not used in analysis due to low samples sizes.

7.4.3.2 Combined risk scores

Combined risk ranged from 0.27 to 0.92, with a mean of 0.59 (S.E. ± 0.04). When testing for associations between combined risk scores and physical farm characteristics only combined risk and water point density were significantly associated (Kendall tau-b: *tau* = 0.38, *P* = 0.01), showing a positive association.

7.4.4 Livestock management and carnivore conservation

The number of non-lethal mitigation methods on farms ranged between zero and three, with a mean of 1.29 methods being used (Table 7.7). Kraaling was the most popular with a total of 46 % respondents using kraals for smallstock, livestock guarding dogs was the second most popular method with 21 % respondents using these dogs (Table 7.8). Shepherds were employed by 17 % of respondents, whilst jackal-proof fencing, electric fencing and border fence patrols were less popular methods, being used by 8 %, 4 % and 4 % of respondents respectively. Only two respondents detailed mitigation methods for cattle; one used a herdsman and the other used a donkey to guard livestock.

Table 7.7: Summary of livestock management variables used by respondents and score for the importance of carnivore conservation to respondents, which is scored on a scale from one to five, with one being carnivore conservation is not important, and five being carnivore conservation being very important

Variable	Mean (S.E)	Range
Mitigation	1.29 (0.23)	0 - 3
Acceptable loss	5.24 (1.14)	0 - 20
Actual Loss	16.4 (3.79)	0 - 45
No of Checks	9.05 (3.55)	1 - 60
Conservation importance	4.12 (0.24)	1 - 5

Acceptable loss ranged from zero to 20 % of livestock with a mean of 5.24 %, whilst actual losses ranged 0 - 45 % of livestock, with no significant difference between acceptable loss and farm type (Mann-Whitney U: *W* = 27.5, *P* = 0.45). No significant association was seen between actual los and acceptable loss (Mann-Whitney U: *W* = 0.19, *P* = 0.55). Mean actual loss was 16.4 % of livestock (range 0 - 45), only one pure cattle farmer reported losses of livestock, with 0.60 % losses, therefore sample size was too low to compare farm types. The mean number of days between checks on livestock was 9.05, with a range of 1 - 60 days, there was no significant difference in the number of days between checks between farm type (Mann-Whitney U: *W* = 55.5, *P* = 0.43).

Table 7.8: Summary of mitigation methods used by the 24 farmers who responded to the questionnaire

Mitigation method	% of respondents using
Kraals	46
Livestock guarding dogs	21
Shepherd	17
Jackal proof fencing	8
Electric fence	4
Fence patrols for holes/damage	4

When testing for significant associations between livestock management variables and carnivore conservation importance, only number of days between checks and actual loss were associated (Kendall tau-b: *tau* = 0.52, *P* = 0.02) (Fig 7.3). However such a result could have been largely influenced by the point where checks were only made once every 60 days. When removing this point, no significant association was seen (Kendall tau: *tau* = -0.16, *P* = 0.52). When considering physical farm characteristics, only actual loss and mountain cover were associated (Kendall tau-b: *tau* = 0.68, *P* = 0.003).

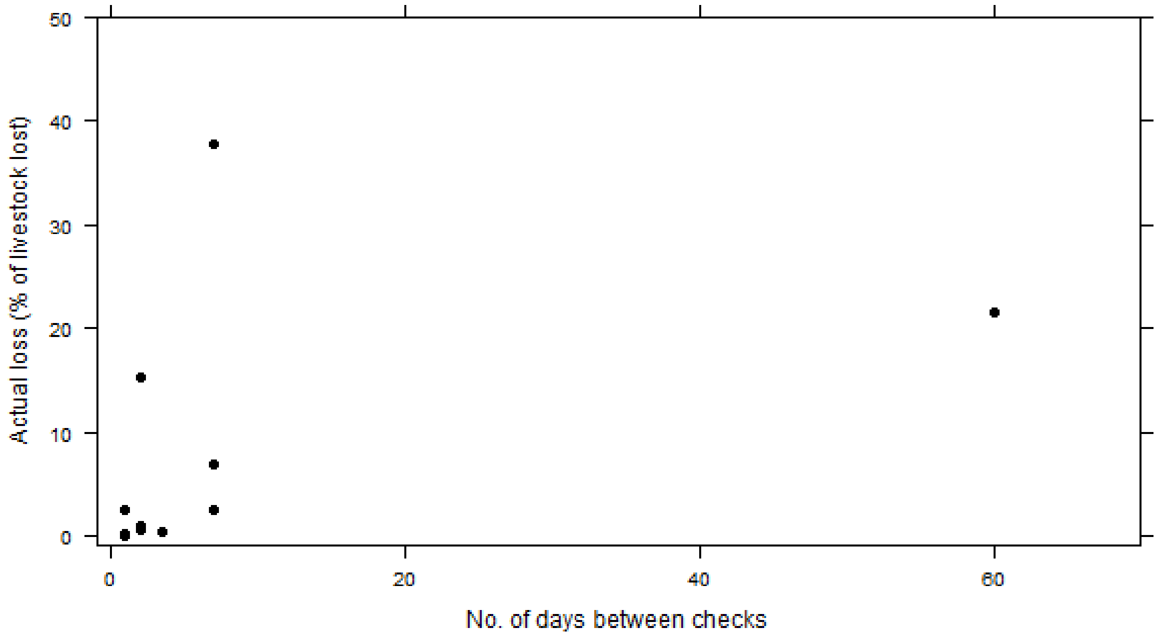


Figure 7.3: Positive, significant ssociation between number of days between checks on livestock and actual losses experienced by respondents (as a percentage of their total number of livestock). N.B. axes started at minus numbers for clarity as some of the points include 0 values. However, it was hypothesised the association was by driven by the extreme point represented by 60 days between checks. When this point was removed, the association failed to be significant (Kendall tau: *n* = 10, *tau* = 0.16, *P* = 0.52).

7.4.4.1. Focal carnivore risk scores, livestock management and carnivore conservation

No significant associations were seen between focal carnivore risk scores and number of mitigation methods, actual loss, acceptable loss or number of checks, for any species. No significant association was seen between focal or combined carnivore risk score and importance of carnivore conservation.

7.4.4.2 Combined risk scores

When testing combined tolerance scores for all carnivores against livestock management variables and importance of carnivore conservation, only importance of carnivore conservation was significantly associated (Kendall tau-b: *tau* = -0.43, *P* = 0.02), where a negative association was seen.

7.4.5 Other causes of livestock loss

Carnivore predation was the most frequently cited cause of livestock loss, with 71 % of respondents having experienced it in the last 12 months, death caused by poisonous plants was the second most frequent cause of death at 50 % of respondents (Fig 7.4). Birthing problems and disease were each experienced by 42 % of respondents, with livestock theft and *veld* injuries having been experienced 29 % and 21 % of respondents respectively.

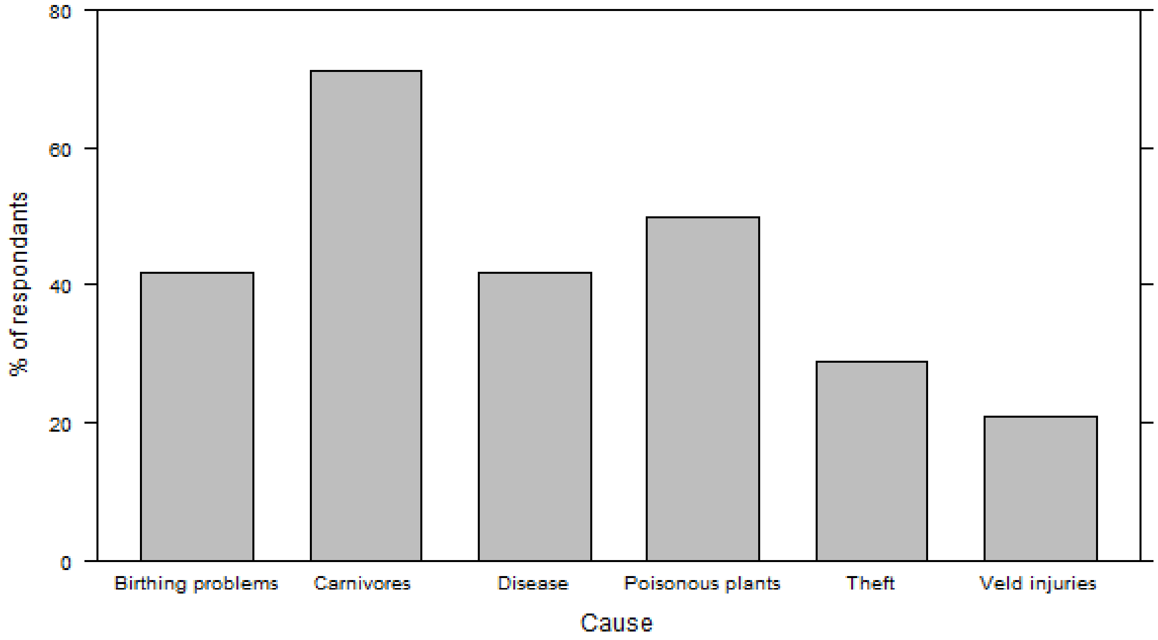


Figure 7.4: Comparison of causes of livestock loss experienced by 24 farmers having farms up to 150 km East of the Sperrgebiet or Namib-Naukluft National Parks borders

7.4.6 Water pipe damage

A total of 70.83 % of respondents had experienced water pipe damage in the last 12 months, however only four reported the use of mitigation methods; three buried the pipe, with a fourth burying or attaching the pipe to the fence line. The most commonly blamed species was porcupine (70.59 % of respondents), followed by baboon (29.41 %) and black-backed jackal (23.53 %). Brown and spotted hyena, oryx, honey badger and bat-eared fox were also blamed for damage by smaller numbers of respondents (Fig 7.5).

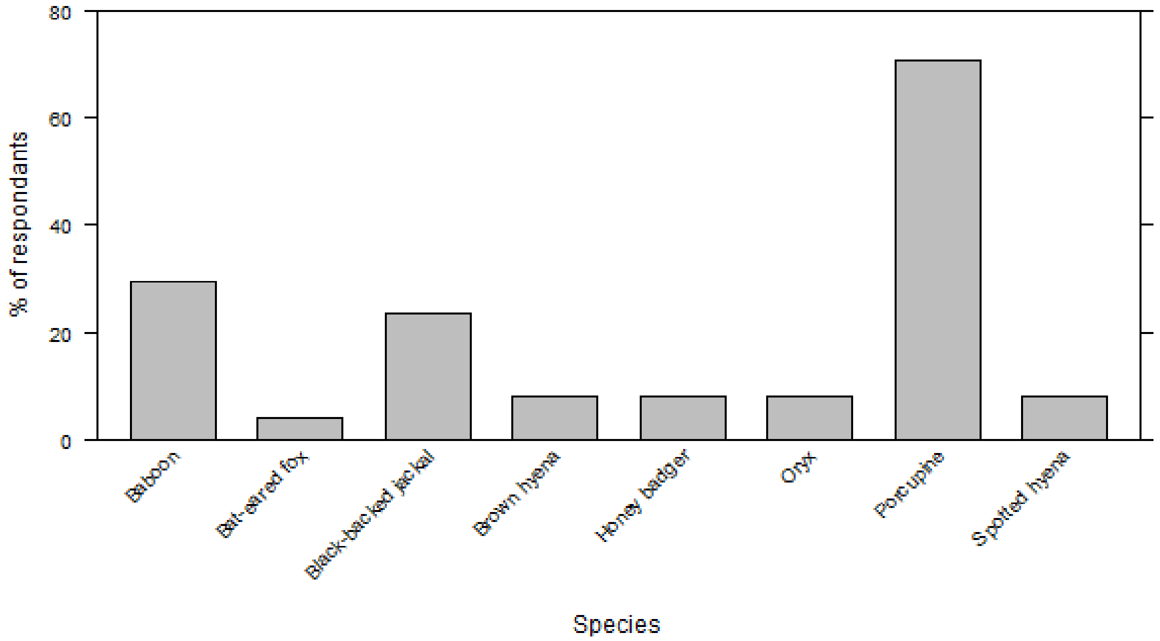


Figure 7.5: Wildlife species blamed for water pipe damage by 17 respondents experiencing water pipe damage, out of a total 24 respondents

7.4.7 Problems with baboons

Problems with baboons affected 62.5 % of respondents, with predation of smallstock being the most frequently cited problem, with one farmer stating they were a bigger problem than any carnivore in this respect. Infrastructure damage was the second biggest problem with it being problematic for 40 % of respondents. Problems with garden damage, eating cattle food, poultry and calf predation each affected 6.67 % of respondents (Fig 7.6).

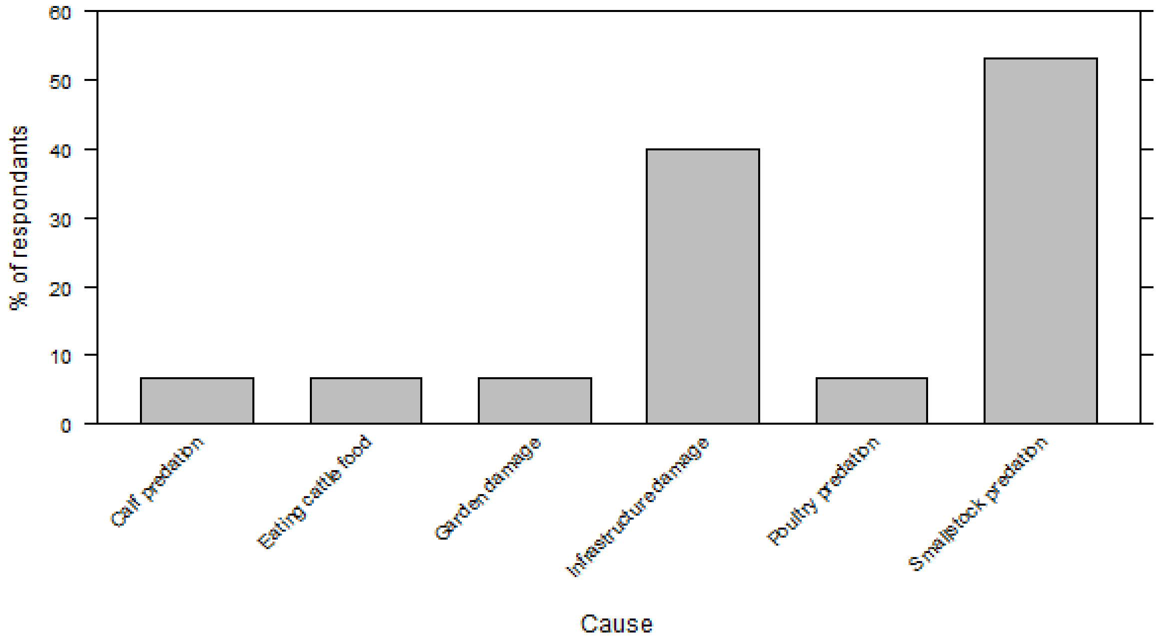


Figure 7.6: Problems caused by baboons as cited by a total of 15 respondents experiencing baboon problems, out of a total of 24 respondents

7.4.8 Non-focal carnivores

Only 29.17 % of respondents reported problems with the non-focal carnivore species, and even those having problems stated they tolerated these species. One respondent named African wild cat as a low risk species for smallstock and another stated honey badger was a low risk species for smallstock. Table 7.9 summarises the problems detailed for smaller species.

Table 7.9: Summary of problems experienced due to small carnivore species by seven respondents

Species	Problem	% of respondents
Cape fox	Killing lambs	4.17
	Digging holes	4.17
Bat-eared fox	Water pipe damage	4.17
	Digging holes	8.33
Honey badger	Biting lamb’s noses	8.33
	Damaging beehive	4.17
	Digging holes	4.17
Aardwolf	Digging holes	8.16
African wild cat	Killing chickens	12.50

7.5 Discussion

Questionnaires conducted with landowners are a commonly used method for assessing the human perspective of human-wildlife conflict, as effective mitigation of such conflicts often relies on thorough understanding of their underlying patterns and causes (Dar et al. 2009). The farmer questionnaire data collected in this study showed few associations between carnivore risk scores and physical farm characteristics or livestock management practices, contradicting the original hypotheses. Only water point density and livestock density were associated with risk scores, and even then only for certain focal carnivore species. Meanwhile, only the percentage of farm covered by mountain habitat was associated with actual losses of livestock. As hypothesised, data regarding water pipe damage by a number of wildlife species and conflict caused by baboons suggest these usually overlooked sources of conflict may be affecting high proportions of farmers in the area and therefore have the potential to be major reasons for conflict between farmers and wildlife.

Black-backed jackal had the highest mean risk score of all carnivore species, followed by leopard, spotted hyena, caracal, brown hyena and lastly cheetah, although no significant differences were seen in mean risk scores between species as hypothesised. Lindsey et al. (2013) found leopard to be the most tolerated large carnivore species in a national farmer survey in Namibia, however this was in comparison to species such as lion and African wild dog, two species not present in the study area. In a study of human-wildlife conflict in the North West Province of South Africa, Thorn et al. (2012) also found black-backed jackal to be perceived as being responsible for most livestock predation, followed by caracal, leopard, brown hyena, cheetah and spotted hyena. In contrast, in Tanzania 97.7 % of livestock loss in areas bordering the Serengeti National Park, was attributed to spotted hyena (Holmern et al. 2007). Rust and Marker (2013) found black-backed jackal and cheetah to be the two species most frequently cited as responsible for livestock predation in Namibia. As these two species were also the most frequently seen predators on farmlands, being diurnal and crepuscular, Rust and Marker (2013) suggested respondents were more likely to rate a frequently seen predator as a problem more than a rarely seen species. Interestingly, cheetah had the lowest mean risk score of all carnivores in this study. Such a difference for cheetah between locations, southern Namibia compared to the north, could be due to cheetah density. In the south cheetah may occur at lower densities, as suggested by the Namibian large carnivore atlas (Stein et al. 2012), potentially explaining why they are not viewed as a high risk species as in the north.

Presence of the three largest species, spotted hyena, cheetah and leopard, were positively and significantly associated across farms. Previous studies of human-wildlife conflict have suggested a 'contagious effect' within conflict situations, where the way a landowner views one species affects the way they view similar species. For example, Dickman et al. (2014) found when pastoralists in Tanzania had a problem with one carnivore species, they were more likely to view others in the same way. Similarly, Marker et al. (2003b) found perceiving a cheetah problem was related to perceiving a black-backed jackal problem for Namibian farmers. Therefore, it is possible that farmers who had a problem with one large carnivore species, may have had negative attitudes towards other species, resulting in removals of all species from farms. Brown hyena was the only large carnivore species whose presence was not significantly associated with other large carnivore presence. However, brown hyenas are known to be outcompeted by socially dominant spotted hyena (Mills 1990). Therefore, that brown hyena is the only large carnivore species whose presence is not significantly associated with other large carnivore presence, is not unexpected.

A significant positive association was seen between actual loss of livestock and percentage of the farm covered by mountain. A similar result was detected by Thorn et al. (2013), who found high elevation to be one of the main determinants of conflict in South Africa. Such a result may not be surprising, given that previous studies have shown carnivore hunting success to be higher in areas with cover (e.g. Hayward et al. 2006; Davidson et al. 2012). Within the general study area, cover in the form of trees and shrubs is relatively rare, with open plains being dominated by grasses with few trees or other forms of taller vegetation. However, mountain habitats are often associated with river beds formed from water run-off from mountains, where a higher density of trees and bushes are seen (*pers. obs.*). Figure 7.7 clearly shows the higher density of trees surrounding the mountains on NBR, in comparison with the open plains area. A higher hunting success in areas with cover is thought to be associated with reduced visibility of prey to approaching predators (Thorn et al. 2012). Alternatively, mountain habitat has been suggested to increase hunting success of leopards, as prey cannot escape quickly up slopes (Swanpoel 2008). Farms with more mountain habitat may therefore be expected to be favoured by a number of carnivore species for hunting, which may include the hunting of domestic livestock, potentially explaining the association between actual loss of livestock and mountain cover.

Figure 7.7: Google Earth image of NBR showing higher density of trees (highlighted within red ovals) associated with mountain habitats in comparison to open plains

Both black-backed jackal and caracal individual risk scores and combined risk scores for all focal species, were significantly and positively associated with water point density. Previous studies have shown water to be associated with livestock predation risk, for example Kaartinen et al. (2009) found the amount of water on farms to have a positive relationship with wolf attacks on sheep in Finland, and Soto (2008) found proximity to water to be a predictor of carnivore conflict in Guatemala. These studies suggested water was attractive to carnivores, drawing them onto the farmlands and thus into contact with livestock. Water sources have also been found to be important carnivore hunting areas, for example Hopcraft et al. (2005) found proximity to water to be an important feature for hunting lions in the Serengeti, suggesting it provides a predictable location for encountering prey. Hopcraft et al. (2005) also suggested that the vegetation around water sources is equally important for hunting lions. However as the majority of water sources on southern Namibian farmlands are artificial, vegetation around water sources does not occur at a higher density than on other areas of the farm (*pers. obs.*), and is unlikely to be associated with higher predation risk.

Water availibility may also be associated with higher densities of game and carnivores. For example, leopard density is known to be positively associated with rainfall (Martin and Meulanaer 1988), and hence prey density (Stander 1997) in sub-Saharan Africa, which may further explain the association between risk scores and water point density. Farmers were asked in the questionnaire to estimate the numbers of each carnivore species present on the farm, however many farmers were unable to answer this question, therefore carnivore density was not used in data analysis. Higher densities of carnivores have been shown to be associated with higher risk scores and livestock predation levels; Kaartien et al. (2009) found wolf density was correlated with predation risk in Finland. Sagør et al. (1997) found brown bear density was significantly correlated with sheep losses in Norway, whilst Stahl et al. (2001) recorded a relationship between lynx abundance and number of sheep losses in France. Stoddart et al. (2001) also found coyote density to be positively correlated with livestock losses in Idaho. Schumann (2009) recorded increasing levels of conflict to be associated with increasing numbers of carnivores on Namibian commercial farmlands. In contrast, in a review of global human-predator-prey conflicts, Graham et al. (2005) found no association between carnivore density and livestock losses. Similarly, Connor et al. (1998) found the number of sheep predation events was not correlated with the number of coyotes removed in a controlled manipulation in northern California. Further studies would be of use to investigate an association between carnivore density and water point density on farmlands, although due to the number of species without individually identifiable markings, such a study would be difficult.

Cheetah risk score was significantly and positively associated with livestock density, however most other studies have failed to detect an association between livestock density and predation, for example Maclennan et al. (2009) found the rate of lion attack was not related to livestock density in Kenya. Schiess-Meier et al. (2007) reported that despite the fact that large farms employed more herders per head of cattle than small farms, the absolute number of livestock losses were similar for small and large farms, suggesting carnivores may see each herd as a unit from which they can take prey items at similar frequencies. In contrast, Hemson et al. (2009) found livestock losses to be positively correlated with the number of livestock owned in Botswana, suggesting such an association was due to predation of stray animals left outside kraals at night, the number of which might increase with herd/flock size. Such an association with livestock density was not expected as carnivores are well known to prefer natural prey to domestic livestock (Norton et al. 1986; Quigley and Crawshaw 1992; Rasmussen 1999; Woodroffe et al. 2005), usually only taking domestic livestock when natural prey density is low (Hemson and Macdonald 2002). However, Schiess-Meier et al. (2007) suggested high livestock densities can result in overgrazing, in turn leading to decreases in densities of natural prey causing carnivores to predate domestic prey. No association was seen between game and livestock densities across farms, however some farmers noted changes in game numbers throughout the year in response to rainfall (W. De Waal, *pers comm.*), which might make an association difficult to observe. Evidence of overgrazing was seen on some of the study farms, for example Weissenborn (Fig. 7.8), as well as changes in game abundance on the study farms throughout the year (*pers. obs.*). Therefore it is possible livestock density may be linked to predation risk through overgrazing, however remedying the situation by decreasing livestock density on farms may not be an option due to loss of income due to reduced numbers of livestock.

Figure 7.8: Example of overgrazing on farm at Weissenborn

Whilst overgrazing may explain the association seen between cheetah risk scores and livestock density, farmer perception of the problem may also provide an explanation. Marker et al. (2003b) found Namibian farmers who removed cheetahs had significantly more smallstock than farmers who did not, yet detected no relationship between cheetah problem and smallstock density. Marker et al. (2003b) also found nearly 60 % of farmers who had no problem with cheetah still removed cheetahs, suggesting carnivores are traditionally removed whether they are a problem or not, as a pre-emptive measure to reduce conflict. Such results might suggest farmer's attitudes towards cheetahs do not reflect the actual risk posed, or problems experienced, as suggested by Rust and Marker (2013) in a study of carnivore conflict on resettled land in Namibia. As cheetah risk scores were not associated with actual losses experienced, it is possible farmers with more livestock were more likely to view cheetahs as a problem and therefore remove them, in comparison to farmers with less livestock.

Many previous studies have shown the level of acceptance of large carnivores by local people is dependent on the level of livestock predation experienced (Rasmussen 1999; Patterson et al. 2004; Woodroffe et al. 2005; Kolowski and Holekamp 2006; Holmern et al. 2007; Schiess-Meier et al. 2007; Gusset et al. 2008). However, the results of this study failed to show an association between actual loss and importance of carnivore conservation. A significant, negative association was seen between the combined risk scores of all focal carnivores and the importance of carnivore conservation. Such a result might suggest that farmer attitudes towards carnivore conservation are rather based on the perceived risk from carnivores, rather than actual losses experienced. Lindsey et al. (2013) found large carnivores were more commonly present on farms where they were wanted, and suggested the attitudes of farmers may be important in determining the fate of carnivores. That the importance of carnivore conservation may be associated with perceived risk rather than actual losses of livestock, is therefore somewhat worrying. Mitigation methods could be used to reduce the levels of actual losses on farmlands, however changing perceptions of conflict and risk are more difficult as ingrained attitudes may mean farmers still kill carnivores regardless of a reduction in problems with them (Dickman 2010). However, Marker et al. (2003b) showed the introduction of even a simple newsletter regarding the

Cheetah Conservation Fund's activities had an effect on farmer tolerance. Before the introduction of the newsletter farmers regarding cheetahs as a problem on average removed 29 cheetah annually, with farmers not regarding cheetahs as a problem still removing 14 cheetahs annually. After the newsletter was introduced, these numbers dropped significantly, to 3.5 and 2.0 respectively. However, Marker et al. (2003b) cautioned that whilst educational programmes can be used to increased tolerance, as farming is a commercial venture, it is much more likely financial incentives will be the tools needed to bring about a sustainable change in tolerance attitudes.

The results pertaining to baboon conflict were of particular interest given that this species is rarely considered or discussed in other human-wildlife conflict studies (Butler 2000). Smallstock predation was the most frequently cited problem caused by baboons, followed by infrastructure damage. Baboons have been noted as predators of sheep in Namibia in times of drought (MET 2005), and as causing 1.6 % of livestock predation in areas bordering the Serengeti National Park in Tanzania (Holmern et al. 2007). Butler (2000) noted baboons to be a major livestock predator in the Gokwe communal lands in Zimbabwe and Butler et al. (2004) reported baboons as livestock raiders in Zimbabwe and male baboons being responsible for killing 11 free-ranging domestic dogs in two and a half years. A total of 6.67 % of respondents in this study cited poultry predation as a cause of conflict with baboons, whilst Holmern and Roscraft (2014) noted 0.5 % of respondents experienced poultry predation by baboons in Tanzania. As no farmers in the area were major producers of poultry, such predation is unlikely to be a significant cause of conflict.

Baboons are known to feed on vertebrate prey in the wild, and along with chimpanzee *Pan troglodytes*, are the only non-human primate species known to stalk and hunt prey (Butynski 1982). Within the central Namib desert they have been observed hunting a klipspringer calf (Davies and Cowlishaw 1996), while in Botswana Hamilton and Busse (1982) recorded baboons taking adult impala *Aepyceros melampus* as their largest prey species. Several studies of predatory behaviour of baboons have noted it is primarily, and sometimes exclusively, males performing hunting and killing behaviour (Hamilton and Cowlishaw 1996; Butler 2000; Butler 2004), with meat intake being related to social dominance rank (Hamilton and Cowlishaw 1996). Baboon livestock predation has previously been recorded as largely seasonal, with most predation occurring when food resources are scarce, for example at the end of the dry season (Butler 2000; Sogbohossou et al. 2011).

Predation of livestock by baboons is potentially a difficult problem to mitigate, as due to their ability to climb, kraals will offer little or no protection, and smallstock is usually targeted rather than cattle (Holmern et al. 2007; Butler 2000; Sogbohossou et al. 2011). However, as baboons are diurnal, all previous livestock predation has been recorded as occurring in the day (Sogbohossou et al. 2011), when livestock is usually out in the field grazing. Anatolian livestock guarding dogs may offer a practical mitigation method for baboon predation whilst smallstock are grazing in the field, and have been recorded as killing baboons in defence of flocks (Marker et al. 2003c). However young dogs have been recorded as being killed by baboons (Marker et al. 2003c), and therefore may be themselves at risk from predation until they are large enough to defend such an attack. A single predation event of a ewe and her newly born lamb on NBR, which had been left in the kraal near the worker houses during the day due to the recent birth, was witnessed (*pers. obs.*). Such a predation event would be difficult to stop, as it is unlikely farmers would station livestock guarding dogs in or near a kraal for single or small groups of animals, however the use of wire or shade cloth roofs on kraals could be used to prevent baboon entry into kraals. Such a mitigation method and further research regarding baboon-livestock predation would be of great use for Namibian farmers, especially those dependent on smallstock.

Water pipe damage was experienced by 70.83 % of respondents suggesting this is a common source of conflict. Damage to infrastructure including water pumps and dams by elephants is commonly experienced in Namibia and is a large source of conflict in the northern areas (MET 2005; Jones and Barnes 2006; Jones and Elliot 2007). However, no previous studies have discussed carnivore, or other wildlife species such as ungulates, as a source of water pipe damage. A camera trap was set up on NBR after the farmer complained of spotted hyenas damaging a water pipe line. The camera trap recorded a spotted hyena with the plastic water pipe in its mouth (Fig. 7.9). However, the pipe was being stored for future use out in the open with no effort being made to protect it from damage. On KAV, water pipe in use was left lying on top of the ground along the road, again with no effort to protect it from damage (Fig. 7.10a). However on Tsirub, all water pipes were buried underground with rocks on top to stop wildlife digging and reaching the pipe (7.10b), with the owner reporting very little damage to pipe lines (J.J. Bosman, *pers. comm.*). Such lack of protection of water pipes is particularly worrying as some farmers admitted shooting or poisoning carnivores for causing water pipe damage (B. Oberholzer, *pers. comm.)*.

Figure 7.9: Spotted hyena with plastic water pipe in mouth on NBR, water pipe damage was noted as a significant problem by respondents within the questionnaire

Porcupine was the most commonly cited culprit of water pipe damage by respondents, and indeed this species was regularly detected on camera trap at both water sources and along roads. Porcupine is commonly recorded as causing conflict by crop damage in Namibia (Mulonga et al. 2003), Ethiopia (Datiko and Bekele 2013) and India (Alkon and Saltz 1985). Additionally it is often blamed for digging holes under fence lines within Namibia, which then allows carnivores access onto farmland (Schumann et al. 2006). Damage to water pipes by porcupine has not been discussed in previous conflict studies, however that such damage occurs is not surprising given porcupines' ability to cause damage with their teeth. Damage to trees, known as ring-barking, where a complete ring of the outer bark of a tree is removed, is common throughout Africa, and is another source of conflict (Yeaton 1988), as it leaves the tree susceptible to fungal infections (Grubb 2008). As water pipe damage affected so many respondents, it is recommended further research into this problem is conducted. The situation can result in carnivore and other wildlife species being lethally removed, as well as large amounts of water being lost, especially if damage to the pipe is not found immediately. In an arid environment, such water loss is potentially extremely costly and therefore should be prevented at all costs.

Figure 7.10: a (*left*) exposed water pipe on KAV, b (*right*) rocks on top of buried water pipe, Tsirub

Non-focal carnivore species (Cape fox, bat-eared fox, honey badger, aardwolf and African wild cat) caused fewer problems than the focal carnivore species. These five non-focal species were all cited as attacking smallstock by small percentages of respondents (4.17 - 12.50 %). Cape fox predation of lambs has been documented previously (Stuart 1981), and is considered a threat to species survival through retaliatory killings, by the IUCN (Stuart and Stuart 2004). Predation of smallstock by bat-eared fox has been a reason for persecution of the species across South Africa, however Nel and Maas (2004), believe farmers may instead be witnessing the species feeding off blowfly (Diptera species) larvae on lamb carcasses, rather than actual predation. Honey badger is most commonly seen as a problem animal for apiculturists, with damage to beehives at ground level frequently recorded (Begg et al. 2008). Whilst livestock predation by honey badgers has been cited previously (Begg et al. 2008), the biting of lambs noses in particular has not been discussed. Little literature exists on the hunting behaviour of vertebrate prey by honey badger, therefore it is difficult to say if such behaviour is normal, or a specialised approach for the area or type of prey. African wild cat has been documented as a pest to both poultry and smallstock producers (Driscoll et al. 2010), and was the only non-focal species not reported to dig holes under fence lines.

Four of the five non-focal carnivore species were blamed by respondents for diggings holes under fence lines, with only African wild cat not identified as causing this problem. The proper maintenance of fence lines on farmlands has long been used as a tool to promote coexistence between carnivores and humans (Wade 1982; Kesch et al. 2013). Species digging holes under fence lines, are seen as conflict causing species as these holes allow problem carnivore species access through the fence and into contact with livestock (Rust et al. 2014). Bat-eared fox and honey badger have previously been identified as potential species for digging holes under fence lines (Kesch et al. 2013). Cape fox also have the potential to dig holes under fence lines, as they are known to rapidly dig for prey and are able to dig their own burrows for denning (Stuart and Stuart 1981). However aardwolf have been noted as weak diggers (Estes 1992), and therefore it is unclear if the species is capable of causing conflict through digging holes, and further research would be useful to determine its role in such conflict.

This study has shown the complexity of assessing the human perspective of human-wildlife conflict situations. Few associations were seen between risk scores given to carnivore species by farmers and physical farm characteristics or livestock management techniques. Therefore trying to produce recommendations for mitigation techniques to reduce conflict based on these data may be difficult. The fact that significant conflict can occur even after damage has been reduced (Dickman 2010), can add further difficulties to the situation. Water point density was positively and significantly associated with risk score for both black-backed and caracal and for focal carnivores combined. Such a result might suggest farms with higher densities of water points should consider using extra mitigation techniques to reduce conflict, however results failed to show an association between actual losses and the number of mitigation techniques used. Such a lack of association may be surprising given in a study comparing livestock losses before and after use of livestock guardian animals, livestock losses were reduced by 70 % in South Africa (Cruise 2014).

The association seen between actual losses and percentage of farm covered by mountain habitat may be an easier situation in which to reduce conflict. As the main cause of conflict in the study was smallstock loss, with very few farmers reporting large numbers of cattle or horse predation, farmers could control areas where smallstock grazed when out in the field during the day by using a shepherd and keeping away from mountain habitats. Alternatively, farmers with higher percentages of mountain habitat on the farm may wish to consider changing to cattle production rather than smallstock as this farming practice seems to suffer less from conflict with carnivores or baboons than smallstock farming. However, such a switch to cattle farming may be unsuitable if grazing is not available within mountain habitats. Thorn et al. (2012) also suggested conflict mitigation methods should be focused on farms with dense cover, which in this study area would be those farmers with the highest percentages of mountain cover.

The results of this study have also highlighted the need to further investigate baboon conflict, especially conflict pertaining to smallstock predation. Few previous studies have focused on this type of conflict, and it is recommended any future human-wildlife conflict studies in southern Africa include baboon conflict in any questionnaires or interviews with farmers and landowners. Additionally, the level of conflict between various wildlife species and farmers regarding damage to plastic water pipe warrants further investigation, especially in arid areas where the loss of water is likely to be significant. Non-focal carnivores were found to cause few problems to farmers and were involved in low levels of conflict, therefore it is recommended any future research into mitigation measures focus on the focal carnivore species only.

8.0 Comparison of methods for surveying a guild of carnivores in an arid environment

N.B. This chapter has been adapted for publication and has been published in the Journal of Arid Environments. See Appendix five.

8.1 Abstract

Whilst carnivores are notoriously difficult to monitor given their elusive behaviour, carnivores in arid environments present a particular challenge given that it in these habitats they occur at their lowest densities and often have the largest home range sizes. In recent years camera traps have become a widely used and established method of surveying carnivores, however low density populations often produce low detection probabilities, which in turn lower the precision of population parameters derived from surveys. Previous efforts to increase detection probability have included the strategic placement of cameras along roads and trails and the use of baits. This study compared two camera trap survey designs, one with cameras placed along roads and trails and another with camera traps placed at water sources, for their efficiency in surveying a guild of carnivore species on two arid, commercial farmlands in southern Namibia. Additionally, as non-invasive hair collection techniques offer additional data to that gained from camera trap, for example the potential for genetic analysis, two non-invasive hair collection devices, rub stations and hair snares were compared to camera traps across four commercial farmlands. All species had higher detection probabilities, although not always significantly so, from the water source survey design, along with lower latencies of detection, higher naive occupancy estimates and a higher diversity of species detection, in comparison to those produced by the road survey design. However, the water source survey design produced lower proportions of photos suitable for individual identification for those species with unique pelage patterns. In comparison to camera traps, non-invasive hair collection devices showed a low detection rate, recording just 44.44 % of species detected by camera trap in the north and 27.27 % of species in the south. These results suggest the water source camera trap survey design to be particularly effective for surveying multiple carnivore species in arid environments; however, when individual identification is required, for example in density estimations, a road survey design would be more suitable given the higher proportions of identification photos captures. Non-invasive hair collection devices, despite their potential to provide data that cannot be collected by camera traps, would not be recommended for use in such environments, given their relatively low detection rates.

8.2 Introduction

Carnivores are notoriously difficult to monitor given their elusive and often nocturnal behaviour, coupled with the fact that they frequently occur at low densities with large home ranges (Long et al. 2007). In arid environments, such problems are likely to be compounded given that densities are often lowest in such habitats (Hayward et al. 2007), for example leopard density in sub-Saharan Africa is positively correlated with rainfall (Martin & de

Meulanaer 1988). Similarly, spotted hyenas in East Africa are known to form clans of up to 90 individuals (Holekamp 2006), whilst in the Namib desert much smaller clan sizes of three to eight individuals are recorded (Tilson and Hamilton 1984). With Namibia having the driest climate in sub-Saharan Africa (Sweet, 1998), large portions of its wildlife populations are likely to occur at low density, further negating the need for efficient and effective methodology for surveying its carnivore populations.

The monitoring of threatened species is especially important (Joseph et al. 2006), with accurately estimating population size and density cited as one of the main goals for conservation research and wildlife management (Gustavo et al. 2010; Harmsen et al. 2010; Gerber et al. 2011; Anile et al. 2012). Carnivores existing at low densities are likely to be more vulnerable to local extinction through lethal removal, following conflict with humans than those living at higher densities (Hemson 2003). Such involvement of carnivores in human-wildlife conflict can have drastic effects on populations, for example a total of 9,588 cheetah removals from commercial farmlands were reported to Namibia's Ministry of Environment and Tourism between 1978 and 1994 (Marker et al. 2003b); in 2008 the estimated cheetah population for Namibia stood at approximately 2,000 adult individuals only (Durant et al. 2008). Therefore carnivores threatened with lethal removal as a consequence of actual or perceived involvement in conflict situations on arid farmlands in Namibia should be seen as priority species for conservation research within the country. However, to date, little data exist regarding such species within the south, with most of Namibia's conservation/research activities being centred in the central and northern regions of the country.

Camera traps have been identified as an important tool for monitoring cryptic species (Karanth 1995), with capture-recapture data of closed populations used as a conventional and increasingly widespread method for density estimation (Griffiths and van Schaik 1993, Gerber et al. 2011). Many density studies for a range of species have used camera traps as the main method (e.g. brown hyena, Thorn et al. 2009; puma, Negroes et al. 2010; jaguar, Soisalo and Cavalcanti 2006; leopard, Chapman and Balme 2010, Chase et al. 2013; serval, *Leptailurus serval*, Ramesh and Downs 2013 and European wild cat *Felis silvestris silvestris*, Anile et al. 2012). Previous studies of carnivores have also demonstrated camera traps to be more effective than other survey methods such as track counts (e.g. leopards in Phinda Private Game Reserve, South Africa Balme et al. 2009), but less effective that non-invasive genetic scat sampling (e.g. snow leopards *Panthera uncia*, Janečka et al. 2011).

Individually identifiable species may make up just a small proportion of those detected in a survey, for example tigers made up just 5 % of the total number of photographs in a survey by Franklin and Tilson (unpublished data, cited by Carbone et al. 2008). For species without such markings many studies have used relative abundance indices for estimating population size. The use of such a measure however is controversial, particularly when making comparisons over space, time and species, as such comparisons rely on the assumption of constant probability of detection (Harmsen et al. 2010, Sollmann et al. 2013). Multiple factors are likely to affect detection probability, such as local density, seasonal or behavioural patterns, size of the species, the amount of area surveyed (Bailey et al. 2004), or survey design (Sollmann et al. 2013), meaning constant probability of detection is unlikely to hold true (O'Connell et al. 2012). Despite the problems associated with comparisons of relative abundance indices between species, space and through time, many studies have done so without validating the assumption of equal detection probabilities (e.g. Dinata et al. 2008; Datta et al. 2008).

Low density carnivore populations are often plagued with low probabilities of detection during camera trap surveys, this is particularly problematic as it results in lower precision of estimates of abundance parameters (White et al. 1982; Karanth and Nichols 2002; Lukacs and Burnham 2005), and an increase in the number of survey days, or sampling periods needed to obtain reliable data (Mackenzie and Royle 2005; Rovero et al. 2010). Therefore researchers often use strategic placement of camera traps to try and increase detection probabilities, and the majority of carnivore surveys using camera traps have used trails and roads for placement of traps (Harmsen et al. 2010), especially in forest environments (e.g. Rios-Uzeda et al. 2007; Lucherini et al.2009). However it has been demonstrated that such a survey design can be biased towards certain species, for example Weckel et al. (2006) found both paca *Agouti paca* and armadilo *Dasypus novincinctus* had higher chances of being captured away from trails in Belize forests. Similarly, in a study of puma and jaguar, Harmsen et al. (2010) showed camera traps placed on trails were biased towards puma captures, stating that comparisons of relative abundance between the two species should be made with caution. Placing camera traps on roads in densely vegetated forest habitats may be practical, as they effectively create a funnel through the dense vegetation, directing animal movement in front of a camera trap, and are the easiest areas for people to traverse (Harmsen et al. 2010). However such an approach may not necessarily be the best option in other habitats where dense vegetation does not restrict animal movement.

Carnivores are also well known to follow roads and trails in open habitats (O'Connell et al. 2011), resulting in many camera trap surveys of large carnivores using such locations for placement of traps in open areas (e.g. Spalton et al. 2006; Trolle et al. 2006). Mann et al. (2014) investigated the differences in detection probabilities of a range of African mammals in an arid environment, and found as a guild carnivore detection probability was influenced by distance from the road, with detection probability sharply decreasing as distance from the road increased. However a large body of literature exists to suggest that whilst apex predators preferentially use roads and trails, in those areas where apex predators are present, mesopredators may avoid such locations (Hayward and Marlow 2014), suggesting such designs could be biased towards larger species. Such biases in road/trail placement of camera traps can mean that the use of this survey design used for multiple species may not be suitable.

Another popular approach to increasing detection probabilities of carnivores has been the use of baits and lures (Dillon and Kelly, 2007), for example Thorn et al. (2009) found fish lure significantly increased encounter rate for brown hyenas *Hyaena brunnea*, whilst du Preez et al. (2014) found bait to significantly increase capture rate for leopards. However, the use of baits in surveys is debated, with concerns being raised regarding violations of the geographic closure assumption of capture-recapture surveys if it causes permanent immigration or emigration onto and off the trapping grid, as well as differences in levels of habituation through time (Balme et al. 2014). Gerber et al. (2011) examined the effects of baited camera traps on Malagasy civet *Fossa fossana* and found baits not to affect immigration or emigration, abundance or density estimates, but to increase precision of these estimates. However, for large African carnivores the use of baits has also been suggested to raise ethical concerns as it potentially increases individual vulnerability to trophy hunting, for which baits are often used (Balme et al. 2014).

Water sources in arid environments are also potentially promising sites for camera trap placement as a number of water dependent species will be attracted to such areas, and therefore might be seen as a natural attractant without being associated with the problems of more traditional baits. However, to date no study exists comparing detection probabilities of carnivore species on roads and at water sources in arid environments. Namibian commercial farmlands provide an excellent opportunity for such a study, as due to low rainfall farmers are forced to provide water and in artificial troughs for domestic livestock and roads are used to connect such troughs.

As an alternative method to camera trapping, non-invasive sampling, in which hair or other genetic material is collected without interaction with the animal (Galaverni et al. 2011), has recently become an increasingly used and important tool for enabling genetic studies of populations of rare and elusive species (Henry and Russello 2011). Furthermore, hair samples can offer more data than camera trap images, for example Jones et al. (2006) used non-invasive sampling to collect grizzly bear *Ursus arctos* hair to examine diet via stable isotope analysis. The DNA from hair is known to be of better quality than that from scats and is less expensive to analyse (Bremner-Harrison et al. 2006). A variety of techniques are used such as simple hair snares that are often baited made from barbed wire placed where an animal is likely to walk so that hair is snared on the barbs as the animal passes (e.g. Gardner et al. 2010). Other studies have used rub stations, where a rough surface such as carpet, often with protruding nails (e.g. Weaver et al. 2010) or wooden stakes (Hanke and Dickman 2013), is used in conjunction with novel or prey related scents to induce rubbing behaviour. Other studies have used pre-existing features within the environment from which to collect hair samples, for example in the Russian Far East Sugimoto et al. (2012) collected Amur tiger hair samples from fences, trees and military barbed wire.

Most studies using non-invasive hair collection devices focus on a single species, such as tigers *Panthera tigris* (Mondol et al. 2009), polar bear *Ursus maritimus* (Herreman and Peacock 2013), Eurasian lynx (Schmidt and Kowalczyk 2006) and ocelots (Weaver et al. 2012), amongst others. Few studies have used or tested the efficiency of such devices for multiple species (but see Zielinski et al. 2012), and the lack of versatile devices for different species, or groups has been noted (e.g. Schmidt and Kowalczyk (2006)). One of the few studies which aimed to use rub stations on multiple felid species used roughened wooden stakes baited with tuna emulsion oil in the Namib Desert (Hanke and Dickman 2013). The technique detected its target species of African wild cat and black-footed cat *Felis nigripes*, as well as feral cat, Cape fox, bat-eared fox, black-backed jackals and several species of

Viverrids, and therefore proves it is possible to detect a range of species with a single device.

Camera traps and non-invasive hair collection devices are both potentially effective means of surveying rare and elusive species, and the few comparative studies available show in general camera traps to be more efficient at detecting carnivores (e.g. Gompper et al. 1999, Long et al. 2007). Monterroso et al. (2013) found camera traps to be 6.7 ± 1.1 times more effective in detecting target mesocarnivores, than hair snares, whilst Reed (2011) found the efficiency of the two methods to vary between species. As non-invasive methods for collecting hair offer the additional options such as genetic and stable isotope analysis, any effective methods are likely to be of great use to carnivore conservation research.

This chapter aims to examine and develop effective and efficient methods of surveying a guild of carnivores in an arid environment. The chapter aimed to forfill the following objectives; to produce relative abundance estimates, latency until first detection and naive occupancy estimates for each carnivore species, for two camera trap survey designs, one with traps set up at water and another where traps are set up along roads. Where possible, to use statistical analysis to compare the metrics listed in the first objective, as a measure of efficiency of each survey design. To compile a list of species detected by non-invasive hair collection devices, namely hair snares and rub stations, to compare to the species inventory as detected by camera traps, with hair samples analysed genetically to species level. Finally, to calculate the proportion of photographs obtained from each camera trap survey design, which could be used for individual identification, for African wild cat, brown hyena and leopard.

Due to the low density of and relative importance of water sources, it is hypothesis the water point camera trap survey design will produce higher relative abundance indices, lower latency until first detection and higher naive occupancies, for all carnivore species. As carnivores are more likely to stop and drink at water points, it is hypothesised the proportion of photographs obtained which are suitable for individual identification, will be higher for the water point survey design. Lastly, it is hypothesised carnivores with a social system will be detected more frequently by rub stations than solitary species, due to the advantages of receiving more attention in the form of allogrooming from conspecifics, which has previously been documented for spotted hyena.

8.3 Methods

8.3.1 Camera traps

Two camera survey designs were used, one set up in the presence of water (project camera traps) and a second where camera traps were set up along roads, (National Leopard Survey camera traps) as described in sections 2.3.1 and 2.3.2 respectively. Camera trap data was entered into Excel spreadsheets as described in section 2.3.1. Due to the low water point density and correspondingly low numbers of water points monitored at the northern study sites (see section 2.1 for more details), comparison between detection probabilities, latency and naive occupancy at water points and roads were only made in the south. As MET/road traps were removed from the south in August 2013, only the winter period (29th May to 3rd August) was analysed.

8.3.2 Detection probabilities

The relative abundance index for each carnivore species was determined (for details see section 4.2.1.2), during both the winter and summer period for the southern sites, and used as a measure of detection probability (c.f. Harmsen et al. 2010; Mann et al. 2014). As road camera traps were interspaced between water camera traps, and stratified by habitat, it was believed no differences in abundance of species would be seen between the two survey designs.

8.3.3 Latency until first detection

The latency until first detection of each species was calculated for all carnivore species for the two camera trap designs. Latency is defined as the time in days from camera trap deployment/the start of each survey period (i.e. winter and summer) until the species was first detected (Foresman and Pearson 1998).

8.3.4 Naive occupancy

Naive occupancy, defined as the proportion of camera traps where the species was detected, was calculated for each species, site and season for each of the camera trap set ups to allow for comparison of methods.

8.3.5 Individual identification

For those species having individually unique markings, with sufficient sample sizes, camera trap images were examined to determine if individual identification could be made based on the clarity of markings. The proportion of images where identification could be made was then calculated from the total number of images from each survey design. As road camera traps were set to take five images per trigger with no delay between triggers, and water camera traps set to take one image per trigger, only the first image per trigger was used from road camera traps. Fisher's exact tests were conducted to examine for significant differences in the proportions of images where identification was possible for each survey design.

8.3.6 Non-invasive hair collection devices

Rub stations and hair snares were used across the five study farms to non-invasively collect hair from carnivores. A full account of the methods, locations and numbers can be found in section 2.3.3. As the hair snare set up at the Tsirub offal pit was placed under the main access to the pit, it was considered a baited hair snare, as animals were using the hole to access offal within the pit.

8.3.7 Genetic analysis

8.3.7.1 DNA extraction

DNA was extracted from 75 hair samples of unknown species, with visible roots or suspected presence of roots. Extractions were performed using a DNeasy blood and tissue extraction kit (Qiagen) following a user-developed protocol ’Purification of total DNA from nails, hair, or feathers using the DNeasy blood and tissue kit’ and the following modification: DNA was eluted in 100 ul instead of 200 ul to increase DNA concentration. Three to seven individual samples were extracted simultaneously. An extraction blank was included in every extraction to detect any potential contamination, and utensils (glass work surface, scissors, and forceps) as well as surrounding work areas cleaned with bleach, water, and ethanol between each sample processing.

The number of hair roots extracted aimed for was 5 - 10, depending on the thickness of the hair; however this number was reduced if the number of hairs of same aspect available in the collection container was less, and increased if fine hairs were present in an entangled bushel. For each extraction 1 to 12 hairs were used and up to 5 mm of the root end of the hair cut into the lysis buffer of the first extraction step. The first lysis step was performed for a length of 2 - 16 hours to increase the success of the tissue and cell lysis. The subsequent extraction steps were performed following manufacturer's protocol (Qiagen).

8.3.7.2 Genetic species identification

Species identification was performed using a small mitochondrial fragment which was verified for use in African carnivores at the Cheetah Conservation Fund, and for which a reference sequence database of African carnivore species was established using voucher specimens (data not published). The reference sequences were then used to identify species from the unknown hair samples.

DNA was amplified using a AmpliTaq Gold Polymerase (Applied Biosystems) and a touchdown PCR program with annealing temperatures ranging from 60 to 50 ^{o}C on a 9700 Thermocycler (Gene Amp® PCR System 9700) (Applied Biosystems). Extraction blanks, as well as negative and positive PCR controls were included in each PCR reaction. If contamination was detected, the laboratory work was repeated. Successful amplification was verified with gel electrophoresis and visualisation of the PCR product on a UV table. PCRs were repeated up to four times, and 0.4 mg/ml BSA was added to the PCR reaction for samples that failed to amplify twice in a row; if no product was obtained after four attempts, the sample was dropped.

All PCR products were purified using illustra Exo-Sap-it (GE health care), after which 1 µl of purified product was included in a sequencing reaction set up with Big Dye® terminator v1.1 cycle sequencing kit (Applied Biosystems). Sequencing products were purified with ethanol precipitation, and run on a 310 or 3130 Genetic analyser. Sequences were initially assessed with sequencing analysis software 5.3.1 (Applied Biosystems) then aligned to reference sequences using the program Geneious v.6.8 (www.geneious.com) to assign a species identity to the sample. Results were accepted when the same species was obtained twice from independent PCRs. Samples which yielded results with contradictory results were dropped as a mixed hair sample was then suspected.

8.4 Results

As MET traps were removed in August 2013, only results from the winter period in the southern sites are presented. During this period a total of 1,106 independent carnivore events were recorded over 1,676 trap nights. Black-backed jackal was the most commonly recorded species, totalling 70.90 % of all carnivore records, whilst cheetah was the least frequently detected species, being captured just once during the entire winter period (Table 8.1).

Table 8.1: Total numbers of carnivore independent events across all camera traps for the southern sites during the winter period (29th May to 3rd August 2013)

Species	Total # of independent events
Cape fox	66
Bat-eared fox	26
Black-backed jackal	894
Honey badger	10
Aardwolf	3
Spotted hyena	3
Brown hyena	41
Leopard	32
Cheetah	1
African wild cat	30
Total	**1,106**

8.4.1 Probability of detection

Mean detection probabilities were highest from the water source survey design for all species (Table 8.2), with Mann-Whitney U tests showing detection probability to be significantly higher from the water source survey design for black-backed jackal (*W* = 100, *P* = <0.001), honey badger (*W* = 74, *P* = 0.03) and brown hyena (*W* = 77, *P* = 0.03).

Table 8.2: Mean detection probabilities for carnivore species from water and road camera trap survey designs, species with significant differences between detection probabilities produced by the two survey designs highlighted in bold

Species	**Mean detection probability (S.E)**	
	Water	**Roads**
Cape fox	6.02 (5.68)	0
Bat-eared fox	4.90 (0.3)	0
Black-backed jackal	**123.13 (33.74)**	**3.87 (2.52)**
Honey badger	**2 (0.70)**	**0.27 (0.27)**
Brown hyena	**5.73 (1.54)**	**1.49 (0.58)**
Leopard	3.01 (1.05)	1.63 (0.77)
African wild cat	3.77 (2.37)	0.48 (0.37)

8.4.2 Latency until first detection

Not all camera traps recorded every species, therefore only data from positive camera traps, i.e. those which detected a species were included. Mean latency until first detection was shorter for the water source survey design for all species (Fig. 8.1), with the exception of honey badger and leopard. Only back-backed jackal (*W* = 0, *P* = 0.006) showed a significant difference in latency until first detection between the two survey designs.

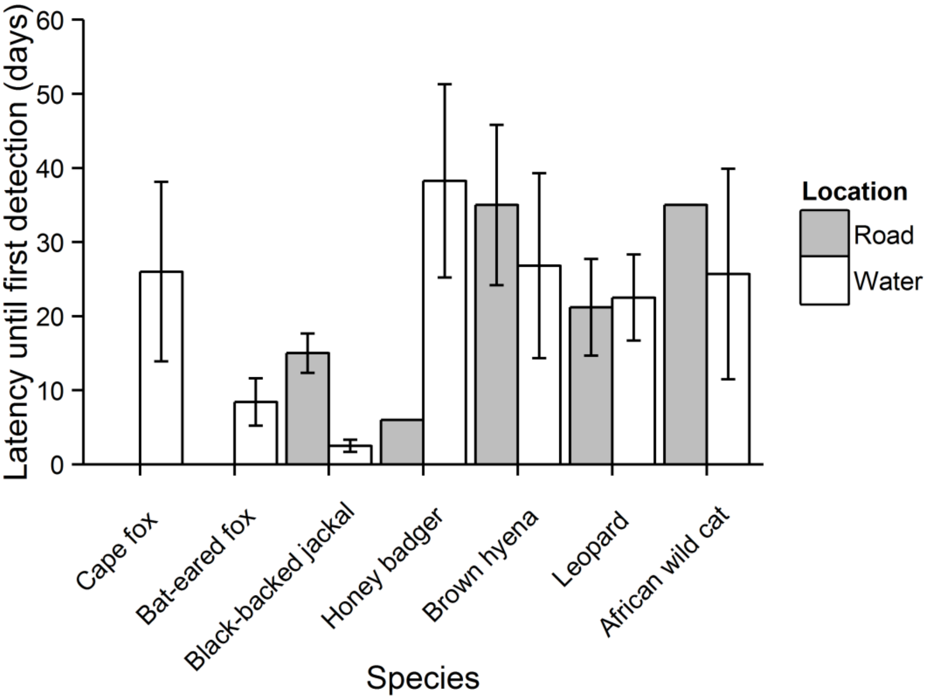


Figure 8.1: Mean latency (days ± SE) until first detection, comparison of placement on roads and at water, across the southern sites during the winter period (29th May to 3rd August 2013), for positive camera traps (i.e. those which detected the species in question) only. A significant difference seen in latency until first detection between water and road camera trap designs for black-backed jackal only (Mann-Whitney U: $W = 0$, $P = 0.006$).

8.4.3 Naive occupancy

Naive occupancy estimates from the two camera trap survey designs were higher at water than on roads for black-backed jackal, honey badger, brown hyena and leopard. Black-backed jackal showed the biggest difference between set ups, naive occupancy at water points was 1.0, indicating all camera traps detected the species, in comparison camera traps set up along roads gave a naive occupancy of 0.4. African wild cat was the only species which showed a higher naive occupancy from the road set up, however it can be seen that the difference between the naive occupancy estimates from the two set ups was much smaller, being just 0.03 for each species. Both Cape fox and bat-eared fox failed to be detected by camera traps set up along roads, with naive occupancy from the water points set up being 0.3 and 0.4 for Cape fox and bat-eared fox respectively (Fig. 8.2).

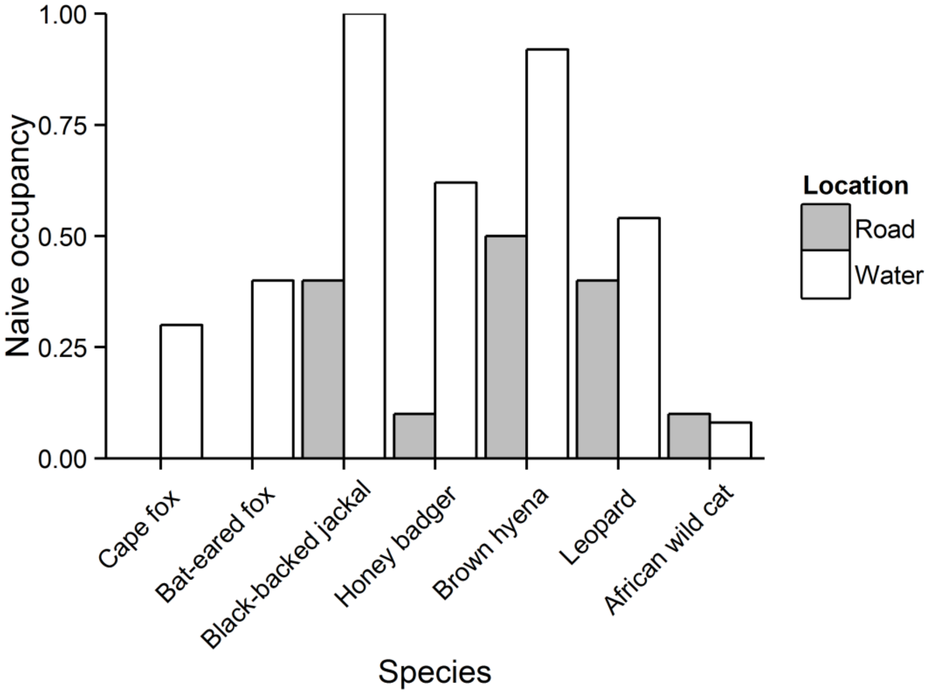


Figure 8.2: Comparison of naive occupancy (proportion of camera traps that detected the species) estimates for carnivore species across the southern sites from the two camera trap set ups; water and road survey designs

8.4.4 Individual identification

The three species having sufficient sample sizes and unique natural markings allowing individual identification, brown hyena, leopard and African wild cat, all showed the proportions of photographs suitable from individual identification, i.e. where the stripe or rosette pattern was clearly visible, was higher from road camera traps than those placed at water sources. A proportion of 0.57 photos from road camera traps were suitable for identification, compared to 0.12 photos from water source camera traps for brown hyena, which was not significantly different (Fisher's exact test, *P* =0.07). Leopard showed no significant differences in the proportions of suitable photos between the two survey designs (Fisher's exact, *P* = 0.41), all photos from road camera traps were suitable for individual identification, compared to 0.61 obtained from water source camera traps. A proportion of 0.67 African wild cat images from road camera traps were suitable for individual identification compared to 0.15 from water source camera traps, which was not significantly different (Fisher's exact test, *P* = 0.19).

8.4.5 Non-invasive hair collection devices

A total of 104 hair samples were collected, 67 from rub stations and 37 from hair snares from the total period that the non-invasive hair collection devices were operational (October 2012 to May 2014). However, only 75 hair samples contained enough hair for genetic analysis; 44 from rub stations and 31 from hair snares. Eighty-seven percent of rub stations collected hair samples whilst 75 % of hair snares collected hair. Rub stations collected a total of 417 individual hairs with a mean of 9.26 hairs per station (range 1 - 45), whilst hair snares collected 750 hairs, with a mean of 24.19 hairs per snare (range 1 - 91). Hair snares collected significantly more hairs per device than rub stations (Wilcoxon rank sum: W= -1.99, P = 0.04).

Genetic analysis could not produce species identification for all hair samples; 60% of rub station samples were analysed to species level, whilst 71.96 % of hair snare samples produced species results (Table 8.3).

Table 8.3: Summary of success of genetic analysis of hair samples gained from non-invasive hair collection devices, as analysed by the Cheetah Conservation Fund genetics lab

Source	*n*	Did not work - No PCR	Mix - dropped	Sample of insufficient quality	Species confirmed
Rub stations	44	1	12	5	26
Hair snares	31	2	5	3	21
All	75	3	17	8	47

Out of a possible 11 species detected by camera traps, only five species were detected as detailed in Table 8.4 below. Brown hyena was the most frequently detected species (53.19 % of samples), whilst Cape fox was only detected once. Both rub stations and hair snares (baited and non-baited) detected four species each, with Cape fox only detected by rub station and aardwolf only detected by hair snares.

Table 8.4: Summary the number of detection events for each species collected from non-invasive hair collection devices across all study sites

Species	Rub station	Non-baited Hair snare	Baited Hair snare	Total
Cape fox	1	0	0	1

Black-backed jackal	8	6	0	14
Aardwolf	0	2	0	2
Brown hyena	13	5	7	25
Leopard	4	1	0	5

8.4.6 Comparison of species inventories

From 1st May 2013 to 1st May 2014 non-invasive hair detection devices in total detected 44.44 % of the species detected by camera traps in the north, however an extra species, brown hyena, was detected by non-invasive hair collection devices which was not detected by camera trap. In the south just 27.27 % of species detected by camera trap were also detected by non-invasive hair collection devices (Table 8.5). Jaccard's indices (Jaccard 1912) of similarity between non-invasive hair detection devices and camera traps were similar for the north and south; 0.30 for the north, and 0.27 for the south.

Table 8.5: Comparison of species inventories as detected by camera traps and non-invasive hair collection devices from May 2013 to May 2014. Ticks representing when a species was detected using that method

	North		**South**	
Species	**Camera traps**	**Non-invasive hair collection**	**Camera traps**	**Non-invasive hair collection**
Cape fox	✓	✓	✓	
Bat-eared fox	✓		✓	
Black-backed jackal	✓	✓	✓	✓
Honey badger			✓	
Aardwolf	✓	✓	✓	
Spotted hyena	✓		✓	
Brown hyena		✓	✓	✓
Leopard	✓		✓	✓
Cheetah	✓		✓	

Caracal	✓		✓	
African wild cat	✓		✓	
Total	**9**	**4**	**11**	**3**

8.5 Discussion

Camera traps have been widely used as a method for inventorying terrestrial mammals (e.g. Srbek-Araujo and Chiarello 2003; Trolle 2003; Azlan 2006; Mugerwa et al. 2012), often aiming to document all species present in a relatively short period of time. The results of this study highlight the effect of fine-scale camera trap placement on detection probability for a guild of eight sympatric carnivore species in an arid environment. That detection probabilities for all species were higher from camera traps placed at water, and for some species significantly so, in comparison to those produced by camera traps placed along roads, would suggest such a design to be suitable for multiple carnivore species in an arid environment. However, that for species with individual identifiable markings, the proportions of photos suitable for identification were higher from the water source survey design, would suggest for studies where identification of individuals is essential, the road survey design would be more appropriate. In comparison to camera traps, non-invasive hair collection devices used showed low success, detecting only 44.44 % of species detected by camera trap in the northern sites and 27.27 % of species detected by camera trap in the south during the same period. Despite this low success, hair snares in the northern sites detected brown hyena which camera traps failed to detect. This might suggest a combination of the two methods would be an ideal situation for inventorying carnivores in such environments, however this is discussed in more detail below.

Camera traps are often placed on roads when surveying carnivores (e.g. Dillon and Kelly 2007; Stein et al. 2010; Negroes et al. 2010), and many studies have used spoor counts on roads as a measure of relative abundance or occupancy for carnivores (e.g. Meville and Bothma 2006; Funston et al. 2010; Stein et al. 2012; Srivathsa et al. 2014). The results of this study showed detection probability to be higher at water in comparison to roads for all species, and significantly so for black-backed jackal, honey badger and brown hyena. Additionally it showed Cape fox, bat-eared fox, aardwolf, spotted hyena and cheetah were not detected by road camera traps, despite camera traps at water sources confirming their presence in the area. Previous studies have shown camera trap placement can affect which species are detected, for example Srbek-Araujo and Chiarello (2005) found camera traps placed along trails to under-represent small mammal (< 1 kg) diversity in neotropical Brazilian forests. Meanwhile, Harmsen et al. (2010) found off-trail camera traps failed to detect puma, ocelots and white-lipped peccary *Tayassu pecari*.

Differences in detection probability could potentially be seen between camera trap brands and models (Kelly and Holub 2008), and in this study two different brands were used for the two survey designs; Reconyx were used on roads, whilst Scoutguards were used at water points. Cove and Jackson (2011) found differences in detection probability for bobcats between Reconyx and Moultrie camera traps in Missouri, with Reconyx detection probability being twice as high as Moultrie (0.23 and 0.11 respectively). Such a difference was suggested to result from the Moultrie's white flash scaring off bobcats before a photo was triggered, compared to the infra-red flash from the Reconyx. Wegge et al. (2004) also found tigers to become trap-shy over time, believing individuals became scared of the white flash and learnt to avoid camera traps. In this study both brands of camera trap used infra-red, however differences in advertised trigger speeds, the amount of time passing between the camera trap detecting a passing target and capturing an image (Rovero et al. 2013), existed. The Reconyx HC 600 advertises a trigger speed of 0.20 seconds, whilst the Scoutguard 560V specifies a trigger time of 1.2 seconds. Such a difference in trigger speed could be expected to result in lower detection probabilities for camera traps placed at water, however the opposite result was seen.

Another potential reason for differences in detection probability between the two camera trap types could be the detection zone, defined as the area in which the camera is able to detect a target through its sensor (Rovero et al. 2013). The models both have a detection angle of 42^{o}, with the Reconyx having a detection distance of 21.34 m, compared to 24.38 m of the Scoutguard. Such a difference could result in differences in detection probabilities, however as camera traps were placed within 3 m of a water trough or in case of road camera traps placed adjacent to the edge of a road which were at most 3 m wide, targets were expected to walk well within the detection range of both camera trap models. Therefore the differences seen in detection probabilities were not thought to result from the different camera traps.

The probability of detecting an animal is thought to correlate with body size, with larger bodied species being associated with higher detection probabilities (Tobler et al. 2008; Rowcliffe et al. 2010). Whilst aardwolf, spotted hyena and cheetah were all undetected by road camera traps, the probabilities of detection at water point camera traps were all low, being less than one event per 100 trap nights, at 0.31, 0.32 and 0.10 for aardwolf, spotted hyena and cheetah respectively. However the two smallest species as determined by shoulder heights from Walker (1996), Cape fox and bat-eared fox, showed higher detection probabilities at water; 6.02 and 4.90 events per 100 trap nights respectively. Data from the northern site showed Cape fox use roads when travelling, and as camera traps were set up approximately 40 cm from ground level, they should be well able to detect bat-eared fox and Cape fox with mean shoulder heights of 30 cm and 31.5 cm respectively (Walker 1996). Therefore it is likely low detection probability associated with roads could be the reason for these species not being detected. As animals are likely to stop in front of a camera placed at water giving the camera trap time to trigger, it follows the probability of detecting the animal is higher than on a road where the animal is most likely to walk past and not stop.

Other studies have examined the effect of fine-scale placement on detection probability of carnivores. Camera traps placed on roads have produced higher detection probability/relative abundance estimates than off-road camera traps at the same site for jaguar (Sollmann et al. 2011), and for both leopard cat *Prionailurus bengalensis* and common palm civet *Paradoxurus hermaphroditus* (Sollmann et al. 2013). Other studies have demonstrated differences in use of different types of roads; Salom-Perez et al. (2007) found sex differences in road use for jaguar, with females avoiding man-made trails, whilst Dillon and Kelly (2007) found ocelots avoid natural trails, preferring to travel along high and low use roads. This study showed detection probability was sometimes orders of magnitude higher at water points in comparison to roads. Such a result is not surprising given that the lack of dense vegetation restricting carnivore movement to roads in the area. Furthermore, given the scarcity of water, water sources are expected to be attractive areas for a number of species.

Biodiversity surveys can often be short in length, for example Mugerwa et al. (2012) used two 30 day periods for a camera trap assessment in Bwindi Impenetrable National Park, Uganda, whilst Swann and Perkins (2003) used a six week sampling period for inventorying terrestrial mammals in the Rincon Mountains, Arizona. As a result, latency until initial detection is often used as a metric for comparing survey methods (Gompper et al. 1999; Barea-Azon et al. 2006; Long et al. 2007), with shorter latencies indicative of more effective methods. Camera traps at water points showed shorter mean latency until first detection for all species in the southern sites, although samples sizes were too small to show if this was significantly shorter. However it can be seen for some species that latency until first detection was much longer for camera traps on roads, for example African wild cat latency was 33 days longer. Therefore it is recommended when conducting carnivore biodiversity surveys in arid environments, that camera traps are placed mainly at water sources to decrease latency until first detection.

Naive occupancy, i.e. the proportion of camera traps to detect a species, was higher for camera traps at water for all species with the exception of aardwolf and African wild cat, where a difference of just 0.03 was seen between the two set ups. High naive occupancies reflect species widely distributed throughout an area (Zeller et al. 2011); as road camera traps were interspaced between water sources where possible, it is likely road camera traps are underestimating the distribution of species across study sites. However MacKenzie and Bailey (2004) caution against the use of naive occupancy estimates, as they do not take into account imperfect detectability of species, i.e. probability of detection being less than one given a species is present at a site. Furthermore, they argued unless detection of probability is exactly equal, the comparison of naive estimates will not be valid. Occupancy analysis showed differences in detection probabilities between the two set ups for all species, therefore such comparisons between naive occupancy estimates are unlikely to be valid.

Several studies have used baits and lures to increase the probability of detecting an animal, and for species with unique markings, also to increase the chances of capturing a suitable shot for identification (e.g. Gompper et al. 1999; Thorn et al 2009; Du Preez et al. 2014). Foster and Harmsen (2012) and Balme et al. (2014) expressed concerns regarding the use of baits, suggesting they could increase individual, behavioural and temporal heterogeneity in capture probability, especially if differences are seen in levels of habituation through time. Water in an arid environment can be considered a natural attractant for most species, and pre-existing water sources are unlikely to change the behaviour of an existing population. Additionally it should avoid sex bias seen with trail use in big cats (e. g. Foster et al. 2010), and therefore can be viewed as good placement for camera traps. However it should be noted that caracal in the northern sites were only detected by road camera traps during the entire study, and aardwolf only detected once at water. Therefore for a full species inventory in an arid environment, a combination of road and water camera traps should be used, and where the number of camera traps is limited, the majority of camera traps placed at water sources.

Spacing of camera traps has long been debated (Dillon and Kelly 2007), and has been shown to affect density estimates for tigers (Wegge et al. 2004) and ocelots (Dillon and Kelly 2007). When the spacing of camera traps is large in comparison to home range sizes of the focal species, density is likely to be underestimated, due to the few individuals covering large distances, for example dispersing individuals, causing inflation of the mean maximum distance moved (MMDM). Whilst it would be cost effective to estimate density for a range of species simultaneously, differences in home range sizes means this is rarely achievable in practice (Dillon and Kelly 2007). Using camera traps to estimate occupancy, or for pure biodiversity studies is much more practical, however the spacing of traps in such situations has received little attention. However the most important consideration is that every species and individual has a more than zero chance of being captured. Therefore it follows that spacing between traps must not be larger than home range sizes of each species (Meek et al. 2014).

This study used a spacing of 4 km between camera traps based on the average walking speed of large carnivores (see section 2.3.1 for more details), whilst the Namibian National Leopard Survey used a spacing of 3.5 km, based on the home range size of a female leopard with cubs from northern Namibia (Stein et al. 2011). Distances between water points on study farms varied, however only two water points on Tsirub and one on KAV were not included as a result of them being closer than 4 km to monitored water points. The small home range sizes of some of the smaller species in the study, for example honey badger at 1 - 2 km^2 and bat-eared fox at 2.79 km^2 (Estes 1992), in comparison to the camera trap spacing could result in such individuals of such species remaining undetected by camera traps. However, as water is a vital resource and rare in the study area, species might be expected to arrange home ranges around water sources, indeed Mizutani and Jewell (1998) suggested female leopards base home ranges around water. Therefore in arid environments placing camera traps at water sources might overcome problems associated with differences between species home range size and spacing between traps, and so the 4 km spacing used in this study is recommended. Spacing of camera traps on roads however is much more likely to result in missing individuals when spacing is large in comparison to home range sizes. When such an approach is used, spacing should be based on the home range size of focal species and as a result may not be an effective method for multiple species.

Examination of camera trap images suitable for individual identification showed for all three species where individual identification was possible, brown hyena, leopard and African wild cat, road camera traps produced higher proportions of suitable photos. Garrote et al. (2012) found baited camera traps produced a higher proportion of images suitable for identification than unbaited traps for Iberian lynx *Lynx pardinus*, suggesting this is a result of lynx spending more time in front of camera traps with bait. Similarly, du Preez et al. (2014) suggested leopards to spend more time in front of baited traps whilst eating thus increasing the number of images captured which improve the accuracy of identification through multiple views of the same individual. Additionally, Garrote et al. (2014) hypothesised baits causing animals to spend more time in front of traps to overcome problems with slow trigger speeds. Whilst carnivores are likely to spend more time in front of camera traps placed at water as they stop to drink, in comparison to road camera traps, often the angle of approach to the water trough may mean the camera triggers whilst the animal is still far from the trap, or a face on shot is obtained, not suitable for identification. In comparison, road camera traps are positioned perpendicularly to roads meaning carnivores pass in front of camera traps, and are usually captured so that the whole flank of the animal is in view and when used in pairs with each trap on one side of a road, images of both the left and right hand side of the animal can be obtained. Therefore, for species where individual identification is needed for density estimation, camera traps placed along roads may provide a better survey design than traps placed at water sources.

Variation in success and efficiency of non-invasive hair collection devices has been seen previously, for example Sheey et al. (2013) collected a total of 158 hair samples collected from non-invasive devices aimed at collecting pine marten *Martes martes* hair, from 24 hair traps in 14 months, 157 of which were successfully confirmed as pine marten using genetic analysis. Castro-Arellano et al. (2012) recorded 74 % of potential target mammal species in just 19 days of field effort in Mexico. In contrast, Comer et al. (2011) paired hair snares and camera traps to survey bobcats and found 15 visits by bobcats to hair snares in 1,680 trap nights resulted in just one hair sample. The low success of hair snares and rub stations seen in this study could be due to a number of reasons such as low encounter rate between carnivores and devices. Whilst care was taken to place rub stations on trees within 5 m of a road in an effort to increase encounter rate, camera trap data suggests lower detection probabilities on roads than at water points for most species, which could have resulted in the low number of hair samples collected. Downey et al. (2012) suggested the presence of gray fox *Urocyon cinereoargenteus* at hair snares as a potential reason for the generally low success of hair snares for surveying felids within gray fox range, and that the odour produced by the fox may be unattractive to felids. It is possible a similar phenomenon could be occurring in the study area, or that rub stations are simply not inducing rubbing behaviour in some carnivore species. However to investigate this further, camera traps would need to be paired with hair snares. Additionally, setting up devices near water could increase chances of encounter, as water troughs are often located next to concrete dams and devices could be attached to dam walls.

It was hypothesised that mainly Canids and Felids would be detected by rub stations, as such devices exploit the natural rubbing behaviours of these families (Kendall and McKelvey 2008). Additionally, social members of these families might be expected to use these devices as odours on the body have been shown to result in increased investigation and allogrooming from conspecifics in spotted hyena (Drea et al. 2002). Three of the four species detected by rub stations belong to Felid and Canid families, whilst the fourth species, brown hyena, is a social species. Therefore, that brown hyenas were detected by rub stations may not be surprising and would suggest this method works for species outside of the Canid and Felid families.

As all of the hair snares, except the Tsirub offal pit snare are passive, requiring only animals to pass through the hole, it was expected a more diverse range of species would be seen in comparison to rub stations. When investigating the use of tyres to facilitate wildlife movement through game fencing, Weise et al. (2014) recorded Cape fox, black-backed jackal, leopard, cheetah and caracal moving through. The low number of species recorded moving through holes in fences in this study could reflect the fact that all farms were not completely fenced, having either sections of the fence line completely down or from the presence of mountain habitat at farm borders where fencing was not used. This could result in carnivores moving over farm borders where there was no fence, however GPS collars or camera traps placed at fence holes would be needed to investigate this further, as it may also be the case some species pass through the holes and simply do not touch the snares. The baited hair snare at the Tsirub offal pit detected only brown hyena and one black-backed jackal sample, despite black-backed jackal being detected regularly in the offal pit by camera trap, and camera trap data suggested the hole where the hair snare was set up was the main point of entry to the pit. Such a result could be due to the barbed wire of the hair being too high to snare hair from the black-backed jackal. As hair snares are set up at pre-existing holes in fences, care must be taken to cover a range of hole heights to ensure species from a range of sizes can be detected.

Brown hyena made up 53.19 % of hair samples, with 28 % of all brown hyena samples coming from the baited hair snare set up under the fence of the Tsirub offal pit, a location where brown hyenas were captured on camera trap eating offal from the pit at a very high rate (mean 108.70 events per 100 trap nights). Previous studies have enjoyed success with baited hair snares (e.g. Foran et al. 1997; Dixon et al. 2006), usually by forming a triangle of barbed wire around three trees and placing a bait in the middle so the animal must pass between the strands of barbed wire to access the bait (Kendall and McKelvey 2008). Such an approach might not be suitable in the study area for two reasons; firstly the general lack of trees would mean finding multiple sites with three trees together would be difficult (for example Gunsbewys only had two trees on the whole farm), secondly such a design could potentially be a danger to game and livestock, especially when running, getting tangled and injuring themselves on the wire. Whilst the results of this study showed baited hair snares on offal pit fences have the potential to be successful, they are likely to be biased towards scavenging species such as hyena species and black-backed jackals.

Overall, the non-invasive hair collection devices showed a low detection rate in inventorying carnivore species in comparison to the camera traps. As mentioned earlier, the fact that brown hyenas in the northern sites were only detected by hair snares might suggest a combination of the two methods as a best strategy for inventorying carnivores in arid environments. However the ecology and behaviour of brown hyenas might explain why this species was not detected by camera traps in the north. Spotted hyenas appeared to be resident in the northern sites, being regularly detected by camera trap on NBR and Weissenborn. Spotted hyenas are socially dominant to brown hyenas and have been recorded chasing brown hyenas from carcasses, raiding brown hyena dens and on occasion killing brown hyenas (Mills 1990). Therefore brown hyenas might not be expected to be resident in the area due to the presence of spotted hyenas. The brown hyena detected by hair snares may have been from nomadic individual/s, which are usually males not living in a clan (Mills 1998), passing through the area, hence not being present for long enough to be detected by camera traps.

Brown hyenas are known to be less dependent on fresh drinking water than spotted hyenas (Skinner and van Aarde 1981). The provision of drinking water in both the Kruger National Park and southern Kalahari has been suggested as the reason for the increase in spotted hyena numbers and subsequent decrease in brown hyena numbers (Mills 1990; Mills and Funston 2003). Therefore due to the frequent use by spotted hyenas of the main water point in the north, and brown hyena's limited dependence on fresh water, it is possible the species did not visit the water point. The total effort and cost of setting up and maintaining the non-invasive hair collection devices along with the final cost of genetic analysis for the benefit of detecting one additional species which was likely not resident in the area is questionable. Due to general low detection rates, it is not recommended to use non-invasive hair collection devices in arid environments, however further studies making the modifications suggested here, i.e. placing devices near to water and ensuring a range of hole heights are covered by hair snares, could be worthwhile to see if success rates could be improved.

A total of 22.66 % of samples contained DNA from more than one species, meaning a species identification could not be ascertained. The design of both the hair snare and rub station meant more than one species could deposit hair on the device, which is known to potentially cause substantive genotyping errors (Pauli et al. 2011). Bremner-Harrison et al. (2006) suggested contamination of DNA on devices by more than one species is less likely to occur with low density populations and territorial species. Previous efforts have been made to develop single-catch snares, but these have largely been developed for small species and involve making a trap for the animal to go into, with a door that allows the animal to exit but stops another individual entering (e.g. Bremner-Harrison et al. 2006; Pauli et al. 2011). Beier et al. (2005), developed a single-use wire hair snare for use with brown bears which they set along trails where bears were known to travel. Such a design is unlikely to be effective on the farm study sites, as it relied on the presence of trees to attach to, which are not common throughout the study area. Additionally, barbed-wire could potentially represent a risk to game species which might become entangled in it. The development of a single-use hair snare or rub station could be a potential way to increase the sample sizes from such designs in an arid environments, however farmland carnivores are unlikely to enter any trap-type design, as farmers often use traps for lethal control, and it has been hypothesised in areas where lethal trapping has been carried out for some time only 'trap-shy' individuals remain (O. Aschenborn, *pers. comm*).

Problems arose with the quality of the DNA from the hair, which may have been degraded due to storage techniques. It was suggested better solutions for storage would have included storing the samples frozen, in ethanol, or in non-hermetic containers at room temperature in a dry environment. Additionally the time between checks may have contributed to the DNA degradation, although this would have been more problematic in a humid environment. Decreasing the time between checks may have also decreased the chance of more than one species depositing hair on the devices. However, due to logistical constraints such as fuel budget and distances between the two sites, decreasing time between checks is not a financially viable option.

8.5.1 Conclusions

This study has shown that camera trap placement at water points is superior to camera trap placement along roads, for surveying a guild of carnivore species in an arid environment. Detection probability, species diversity and naive occupancy were higher and latency until first detection lower in the water survey design, showing camera traps placed at water points to be more effective. However, it is important to note that for studies where individual identification is required, such as for capture-recapture surveys, a road camera trap design would be more appropriate given the higher proportions of photos suitable for individual recognition from this survey design. Non-invasive hair collection devices had a low success, failing to detect even half of the species detected on camera trap at either site. Reasons for low success could be low encounter rates between carnivores and hair snares and rub stations, especially for rub stations placed along roads, as the results of camera trapping shows lower probability of detection at such locations. The success of camera traps at water points in comparison to roads, points towards placing rub stations at water points to try and maximise encounter rates with carnivores. It is recommended a further study using water points as locations for rub stations be conducted to see if success rates of the devices can be improved, whilst pairing camera traps with rub stations to monitor behaviour at stations. The survey design used for non-invasive hair collection devices in this study would not be recommended, especially when camera traps are available for surveying carnivores.

9.0 Discussion

9.1 Summary

Human-wildlife is a growing and global problem, and within Namibia is one which represents an increasing risk to the conservation of carnivores, whilst threatening the viability of farming practices both at an individual and national level. This thesis represents the first ecological study of human-wildlife conflict in southern Namibia, attempting to find a link between the microhabitat features favoured by carnivores and those features identified by farmers as being associated with higher levels of conflict. Whilst the questionnaire data was in general agreement with many previous studies in highlighting the complexities of assessing human-wildlife conflict, by showing a general lack of associations in the data, some data did link to the ecological findings. Carnivores were highly attracted to water points, the density of which was positively associated with the perceived risk of both black-backed jackal and caracal individually, and with combined perceived risk score for all carnivores. Additionally, open plains/mountain transitional habitat was favoured by a number of carnivores, and the percentage of mountain cover on farms was positively associated with livestock losses. Somewhat worrying was the lack of association between perceived risk and actual livestock losses, which should be seen as a key issue to address when mitigating conflict. The study illustrated the difficulties of surveying carnivores in arid environments, but developed methodologies for improving probability of detection and thus precision in this habitat. Also, it illustrated which methods are not suitable. Due to the low levels of cattle losses, it is recommended where possible, cattle rather than smallstock, consisting of sheep and goats, are farmed. However, where this is not possible, the data would suggest locating kraals away from water sources, mountain habitat and offal pits.

9.2 Introduction

As an arid country, with the driest climate in sub-Saharan Africa (Sweet 1991), farming in Namibia is difficult, with dry conditions resulting in low rangeland productivity, and limited potential for arable crop production in many areas of the country. Despite this, the agricultural sector is an important part of the Namibian economy (Directorate of Planning 2005) as well as the biggest employer nationwide (IFAD 1997). Any challenges to farming success, such as predation of livestock by carnivores, is likely to represent a serious problem, from the scale of the individual farmer, whether this be on a commercial or subsistence level, to the agricultural sector as a whole. With Namibia having a strong conservation ethos, as illustrated by the success of the conservancy concept, the protection and sustainable management of its carnivore populations is key. However, due to the importance of the agricultural sector to the Namibian economy, maintaining carnivore populations must be done in balance with having a productive and financially successful farming industry.

This study set out to explore the extent of human-wildlife conflict on commercial farmlands in southern Namibia, by attempting to link ecological data to data pertaining to the human perspective of the conflict situation, to give a more holistic picture of the conflict situation. This study represents the first attempt to examine conflict in such a way within Namibia, and did so with two general aims firstly, what are the key environmental features across the farmlands that carnivores are attracted to? Secondly, are these features also identified by farmers as those associated with higher levels of conflict? Additionally, as researchers often avoid working in arid environments due to difficulties associated with low densities of carnivores, the study sought to identify the most effective methods for surveying carnivores in such habitats.

9.3 Addressing the main aims

9.3.1 What are the key environmental features across the farmlands carnivores are attracted to?

One of the main microhabitat features carnivores were attracted to across farmlands were water sources, both the artificial troughs farmers maintain for domestic livestock and wild game, and natural springs. As free-standing water is known to be a critical resource in arid environments (Sheilds et al. 2012), as well as a long recognised limiting factor for large-bodied mammals (Rautenstrauch and Krausman 1989), such a result is not surprising. Evidence for carnivores being attracted to such areas was found in two of the experimental chapters. Firstly, the occupancy analysis undertaken in Chapter three, showed presence of water was the microhabitat feature most frequently included in top-fitting models, where it always resulted in an increase in probability of occupancy. Additionally, Chapter eight demonstrated that carnivores were always recorded with higher probabilities of detection by camera traps at water sources in comparison to camera traps placed along roads.

Previous studies have also shown carnivores to be attracted to farmland water sources (e.g. Soto 2008; Schuette et al. 2013), with Atwood et al. (2011), finding them to be focal attractors to three sympatric carnivore species in a desert environment. As the bordering National Parks do not provide artificial water sources, with the exception of the Garub feral horse water trough in the Namib-Naukluft National Park, farmlands provide water sources at a higher than natural density, and therefore have the potential to affect carnivore and herbivore spatial ecology at a landscape level. However, it is not known if the attraction of carnivores to water sources would result in higher densities of carnivores than would be found naturally, due to the territorial behaviour of carnivores, which may limit the number of animals utilising each water point. It has been suggested that carnivore home range sizes often vary in relation to water availability (Bowers et al. 1990; de Beer and van Aarde 1998), which for territorial carnivores could lead to changes in population density. Furthermore, provisioning of artificial water in Kruger National Park has thought to have led to an increase in the number of lions owing to a year round availability of prey around these permanent water sources (Smuts 1978).

Although carnivores, including leopards, were attracted to water sources, the density of leopard was found to be higher in the north where water point density was lower than across the southern sites. The results of the leopard density estimates from this study in context of the entire National Leopard Survey, i.e. having the lowest density of leopards and the lowest annual rainfall, lend support to Martin and Meulanaer's (1988) findings that leopard density is positively correlated with rainfall across sub-Saharan Africa. Therefore, it may be tempting to imply the comparison of leopard density estimates between the northern and southern sites is in disagreement with Martin and Meulanear's (1988) finding, as a higher water point density was associated with a lower leopard density. However, it is most likely leopard density is positively correlated with rainfall due to its secondary effects on herbivore abundance through increased grazing availability (Stander 1997). As the majority of water sources across the farmlands are artificial, this source of water availability has no influence on grazing. Therefore it is unlikely the density of water sources is likely to influence natural herbivore abundance via increased grazing effects, and indeed the questionnaire data showed no association between wild ungulate abundance and water point density.

With a number of carnivore and herbivore species being attracted to water points, it was hypothesised they would become areas associated with a higher risk of predation, and potential sites for human-wildlife conflict to occur. Previous studies have shown the aggregations of herbivores at water sources are attractive to carnivores, who have been recorded as concentrating their hunting activity there (Hopcraft et al. 2005, Valeix et al. 2009). Carnivores also face the risk of predation at such sites in the form of intraguild predation, which is classified as an extreme form of interference competition (Holt and Polis 1997). Meanwhile, for herbivores this would be in the more traditional form of predation, between trophic levels. However, empirical evidence from Chapter four, suggests both carnivores and herbivores use temporal resource partitioning to avoid direct encounters at water points. Additionally, they do this in a way which reflects risk of predation, as evidenced by the relative differences in body mass between species pairs being associated with the degree of partitioning seen. Such data was important and encouraging not only for human-wildlife conflict, but also from a conservation standpoint as it is believed intraguild predation has the ability to reduce the carrying capacity of an area to lower densities than would be predicted from prey abundance alone (Linnell and Strand 2000). Therefore, although intraguild predation has been previously recorded between several members of the carnivore guild present on the farmlands, species are able to avoid each other at water sources, decreasing the risk of predation, thus allowing the coexistence of a diverse carnivore guild, including species of conservation concern.

Another key microhabitat feature preferred by carnivores was the open plains/mountain transition habitat, i.e. those areas between 0.5 and 1 km from a mountain base or mountain habitat. Evidence for this came from Chapter three, which showed open plains/mountain transition habitat to be included in the top fitting occupancy models for a number of species. This habitat was usually associated with increases in probability of detection, which is believed to be positively correlated with abundance (Royle and Nichols 2003). It is hypothesised such habitat is favoured as it is associated with increased hunting success (Hayward et al. 2006; Davidson et al.2012) with the cover resulting in a reduced visibility of carnivores to prey (Thorn et al. 2012). Therefore such areas have the potential to be sites where human-wildlife conflict may occur if prey includes livestock species.

Carnivores showing a preference for open plains/mountain transition habitat was believed to be due to increased cover in such areas being associated with increased hunting success. In contrast, stable isotope analysis of carnivore diet showed all carnivores to feed predominantly on prey based upon the C4 food web, namely herbivore species feeding on grasses and sedges (Bender 1971). Such data might suggest they are hunting in open plains habitats (Codron et al. 2006). Although stable isotope data from springbok came from a small number of samples, it could be seen all samples placed springbok within the C4 food web, even though it is traditionally considered as a browser (Estes 1992). Such a result is not surprising given that springbok in northern Namibia were recorded eating both C3 (trees and shrubs) and C4 plants (Lehmann et al. 2012), combined with the relatively low abundance of trees and shrubs across the study area. Therefore, whilst the suggestion of carnivores hunting in areas with increased cover is in contrast with isotope data, it is likely even those species traditionally viewed as browsers are also feeding on grasses due to the scarcity of trees in the landscape and may spend time in both open plains habitats and those habitats with more cover.

The presence of an offal pit, which represented an accessible and reliable anthropogenic food source, was highly attractive to both brown hyena and black-backed jackal in the south. Camera trap data showed high frequencies of visits to the pit by both species, with relative abundance indices being much higher than any water source camera trap for either species. Although sample sizes for stable isotope analysis were small, the data suggested diet of these scavenging species is affected by the offal pit, in comparison to those same species in the north. Such data would be in agreement with a number of previous studies which suggest anthropogenic food sources are widely and extensively used by mesopredators, with felids generally not utilising such resources given their preference for fresh meat (Newsome et al. 2015a). In contrast to other studies which have recorded carnivores as avoiding areas of human activity (e.g. Eurasian lynx Basille et al. 2009; puma Sweanor et al. 2008), this study showed scavengers were attracted to the offal pit which was located approximately 400 m from the main farm house, with staff dumping offal within the pit two to three times a week.

Debate in the literature exists regarding the effectiveness of human activity as a deterrent to carnivores predating livestock. Ogada et al. (2003) found livestock which were kraaled at night in bomas with high levels of human activity were less likely to be predated by large carnivores in Kenya. However, in contrast Kolowski and Holekamp (2006) found high levels of human activity around bomas were not associated with lower levels of livestock predation in Kenya. They suggested spotted hyena, being opportunistic feeders, were more likely to be visiting bomas to feed on waste materials there. Furthermore bomas with more human activity and hence more waste were more likely to be more attractive to hyenas, and were consequently associated with higher levels of opportunistic livestock attack when hyenas visited the area. This study has shown brown hyena and black-backed jackal to be highly attracted to the offal pit despite it being the only location on the farm with constant human activity. Although no kraal or boma was located at the house, due to Tsirub being a game farm, it is possible increased visits by these species, especially black-backed jackal, could result in increased opportunistic livestock predations if a kraal was located in the area. With many farmers in the area locating kraals for smallstock close to houses (*pers. obs*.), the presence of an offal pit in the same area may therefore represent an increased risk of predation from carnivores utilising the offal pit.

When examining the microhabitat features carnivores are attracted to across the commercial farmlands, it is interesting to note two of the main features identified as attractive, water sources and offal pits, are unnatural in the environment. Although carnivores were attracted to both artificial and natural water sources, the provisioning of artificial water sources by farmers means the overall density of water sources occurs at a higher than natural density across the farms. The offal pit monitored represents a large, accessible and reliable food resource, available to carnivores without the need for hunting. Whilst carcasses of both domestic livestock and herbivores are also large, accessible food sources, they are not usually available permanently as food from the offal pit was. Maude (2005) found livestock carcasses to be available in large numbers throughout the year, and suggested predation by lions, spotted hyena and black-backed jackal, as well as seasonal droughts resulting in cattle mortality were the cause. However, in this study cattle farmers reported generally low levels of livestock predation by carnivores, and cattle carcasses were only seen during before the arrival of the summer rains in 2013 (*pers.obs.*).

9.3.2 Are the microhabitat features identified by question one also identified by farmers as those associated with higher levels of conflict?

Identifying the features on farmlands attractive to carnivores is of interest, however when examining human-wildlife conflict, it is important to examine if these features are those associated with higher levels of livestock losses. Hence, addressing the second research question is vital in the progress of making informed mitigation recommendations. Data from the farmer questionnaire demonstrated the complexities of trying to assess the human perspective of human wildlife conflict. Few patterns were seen in the data, with only water point density and livestock density being associated with perceived risk, although not for all carnivore species. This data fits into the general pattern of the human perspective of conflict being complex and diverse (Hermann et al. 2001; Dickman 2010), perhaps suggests there is no 'one fits all' solution to mitigating conflict.

Ecological data showed carnivores were attracted to water points, with questionnaire data suggesting density of water points being positively associated with perceived risk of both black-backed jackal and caracal individually, and with combined perceived risk score for all carnivores. However, water point density was not associated with livestock losses. Such data strengthens that presented in Chapter four which suggested that although water points were attractive areas for both carnivores and herbivores, temporal partitioning was used by domestic livestock, to avoid visiting water points at peak carnivore activity times, thus decreasing the risk of predation at such sites. Therefore the association between water point density and perceived risk score needs some discussion. It was suggested in the Chapter seven that this association may have resulted from water point density being positively correlated with carnivore abundance. Previous studies have shown carnivore abundance and predation risk to be positively associated (Kaartien et al. 2009; Schumann et al. 2009). However, data from the Chapter five suggested leopard density was higher in the north where water point density was lower. Data for other species' densities in relation to water point density is not available.

A possible explanation to the association seen between perceived risk scores and water point density may lie in the relationship previous studies have noted between visibility of a carnivores, and culpability. Rasmussen (1999) suggested the high visibility of

African wild dogs related to their large pack sizes and diurnal nature, results in their culpability being more often related to visibility, rather than direct evidence. Similarly, Rust and Marker (2013) suggested that the crepuscular and diurnal natures of black-backed jackal and cheetah, and resulting high visibility in comparison to other carnivore species, resulted in them the most commonly cited species responsible for livestock predation in north central Namibia. It is possible, therefore, that the association between perceived risk and water point density may be due to the increased visibility of spoor at water points, as a result of them being attractive areas for carnivores. A farmer with more water points may see carnivore spoor in more locations and more frequently than a farmer with fewer water points, and thus perceive carnivores to be a bigger risk.

Questionnaire data suggested a positive association between the percentage of mountain habitat on a farm and the level of livestock losses. As previously discussed such an association may be a result of the higher hunting success for many carnivore species in areas with increased cover (Hayward et al. 2006). Data from the occupancy analysis in Chapter three showed whilst leopard preferred mountains in summer, a preference of sites away from mountains was preferred in winter, with camera trap data showing six new locations, all in open plains or open plains/mountain transition habitats, being recorded for leopard in summer. Additionally black-backed jackals preferred sites away from winter in the winter in the north. Baboons are also known to favour mountainous habitats (Estes 1992) and were identified by a number of smallstock farmers as being responsible for smallstock predation. The majority of farmers could not comment when asked if livestock predation was associated with a particular season, however areas with cover are likely to represent optimal foraging grounds all year round, which may explain the association between mountain cover and livestock losses.

9.3.3 What methods are suitable for surveying carnivores in arid environments and how can existing methods be modified to increase success in arid environments?

The third research question asked which methods were particularly effective for surveying carnivores in arid environments. Data from this study, specifically empirical data from Chapter eight, was in agreement with the general consensus within the field of ecology that camera traps are an effective method of surveying cryptic carnivores (Karanth 1995). Non-invasive hair collection devices only detected 44 % and 27.27 % of species recorded on camera trap in the northern and southern sites respectively. These results agree with the findings of Hanke and Dickman (2013), the only other study to test the efficiency of non-invasive hair collection devices in Africa, who found wooden stakes baited with tuna in the Namib and Kalahari Deserts to collect small felid hair samples at a low rate.

Camera traps placed at water sources resulted in higher detection probabilities, which in turn is known to be associated with higher precision of population estimates (White et al. 1982; Karanth and Nichols 2002), for all species than camera traps placed along roads and trails. As many studies have previously placed camera traps along trails and roads in an effort to increase probability of detection (Harmsen et al. 2010), the results of this study are important as they show for arid environments the placement of camera traps at water sources is a more effective and efficient way to survey carnivores. However, the study also demonstrated such a camera trap placement results in lower numbers of photographs suitable for individual identification, in comparison to when camera traps are placed along roads. Whilst it is possible that such problems may be overcome with the use of baits (du Preez et al. 2014), multiple problems with such use, such as violating the geographic closure assumption and habituation of carnivores to attractants (Balme et al. 2014) as discussed in Chapter eight, would warn against the use of baits. Therefore, it is recommended the final outcome of the particular study must be considered by researchers when choosing the most suitable camera trap placement.

A comparison of the farmer estimates of leopard numbers on their property to those gained from camera trap data might suggest using landowner questionnaire data to examine the population status of a species is not a reliable method. Very few previous studies have made comparisons between data gathered from local communities in comparison to ecological data, with White et al. (2012) finding in a review of 89 questionnaires in which the factual information collected could be checked by field work, just 6.7 % actually conducted ground-truthing work. However, when comparing data gathered from local communities and camera trap data regarding the presence of mammals in Yenice Forest in Turkey, Can and Togan (2009) found local people were unaware of the presence of jackal *Canis aureus* and brown hare *Lepus europaeus*, whilst they failed to detect lynx *Lynx lynx* that local inhabitants believed to be present. Therefore the data from

Chapter five follows the pattern of Can and Togan (2009), showing data collected from local communities and landowners regarding carnivore populations may not be reliable, and would not be recommended in lieu of field work (Edwards et al. 2015). The implications of this finding show a very real value given that the National Leopard Survey (Stein et al. 2011a), used farmer questionnaire data to estimate leopard density in areas where field work had not been conducted, which contributed to the overall national leopard population estimate. As leopard trophy hunting quotas in Namibia are based on a sustainable off-take of 3 - 4 % of its adult male population (Stein et al. 2011a), estimation of population size from unreliable data could result in a quota set above a sustainable level, which may ultimately be detrimental to the leopard population.

9.4 Limitations

The low success of the non-invasive hair collection devices in this study has led to one of the main limitations; low sample size of hair samples for stable isotope analysis. The study originally aimed to examine the relative contribution of domestic livestock to the diet of carnivores, however the sample sizes were too low for the necessary isotope mixing models. Whilst Chapter six has discussed the low number of carnivore hair samples, it is worth discussing the issue here in relation to the study as whole. Knowing to what extent carnivores feed upon domestic livestock would have allowed a comparison of those species identified by farmers as high risk to livestock, to those species identified by stable isotope analysis as having high proportions of their diet consisting of domestic livestock. However, due to felids having a preference for hunting their prey, rather than scavenging food (Newsome et al. 2015a), perhaps such a comparison could only be made for felids, which would have still been of importance given that leopards were ranked second by farmers for perceived risk. Any domestic livestock in the diet of scavengers could be the result of scavenging rather than predation. Such a comparison for felids would have been extremely useful given that farmers and landowners have been recorded as deliberately inflating losses or blaming carnivores as responsible for livestock loss without having direct evidence (Hermann et al. 2001).

Another limitation of the study has been the absence of data regarding the spatial ecology of carnivores across the farmlands, with particular reference to water points and the offal pit. The presence of both features may have influenced home range size and seasonal shifts in home ranges of carnivores (Newsome et al. 2015a). Previous studies have suggested carnivores base their home ranges around resources such as water, and that water availability can influence home range size (Bowers et al. 1990; de Beer and van Aarde 1998). Anthropogenic food sources have been shown to result in reduced home range sizes of a number of carnivore species, as well as reducing shifts in size and space related to seasonal effects (Newsome et al. 2015a). Examining such effects using GPS collars fitted to focal carnivore species would have demonstrated the effects of these anthropogenic resources on carnivore ecology. Previous research has also demonstrated anthropogenic food sources can result in increased abundances of carnivores with access to them (e.g. coyote; Fedriani et al. 2001). Examining the effect of the offal pit on carnivore densities will be more difficult due to the problems associated with surveying species without individually unique natural markings (see Chapter eight for a more in-depth discussion). A potential solution may be to use individual ear tags, which have previously been used with coyotes (Newsome et al. 2015b) and kit foxes (Dempsey et al. 2014), in combination with capture-recapture analysis of camera trap data (Karanth 1995). However, given black-backed jackal's reputation amongst farmers as extremely difficult to catch in a trap (JJ Bosman, *pers. comm*.), the viability of this method is questionable.

The use of biologgers, minature animal attached tags for logging and relaying information regarding an animal's movements, behaviour, physiology or environment (Rutz and Hays 2009), may have been extremely useful in this study. Accelerometers, a particular type of biologger, are able to measure changes in velocity of the body through time, and have been used with over 120 species to date (Brown et al. 2013). Accerelation movements are usually collected in three dimensions of animal movement at a typically high resolution of over 10HZ, and particularly useful for carnivores, given that acceralation can be linked to hunting behaviour and energy expenditure (Brown et al. 2013). Accelerometers have previously been used to identify temporal and spatial patterns of hunting behaviour in carnivores. For example, Williams et al. (2014) used accelerometers within a collar, on pumas, and were able to continously monitor the energetic movement and behaviour in four wild individuals. From the information gained, the authors were able to identify different hunting behaviour patterns, ranging from a sit and wait approach to those individuals using constant movement when foraging (Williams et al. (2014).

Biologgers, and in particular accelerometers with GPS collars, used on the focal carnivore species within this study may have been particularly useful for highlighting spatial patterns in hunting behaviour, especially if used simultaneously with biologgers on domestic livestock herds. Such an approach has recently been investigated with leopards in South Africa, where Frohlich et al. (2012) were able to detect prey remains at 57.4 % 54 potential kill sights, and analysis of activity patterns showed a difference between small kills (e.g. rock hyrax *Procavia capensis*) and large kills, such as antelope, although did difference was not significant. However, in the case of human-wildlife conflict, due to the similar size of cattle and oryx, is it unlikely activity patterns would be able to detect if a domestic or wild game species was predated. Whilst accelerometers on brown hyena would not necessarily show hunting behaviour, given this species' preference of scavenging, they may have allowed insights into energy expended whilst foraging for carcasses, and could have been particually useful in comparing the energy expended by individuals in the north, to those in the south, where an active offal pit is present. Being able to see where, in particular in which habitats, and when focal carnivores were hunting may have allowed more accurate insights as to whether these species were actually causing conflict by predating livestock.

Another particually useful method for identifying hunting sites, when accelerometers are not available, is the analysis and ground-truthing of temporal and spatial GPS clusters, i.e. clusters in time or space of GPS positions, indicating an animal has spent time in one particular locale. When analysing such clusters from leopard GPS collars, Pitman et al. (2014) found the approach to increase the detection of kill sites by 20 - 23 %, over using VHF tracking of leopards. Similarly, Krofel et al. (2012) found 99 % of Eurasian lynx kills using GPS cluster analysis. This approach may have been useful in the study for the felid species, as due to their scavenging nature, GPS clusters for both hyena species and black-backed jackal may have simply represented their attendance at a carcass, which they did not kill themselves. The suitability of this approach for cheetah may also be questionable given their habit of quickly eating food and moving on so as not to attract attention from larger carnivores (Estes 1992). Leopards are well known to go back to their prey (Estes 1992), and so this approach may have been most effective for this species only.

9.5 Future research

This study has clearly demonstrated the attractiveness of water sources to the many members of the carnivore guild across the study farmlands. Examining the role of these off-Park water sources on the ecology of carnivores within the National Parks would be a next logical study to lead on at this point. The provisioning of artificial water in protected areas, one of the main management techniques available to wildlife managers, is a contentious issue which is generally supported by park managers and landowners, but widely opposed by ecologists, given the potential unnatural effects on both carnivore and herbivore ecology (Owen-Smith 1996). Although the decision was made to not provide artificial water sources within the Sperrgebiet and Namib-Naukluft National Parks, the provision of such resources on bordering farmlands could potentially influence the ecology of both herbivores and carnivores within the Park. A case study of the central Kalahari region of Botswana demonstrated that oryx, springbok, eland *Taurotragus oryx* and wildebeest *Connochaetes taurinus* were present within the region year round despite a lack of surface water in the dry season. However, during an extreme drought in 1983 wildebeest started to move towards the Makgadikgadi Pan in search of drinking water, and the presence of veterinary fences blocking access to the Pan resulted in large numbers of mortalities (Williamson et al. 1988). Therefore, it is possible during extreme droughts, herbivores within the Park may move onto the farms to access drinking water.

Movement of herbivores between the National Parks and bordering farmlands may in turn influence the spatial ecology of carnivores, which may move onto the farms following herbivore movement from the Park, or to access drinking water themselves. Such movements of carnivores have previously been recorded in the Kruger National Park, where a mass movement of zebra and wildebeest northwards during the 1982 - 1983 drought, to access permanent water and food there, led to an increase in lion numbers in the region (Owens-Smith 1996). Such an increase was also believed to be a major factor in the regional decline of the roan *Hippotragus equinus* during that time (Harrington 1995).

Such a study would be important for a number of reasons. Firstly, if carnivores from within the National Parks are forced to make use of these farmland water sources for at least part of the year due to no water being available in the Park, they have the potential to be exposed to human-wildlife conflict when visiting these resources. Involvement in such conflict often results in the lethal removal of carnivores in the study area, which means the conservation efforts of the Park are likely to be compromised if its carnivore populations are exposed to potential conflict situations if forced to visit off-Park water sources. There is the potential for lethal removal of animals moving from the Parks to farmlands to result in sink-source dynamics (Pulliam 1988) at a landscape level. Secondly, it will add to the growing debate on the provisioning of water sources in protected areas across the globe, providing a unique example from an arid environment where the effects of such resources are likely to be more extreme than in other areas. Finally such data could be used by the Park management to better manage both its carnivore and herbivore populations for conservation.

9.6 Recommendations

One of the main recommendations of this research would be the farming of cattle and game in preference to small stock species within the study area, especially on farms with higher levels of mountain habitat which were associated with higher levels of livestock loss. The questionnaire data showed farmers experienced much lower losses of cattle in comparison to smallstock, and that cattle were not usually predated upon by baboons. This data is in contrast to Stander (1997) and Wint (1997) who suggested the lack of close herding of cattle in Namibia and Botswana creates conditions in which controlling livestock predation without killing carnivores is difficult, and could lead to unsustainable levels of livestock predations. It is suggested that the absence of lions, and low density of large carnivores capable of killing adult cattle, i.e. spotted hyena and leopard, coupled with the anti-predator behaviour of cattle could be responsible for this contrast.

The recommendation of farming with cattle rather than smallstock is also supported by data from Chapter four which demonstrated that cattle show anti-predator behaviour by avoiding water points during carnivore peak activity time, in a way which reflected risk from different carnivores species. Furthermore, Rasmussen (1999), recorded cattle showing anti-predator behaviour by forming a protective circle around calves in the presence of African wild dog, and even recorded a cow injuring an African wild dog with its horns. In contrast, smallstock are known to fall into a state of shock when faced with a predator, often standing still during an attack (W. Theile*, pers. comm.*).

Smallstock require more intensive management than cattle, which are largely left unattended throughout the study area, requiring the presence of a shepherd or livestock guarding dog in the day and being kraaled at night to avoid high levels of predation. Many farmers in the area already seem to be making the move towards pure cattle farming, with all smallstock from NBR being sold during the study period due to unreliable shepherd labour (T. Theile, *pers. comm*.), and two other farmers stating labour costs and high livestock losses as their reasons for stopping farming with smallstock (W. Izko and W. De Waal, *pers. comm.*). Therefore, although this recommendation may seem drastic due to it involving major changes in farming practice, it is one already being carried out within the study area.

Farmers wishing to continue with smallstock farming, or those who not be able to switch to cattle farming given environmental conditions on their land, are recommended to avoid positioning kraals in open plains/mountain transition habitat and avoid shepherding livestock in mountainous areas due to many carnivore species having a preference for this habitat. Many farmers in the area locate kraals close to the main farm house in an attempt to deter carnivores from entering them. Data from Chapter six demonstrated that both brown hyena and black-backed jackal visited the offal pit at Tsirub very frequently despite it being located close to the main farm house. Therefore, farmers with offal pits must be careful not to place kraals near to offal pits, even if they are also close to houses, as visits to the offal pit by carnivores may result in opportunistic livestock predation.

Making recommendations regarding the issue of the perceived risk of carnivores by farmers not being associated with livestock losses is difficult, given the complexities of human attitudes towards wildlife (Dickman 2010). Although environmental education is a widespread strategy for reducing human-wildlife conflict (Espinosa and Jacobson 2012), communications with farmers during this study would suggest such an approach is unlikely to be effective, especially with those farmers whose families have been farming in the area for many generations. The Cheetah Conservation Fund, based in north central Namibia, demonstrated the use of a simple newsletter regarding their activities was effective in increasing farmer tolerance of cheetah (Marker et al. 2013b). Such an approach may be more effective in the study area and could be used by Naan Kuse, an NGO which recently started working on carnivore conflict within the study area (K. Fester, *pers. comm.*).

Another approach to mitigating the problem of farmer perceived risk not being associated to actual livestock losses could be encouraging farmers to use camera traps to monitor predators on their land. This way, farmers would be able to see for themselves which carnivores are active in which locations on their land, and could be provided with a manual on identifying individual animals by their spot or stripe patterns. As camera traps have recently started to become more available to the general public in Namibia, through outdoor and hunting shops selling them, many farmers already are using them for both monitoring carnivores and in the fight against stock theft (T. Miller, *pers. comm.*). Such a solution could have several benefits; farmers may start to gain a better idea of the numbers of large carnivores in the area by seeing the data themselves firsthand, which could lead to a reduction in killings, when they realise, for example, that they only have three leopards on their farm rather than 15. It also gives farmers a chance to see elusive species such as leopard, which they may rarely see live on the farm, which may lead to an appreciation of their aesthetic value.

An example of why this recommendation has the potential to work comes from this study. At the start of the study Mr Bosman, the owner of Tsirub, was very anti-predator, often using shooting or snaring as a first response to perceived conflict. He asked to see some of the camera trap photos of large carnivores from his farm, which he then forwarded to his children and grandchildren as far away as New Zealand, perhaps suggesting a certain pride in showing 'his' animals to his family. At the end of the project Mr Bosman forwarded a photo of a cheetah he had taken on Tsirub, which he had photographed rather than killed, and asked for advice on which camera trap to buy for personal use. Farmers could be encouraged to buy camera traps by promoting their use, and even offering to order camera traps, at Farmer Association meetings and providing a simple, short manual on how to individually identify those species with unique markings.

Chapter seven illustrated the widespread problems farmers experience with baboons and water pipe damage. As discussed within the chapter, problems with baboons are not commonly included in human-wildlife conflict studies, but the few studies considering them have noted them as problematic to smallstock farmers (Butler 2000; Holmern et al. 2007), whilst no previous studies have noted water pipe damage as a cause of conflict. It is recommended any future conflict studies within Africa, especially those in arid environments include both water pipe damage and conflict with baboons. Many farmers cited carnivore species as being responsible for water pipe damage which may add to negative attitudes towards carnivores. Additionally, it is suggested future research into baboon predation of smallstock including spatial and temporal patterns as well as the development of effective mitigation techniques is likely to be extremely useful for farmers in southern Namibia.

Lastly, it is recommended the Namibian Ministry of Environment and Tourism use the leopard density estimates from this study to reassess the leopard population in the south, and ultimately reassess the national population estimate. Once this has been done, a new, more sustainable annual trophy hunting quota can be made, which reflects 3 - 4 % of the true, adult male population. Due to the large variations in farmer estimates of leopard numbers on their land compared to those detected by camera trap, it is recommended the National Leopard Survey stops relying on questionnaire data when assessing population size, using camera trap data as the only reliable source of information regarding leopard numbers. Additionally, it is recommended the number of animals killed as result of human-wildlife conflict should be considered when calculating the trophy hunting quota. At the time of writing, this recommendation is being followed, with the MET requesting this data for the updated Namibian Large Carnivore Atlas, which maps population densities of all large carnivore species across Namibia, as well as estimating national population sizes of each species.

9.7 Conclusions

In conclusion, the study has demonstrated that human-wildlife conflict in southern Namibia, like elsewhere, is complex, as demonstrated by the human perspective of the problem not being associated with actual levels of livestock loss, the main cause of conflict. However, two links were found between the ecological data and the questionnaire data, suggesting clear areas for mitigation techniques to focus on. It is recommended that farmers, where possible, switch to cattle farming in preference to smallstock farming due to the low levels of livestock predation experienced by cattle farmers. Additionally, the study has identified the most effective methods to survey carnivores in these difficult environmental conditions. Whilst the study could not answer questions regarding the relative contribution of domestic livestock to the diet of carnivores, it has suggested anthropogenic food resources are highly attractive and heavily used by scavengers, having the potential to influence various aspects of their ecology. Ultimately, the study has demonstrated the merits in assessing both ecological data and the human perception of the problem in identifying those areas as being high risk for conflict to occur. Being the first study to conduct field work on human-wildlife conflict within the area, it has provided valuable insights into the ecology of a diverse carnivore community, along with setting clear objectives for future research which will allow a greater depth of understanding of the complex and multifaceted problem of human-wildlife conflict.

10.0. References

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Appendix one: Edwards, S., Gange, A. C., & Wiesel, I. (2015). Spatiotemporal resource partitioning of water sources by African carnivores on Namibian commercial farmlands. *Journal of Zoology*, DOI:10.1111/jzo.12248

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Spatiotemporal resource partitioning of water sources by African carnivores on Namibian commercial farmlands

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activity pattern; camera trapping; carnivores; partitioning; interspecific competition; Namibia.

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Abstract

Interspecific competition often occurs when sympatric carnivores compete for the same, limited resources, although the degree of competition between species pairs may vary with biotic factors such as body size, diet and population density. Avoidance of dominant competitors along the axes of space and time is a potential mechanism for reducing chances of direct encounters between species. However, when resources are essential and spatially fixed, options for spatial partitioning may be limited. We examined resource partitioning within a guild of eight carnivore species at water sources across two commercial farmlands in southwest Namibia. In this semi-desert environment, surface water is scarce and farmers are forced to provision water for livestock through artificial means. Camera traps were used to record spatial and temporal activity patterns of carnivore species at artificial and natural permanent water sources. We found that carnivores use either spatial or temporal resource partitioning, with temporal partitioning being most frequently seen. An association was seen between difference in body mass and degree of spatial partitioning, where species pairings with larger differences in body mass showed the greatest degree of partitioning. These results show that while in arid environments water is rare and used by a number of carnivore species, resource partitioning allows a guild of carnivores, including species of conservation concern, to coexist outside of protected areas.

Introduction

In ecosystems with multiple carnivore species, interspecific competition for the same limited resources such as food and habitat can occur. Such competition can have a strong and widespread impact on community composition, ultimately determining which species are able to coexist (Begon, Harper & Townsend, 2006). Such an impact can have direct consequences for the conservation of rare species, for example densities of both wild dog *Lycaon pictus* and cheetah *Acinonyx jubatus* show a negative association with the densities of lions *Panthera leo* and spotted hyaenas *Crocuta crocuta* across their range (Durant, 2000). The competitive exclusion theory suggests that species with similar ecology cannot coexist (Hardin, 1960). However, ecological separation, occurring on the axes of space, time and diet, can provide a mechanism for species coexistence (Schoener, 1974). The ways in which multiple carnivore species utilize and partition resources are currently poorly understood (Vanak *et al.*, 2013), but can be important for understanding which mechanisms structure communities (Vieira & Port, 2007).

Schoener (1974) argued that although temporal resource partitioning is rare in ecology, it is seen more frequently in carnivores than other groups. Hayward & Slotow (2009) examined temporal overlap between cheetah, wild dog, spotted hyaena and lion and found subordinate guild members use temporal resource partitioning, having evolved activity patterns which minimize overlap with dominant species, to avoid both kleptoparasitism and intraguild predation. Similarly, Di Bitetti *et al.* (2010) found temporal partitioning in the activity patterns of the most morphologically similar species in a community of six species of neotropical felids. Spatial partitioning is also seen between carnivores; Swanson *et al.* (2014) recorded spatial avoidance of lion by wild dog and Kamler *et al.* (2012) found spatial avoidance of black-backed jackal *Canis mesomelas* by Cape fox *Vulpes chama*.

Carnivore species may be able to coexist and avoid the effects of competition by utilizing different prey. Hayward (2006) found that although lions and spotted hyaena had high levels of dietary overlap, the unselective nature of hyaenas allowed the two species to coexist. Similarly, leopards *Panthera pardus* were found to take smaller prey items than other guild members allowing them to coexist with competitors (Hayward & Kerley, 2008). Within a diverse carnivore community, competition is likely to differ between each species pair, for example competitive theory predicts species that differ significantly in body mass do not compete (Wilson, 1975). Larger species benefit from size (Persson, 1985), meaning smaller species often have decreased access to limited resources (Amarasekare, 2003). However, smaller species may avoid larger species as they are more at risk from intraguild predation (Woodward & Hildrew, 2002), an extreme form of interference competition where two species that compete for the same resources kill and sometimes eat each other (Polis, Myers & Holt, 1989). Therefore, examining partitioning in a sympatric carnivore assemblage where a range of body sizes, diets and densities are present is likely to advance current knowledge in the field of ecological community structure.

Africa presents the perfect opportunity to study carnivore guild interactions as it is the only continent with an intact carnivore guild (Cozzi *et al*., 2012). Furthermore, Namibia is the ideal place to examine resource partitioning at water sources as one of the driest climates in sub-Saharan Africa. Such locations represent important and spatially fixed resources for a number of species and as a result these water sources become high-risk areas for predation (Valeix *et al*., 2009). How carnivores avoid each other at water sources in such arid environments has received little attention (but see Atwood, Fry & Leland, 2011).

This study used camera traps to examine temporal and spatial resource partitioning at 13 permanent water sources in a sympatric guild of 11 carnivore species on two commercial farmlands in southwest Namibia. In this environment, natural permanent water sources are rare, with most rainfall water seeping underground and ephemeral pools seen only in the wet season. Temporal and spatial activity patterns of carnivores were determined over the period of 1 year. As water sources are both scarce and spatially fixed, it was hypothesized that temporal partitioning would be the main method used by guild members to avoid direct encounters. Furthermore, it was hypothesized that associations between differences in body mass and degree of resource partitioning would be observed, with species pairings with large differences in body mass showing higher levels of partitioning than species pairs of similar size.

Methods

Study area

The study was conducted across two bordering commercial farmlands Tsirub (S 26°49′14″, E 16°05′55″) and Klein Aus Vista (KAV) (S 26°42′00″, E 16°06′09″) near the settlement of Aus, Karas region, southwest Namibia (Fig. 1). The farms directly border the Tsau//Khaeb (Sperrgebiet) National Park and total 400 and 500 km^2, respectively. The area consists of Namib Desert and Nama Karoo biomes (Giess, 1971) characterized by mountains and flat grassy plains dominated by *Stipagrostis* grass species with relatively few trees and shrubs. The mean annual rainfall is 80 mm and the mean annual temperature is 17.5°C (22.8°C summer, 15.2°C winter) ranging from −5 to 42°C (Namibia Weather Network, 2014). Altitude lies between 1000 and 1500 m. The area is positioned within a winter-summer rainfall transitional zone (Burke, 2004), although most rain falls during the summer months (November to March).

The main agricultural activity was livestock and game production for meat, Tsirub farmed game, namely springbok *Antidorcas marsupialis* and oryx *Oryx gazella*, while KAV farmed cattle *Bos taurus* but also had oryx and springbok present. Tsirub had no internal fences, while KAV was divided into four main grazing camps through which cattle were rotated. However, spacing of wires within the fence line was wide enough to allow passage of carnivores through and was not considered a barrier to movement. Density of artificial

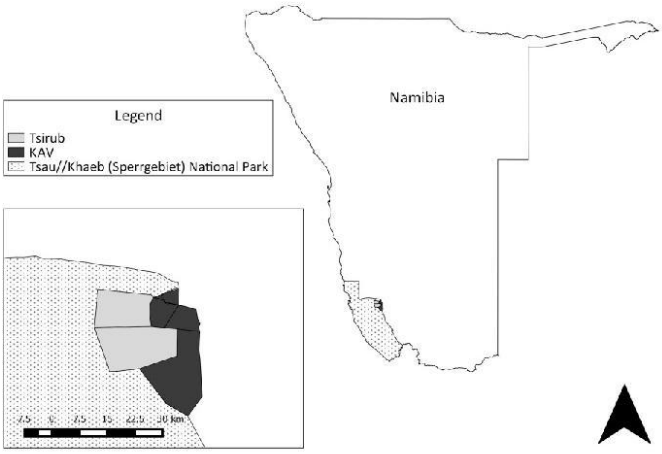


Figure 1 Study farms Tsirub and Klein Aus Vista (KAV), Karas region, southern Namibia.

water points varied between farms with Tsirub having a density of 7.25 points per 100 km^2, while KAV had 3.92 per 100 km^2.

Previous studies have shown differences between domestic livestock and game farmers in tolerance levels of carnivores which in turn affect removal (Lindsey *et al*., 2005). However, during the study period, no carnivores were killed on either farm with the exception of Tsirub's owner occasionally shooting black-backed jackals during normal game hunting activities. Blaum, Tietjen & Rossmanith (2009) found the stocking density and associated changes in vegetation structure to have a negative relationship with abundance of small carnivores. Due to the arid environment, both farms stocked at low density (KAV stocked cattle at a density of 80 cattle per 100 km^2) and the density of wild game across the two farms was similar. Therefore, the differences between the farms in stocking density were not believed to affect the carnivore guild.

Methods

A total of 12 artificial water sources (Tsirub $n = 7$, KAV $n = 5$) and one natural, permanent spring on KAV, were chosen randomly and monitored by camera trap from May 2013 to May 2014. A single Scoutguard SG560V (HCO Outdoors, Norcross, GA, USA) camera trap was positioned at an average height of 40 cm from the ground and angled so the entire water source was in view. Camera traps were spaced at least 4 km apart, which was considered as spatially independent, and programmed to take one photo per trigger, with a minute delay between and checked every 2 weeks when batteries and SD cards were changed.

Statistical analysis

Temporal partitioning was analysed separately for each farm. Due to small sample sizes, data were combined for the two farms to test for spatial partitioning and the association between difference in body mass and resource partitioning. Because the 2014 rains only reached 50% of the annual mean of 80 mm and the seasonal pools only filled for a few days at a time (S. Edwards, pers. obs.), differences in natural water availability were thought to be minimal and thus seasons were not controlled for. Carnivore images were identified to species level and classed into independent events using a criterion of a minimum of 30 min between consecutive photos of the same species (O'Brien *et al*., 2003), except for species with individual markings where detection of a different individual was always recorded, but the criterion earlier holds valid for same individual detection. Analyses to examine temporal and spatial partitioning between each carnivore species pair were conducted using R 3.1.1 (R Development Core Team, 2014).

Temporal and spatial resource partitioning

Temporal partitioning activity patterns at water sources were compared with the non-parametric circular Mardia-Watson Wheeler test (Batschelet, 1981) using Oriana (Kovach Computing Services, Pentraeth, Isle of Anglesey, UK; Kovach Computing Services, 2013) to test the null hypothesis that activity patterns were identical for each species pair. As the test requires $n \geq 10$, not all species could be analysed. Additionally, Oriana was used to calculate the mean vector (activity time), length of mean vector which ranges from 0 to 1, where a higher value indicates that the observations are clustered more closely around the mean and circular variance, standard deviation and 95% confidence intervals, which are equivalent to their linear counter parts. Secondly, independent events for each species and camera trap location were grouped into 2-h time periods (i.e. 00:00–02:00 h etc.) and the proportion of events in each period was calculated. Pianka's index of niche overlap (Pianka, 1973) was then calculated for each species pair using R package 'pgirmess' version 1.5.9 (Giraudoux, 2014).

Finally, in order to examine if different carnivore species avoid using the same water point on the same day, a bootstrapping procedure was used to test if the number of joint occurrences observed differed from the number expected randomly. For each species pair and camera trap location, two sets of random numbers were generated, the *n* of the first set equal to the number of days the first species had been detected at that particular camera trap and the *n* of the second set equal to the number of days the second species in the pair had been detected. The total number of operational camera trap nights determined the range the random numbers were generated from. For example, if a camera trap had 250 camera trap nights and a cheetah had been detected there on 50 nights and an aardwolf on 100 nights, one set of 50 random numbers between 1 and 250 would be generated and another set of 100 between 1 and 250 would be generated. The number of times the same number was seen in each set of random numbers represented the number of joint occurrences expected to occur at random. Each resampling procedure was repeated 10 000 times for each species pair at each camera trap location and the mean was used for analysis. Wilcoxon-matched pairs tests where then used to examine differences between observed and mean expected joint occurrences for each species pair.

To examine spatial resource partitioning between species, the proportion of independent events at each water source was calculated for each species. Spearman's rank correlation was used to examine associations in the relative abundance of each species pair at camera trap locations. Relative abundance was calculated as the number of operational camera trap nights, using the formula from Negr es *et al*. (2010):

$$\mathrm{RAI}_i = \left(\mathrm{g}_i \sum \mathrm{jP}_{ij} \Big/ \sum_j \mathrm{tn}_j\right) \times 100$$

where g_i is the average group size for the i^{th} species, P_{ij} is the number of independent events for the i^{th} species and tn_j is the total number of trap nights at the j^{th} location. For social species, such as black-backed jackal, bat-eared fox *Otocyon megalotis* and brown hyaena *Hyaena brunnea*, mean group size was determined from the literature or where possible from direct field observations across the study sites.

Association between differences in body mass and degree of resource partitioning

To examine associations between differences in body mass between species pairs and the degree of resource partitioning, Spearman's rank correlation was used with the Pianka's indices for both temporal and then spatial partitioning against the difference in relative body mass (taken from Estes, 1992) for all carnivore species pairs.

Results

A total of 11 species were detected over 4507 camera trap nights across the two farms. Species detected were Cape fox ($n = 140$), bat-eared fox ($n = 376$), black-backed jackal ($n = 4482$), honey badger *Mellivora capensis* ($n = 46$), aardwolf *Proteles cristata* ($n = 12$), spotted hyaena ($n = 11$), brown hyaena ($n = 399$), leopard ($n = 148$), cheetah ($n = 22$), caracal *Caracal caracal* ($n = 8$) and African wild cat *Felis lybica* ($n = 52$). Due to low sample sizes and presumed low densities, spotted hyaena, aardwolf and caracal across the two sites and African wild cat on KAV were excluded from analysis.

Temporal and spatial resource partitioning

Almost all species showed predominant nocturnal activity (between 18:00 and 06:00 h) with less than 1 h differences in within species mean activity times across study sites (Table 1). Cape fox showed strictly nocturnal activity patterns with peaks of activity around midnight and dawn (Figs. 2 and 3). Bat-eared fox was mainly nocturnal, but showed some activity during the day at Tsirub, but was strictly nocturnal at KAV with a peak in activity at 21:00 h. At both sites, black-backed jackal showed activity throughout the day and night, but with the least activity recorded from mid-morning to late afternoon. Honey badger at Tsirub showed activity throughout the day and night, with peaks in the early morning and early evening, while on KAV nearly all activity was nocturnal. Brown hyaena at both sites showed predominant nocturnal activity, with peaks on Tsirub around 22:00 and 03:00 h, and similar peaks between 21:00 and 22:00 h and at dawn at KAV. On both sites, leopards were most active during the first half of the night and dawn, with some activity throughout the day. Cheetah and African wild cat were predominately nocturnal. Cheetah showed increased activity in the early evening, at dawn and early morning, whereas African wild cat had a clear peak in activity at 01:00 h.

Mardia-Watson Wheeler tests revealed significant differences in temporal activity between species at water points across both sites. On Tsirub, brown hyaena temporal activity was significantly different to the temporal activity of leopard ($W = 13.17$, $P = 0.002$), black-backed jackal ($W = 94.61$, $P < 0.001$), bat-eared fox ($W = 12.52$, $P = 0.001$) and honey badger ($W = 36.3$, $P < 0.001$). Leopard temporal activity was significantly different from Cape fox ($W = 6.84$, $P = 0.03$) and honey badger ($W = 6.52$, $P = 0.04$), black-backed jackal was significantly different from African wild cat ($W = 10.6$, $P = 0.005$), bat-eared fox ($W = 20.53$, $P = 0.002$) and Cape fox ($W = 10.08$, $P = 0.006$) and honey badger temporal activity was significantly different from African wild cat ($W = 12.03$, $P = 0.002$), bat-eared fox ($W = 13.54$, $P = 0.04$) and Cape fox ($W = 20.92$, $P < 0.001$) (Table 2).

Table 1 Circular descriptive statistics for carnivore species across Tsirub and KAV commercial farmlands, southwest Namibia

	Tsirub								KAV					
Variable	Cape fox	Bat-eared fox	Black-backed jackal	Honey badger	Brown hyaena	Leopard	Cheetah	African wild cat	Cape fox	Bat-eared fox	Black-backed jackal	Honey badger	Brown hyaena	Leopard
Number of events	19	358	3332	34	265	55	22	51	121	18	1150	12	134	93
Mean vector	01:17	23:48	00:47	02:11	01:23	01:03	02:14	23:23	01:26	22:21	23:57	02:33	01:42	00:18
Length of mean vector	0.69	0.36	0.25	0.08	0.63	0.32	0.45	0.55	0.63	0.80	0.18	0.73	0.58	0.40
Circular variance	0.31	0.64	0.76	0.93	0.37	0.68	0.55	0.45	0.69	0.20	0.82	0.27	0.42	0.60
Standard error of mean vector	00:45	00:22	00:11	06:09	00:13	01:06	01:11	00:37	00:20	00:36	00:26	01:00	00:21	00:39
95% confidence interval	23:48–02:45	23:03–00:33	00:25–01:09	14:06–14:16[a]	00:56–01:50	22:53–03:12	23:53–04:35	22:09–00:37	00:46–02:06	21:10–23:32	23:05–00:50	00:35–04:31	01:00–02:25	23:00–01:36

[a] Oriana cautioned value may be unreliable because of low concentration/uniform distribution. KAV, Klein Aus Vista.

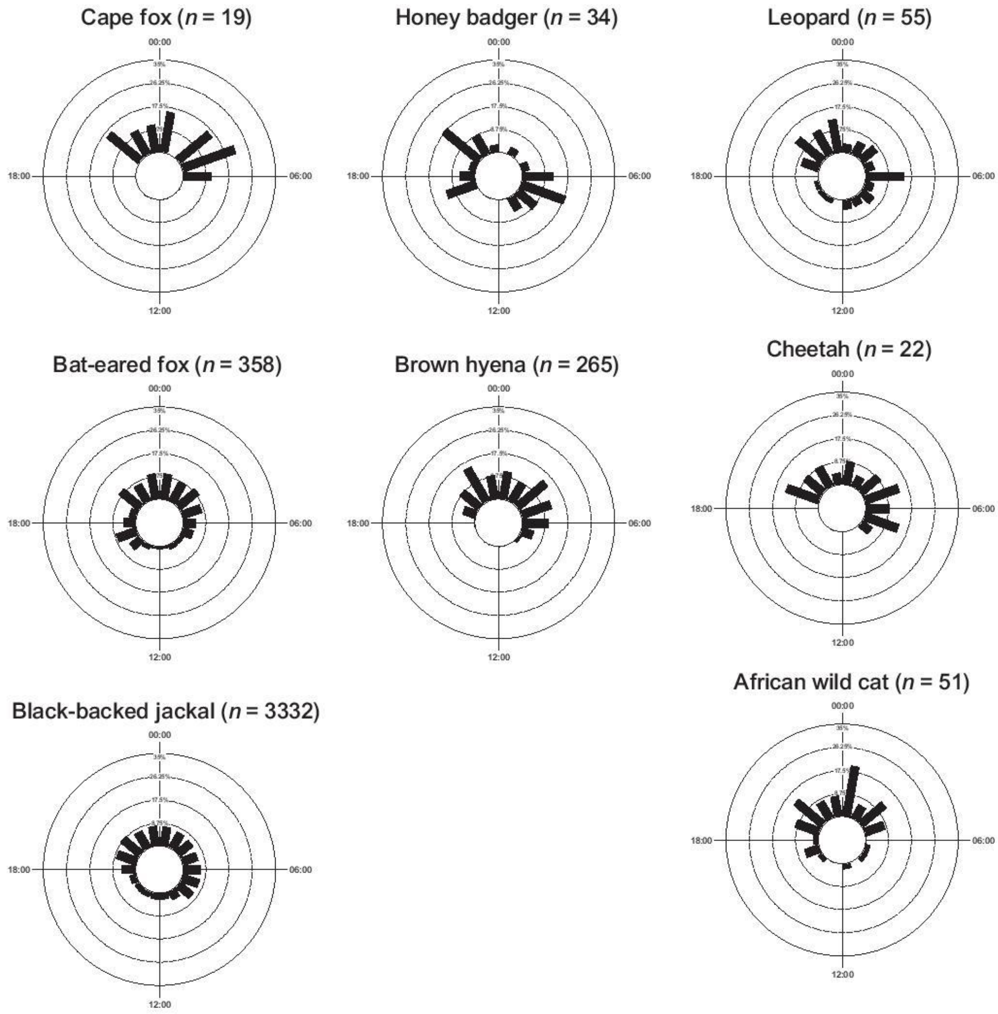
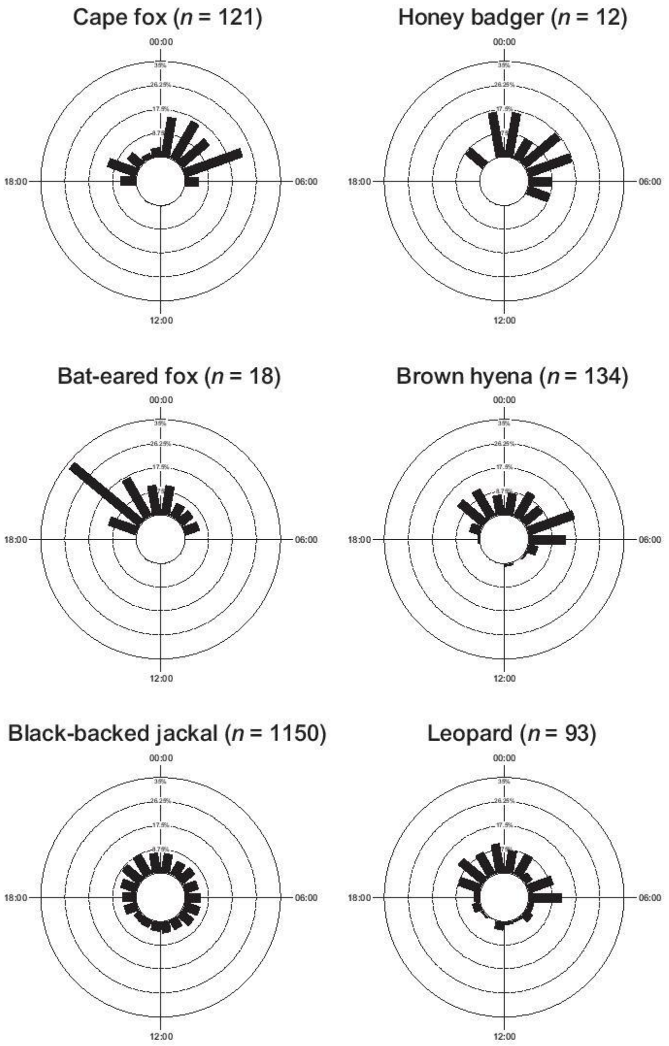


Figure 2 Temporal activity of carnivores on Tsirub, black bars show activity seen throughout the 24-h period, with length of black bars representing the proportion of activity seen. Longer bars represent peak times of activity.

At KAV, there were significant differences in temporal activity at water points between all carnivore species, with the exception of brown hyaena and honey badger (W = 1.63, $P = 0.44$) and honey badger and Cape fox (W = 0.07, $P = 0.95$ (Table 2).

Bootstrapping procedures showed significant differences in the number of observed and expected numbers of joint occurrences for only three of the 28 species pairs; bat-eared fox and African wild cat (V = 0, $P = 0.03$), honey badger and African wild cat (V = 0, $P = 0.03$) and honey badger and cheetah (V = 0, $P = 0.03$) on Tsirub. This meant the number of days the two species were seen at the same water source was significantly different than would be expected to happen at random. Observed values were always less than expected for significant values, suggesting avoidance at water points. No species pairs showed significant differences between the


Cape fox (n = 121)

Honey badger (n = 12)

Bat-eared fox (n = 18)

Brown hyena (n = 134)

Black-backed jackal (n = 1150)

Leopard (n = 93)

Figure 3 Temporal activity of carnivores on Klein Aus Vista, black bars show activity seen throughout the 24-h period, with length of black bars representing the proportion of activity seen. Longer bars represent peak times of activity.

numbers of observed and expected joint occurrences on KAV. It should be noted that as Cape fox was only recorded at one location on KAV, paired t-tests could not be performed for this species.

Spearman's rank correlation tests showed significant, negative associations between difference in body mass and degree of spatial partitioning for only three species pairs out of 28: black-backed jackal and leopard, brown hyaena and cheetah and between leopard and cheetah (Table 2).

Association between differences in body mass and degree of resource partitioning

Spearman's rank correlation showed no significant association between difference in body mass and Pianka's index of

Table 2 Results of temporal and spatial resource partitioning analyses between carnivores on commercial farmlands, southwest Namibia

	Temporal				Spatial
	Activity patterns		Joint occurrence		Spatial avoidance
	Mardia-Watson-Wheeler test		Wilcoxon-matched paired test		Spearman's rank correlation
Species	Tsirub	KAV	Tsirub	KAV	r_s
Cape fox and bat-eared fox	2.34	**8.08**	12	NA	**0.78**
Cape fox and black-backed jackal	**10.08**	**52.87**	10	NA	0.44
Cape fox and honey badger	**20.92**	0.07	4	NA	0.16
Cape fox and brown hyaena	0.20	**8.00**	0	NA	0.28
Cape fox and leopard	**6.74**	**20.09**	0	NA	–0.38
Cape fox and cheetah	2.49		4	NA	0.42
Cape fox and African wild cat	0.48		0	NA	–0.18
Bat-eared fox and black-backed jackal	**20.53**	**15.54**	15	4	**0.61**
Bat-eared fox and honey badger	**13.54**	**7.33**	11	0	0.38
Bat-eared fox and brown hyaena	**12.52**	**8.83**	0	3	0.47
Bat-eared fox and leopard	1.36	**8.92**	6	0	–0.53
Bat-eared fox and cheetah	1.12		11		**0.63**
Bat-eared fox and African wild cat	2.33		**0**		–0.40
Black-backed jackal and honey badger	4.66	**10.26**	17	4	–0.20
Black-backed jackal and brown hyaena	**94.61**	**43.64**	17	7	0.24
Black-backed jackal and leopard	0.76	**8.41**	5	7	**–0.79**
Black-backed jackal and cheetah	2.32		20		**0.61**
Black-backed jackal and African wild cat	**10.60**		8		–0.53
Honey badger and brown hyaena	**36.30**	1.63	18	4	0.15
Honey badger and leopard	**6.44**	**6.69**	0	1	0.25
Honey badger and cheetah	2.49		**0**		0.05
Honey badger and African wild cat	**12.03**		**0**		–0.07
Brown hyaena and leopard	**13.17**	**6.98**	8	9	0.03
Brown hyaena and cheetah	3.64		6		**–0.79**
Brown hyaena and African wild cat	1.67		**0**		–0.11
Leopard and cheetah	1.22		0		**–0.79**
Leopard and African wild cat	2.75		4		0.12
Cheetah and African wild cat	3.74		5		–0.34

Significant results shown in bold. KAV, Klein Aus Vista; NA, not applicable.

temporal overlap for data combined from all two study sites ($r_s = -0.15$, $P = 0.33$). However, a significant, negative correlation was seen between difference in body mass and Pianka's index of spatial overlap for all data combined ($r_s = -0.43$, $P = 0.004$).

Discussion

Partitioning between carnivores has been documented for a number of species, either temporally (Di Bitetti *et al*., 2010; Ramesh *et al*., 2012), spatially (Schwartz *et al*., 2010; Vanak *et al*., 2013) and occasionally both (Atwood *et al*., 2011). Our results show carnivores exhibited either temporal or spatial resource partitioning at water points, with a significant, negative association between spatial overlap and difference in body mass between species pairs. Only leopard and black-backed jackal showed both temporal and spatial resource partitioning, while some of the species pairings involving cheetah and African wild cat showed no resource partitioning. Most previous studies have focused on two or three species or multiple species of the same family, this study is the first to focus on a guild of eight sympatric carnivore species representing the Canidae, Felidae, Hyaenidae and Mustelidae families.

Temporal partitioning was more common than spatial resource partitioning; of the 28 species pairs, 17 showed temporal partitioning compared with three showing spatial. Schoener (1974) stated temporal partitioning to be less common than spatial, while Hayward & Slotow (2009) predicted temporal resource partitioning being the main mechanism for the coexistence of large African carnivores. Partitioning at spatially fixed resources may represent a special case; Atwood *et al*. (2011) also recorded temporal partitioning between three carnivore species at artificial water points. As the two dominant species were recorded at all and most of the water points, it was argued that there was little opportunity for spatial partitioning by subordinate species. Romero-Muñoz *et al*. (2010) also suggested spatial rarity of travel routes to explain the wide overlap between puma *Puma concolor* and jaguar *Panthera onca* on roads and trails. As carnivore species occurred at 46–100% of water points monitored, limited opportunity for spatial resource partitioning existed, meaning carnivores must use another mechanism to avoid direct carnivore encounters at water.

Differences in the density of water points between the two farms might affect the degree of partitioning seen, for example a higher density of water may be expected to be associated with lower levels of temporal partitioning as more options for spatial partitioning are available. Density of water on Tsirub was almost twice that of KAV and had a total of 57% of species pairs showing temporal partitioning compared with KAV where 86% of pairings exhibited temporal partitioning. Differences in water density and options for partitioning may also explain why certain species, for example cheetah, were not detected on KAV.

Temporal partitioning occurred on a finer scale than simple nocturnal, crepuscular and diurnal partitioning recorded in other studies (e.g. Crooks & Vuren, 1995). All carnivores showed the majority of activity to occur at night, with the exception of black-backed jackal and honey badger which showed activity throughout both day and night. Harrington *et al.* (2009) recorded American mink *Neovision vison* switching from primarily nocturnal to diurnal behaviour with increasing abundance of competitors. While it may aid temporal partitioning for some species to show diurnal activity at water points, Daan (1981) argued diurnal and nocturnal activity require very different evolutionary adaptations and that recorded shifts in activity patterns are usually seen within the normal diel cycle of the species. Furthermore, increased daytime activity may result in increased contact and conflict with humans; carnivores have been shown to shift activity patterns in order to avoid human activity (e.g. Henschel & Ray, 2003). In this study, cheetah was seen to be primarily nocturnal, although usually described as diurnal (Cooper, Pettorelli & Durant, 2007), such a difference in behaviour could be a tactic to avoid persecution.

More species pairs showed temporal partitioning in the form of significant differences in activity patterns rather than complete avoidance of a water point on the same day another carnivore species was present. Data pertaining to the water requirements of carnivores are scarce, with Bothma (2005) recording Kalahari leopards drinking, or having access to moisture in the form of kills, at intervals of 2.5, 2.2 and 1.6 days for males, females without cubs and females with cubs, respectively. Metabolic water requirements may halt avoidance of water points on the same day as competitors; alternatively, fine scale shifts in temporal activity at water points may be sufficient to minimize risk of intraguild predation.

No partitioning at either scale was seen between cheetah and Cape fox, and between African wild cat and Cape fox, bat-eared fox, leopard or cheetah. Abundance of competitors has been cited as the most important factor influencing competition between interacting species (Creel, Spong & Creel, 2001). Romero-Mu oz *et al.* (2010) suggested low densities of competitors decrease the probability of encounter, making partitioning unnecessary. This may explain the lack of partitioning between species pairings involving cheetah and African wild cat; cheetah only occurred on Tsirub where just two individuals were recorded, while African wild cat had a mean photographic rate of just 3.05 events per 100 trap nights.

A significant, negative association between spatial, but not temporal, overlap and difference in body mass between species pairs was recorded. Relative body mass is cited as one of the most important factors influencing interspecific competition (Polis *et al.*, 1989). While closely related species are prime candidates for competition (Wilson, 1975), carnivores with relatively large differences in body size are prime candidates for intraguild predation. As there is a risk of intraguild predation for carnivores at water points, a negative association between spatial partitioning and difference in body mass may be expected. Prior to data collection, camera traps were positioned and tested so that all movement was believed to trigger, as sample sizes were too small for occupancy analysis, therefore differences in detection rates between species were believed to reflect differences in visits to water rather than in detection probabilities. This result could suggest carnivores are able to partition themselves in a way that incorporates risk of intraguild predation in relation to body size. However, such a result was also expected for temporal resource partitioning, yet no significant association was seen, which may mean resource partitioning is not the reason for the spatial association.

The results of this study show temporal resource partitioning to be the main driver for coexistence of a large number of sympatric carnivore species and suggest commercial farmlands have the potential to accommodate a diversity of carnivore species even with limited water resources. As some of the species recorded are of conservation concern, these results are encouraging and highlight the importance of farmlands and their management strategies for wildlife. Further studies to investigate partitioning of home ranges around water sources both within and between species would be of interest as home range size variations have been related to water availability (De Beer & van Aarde, 2008). As a result, density and positioning of artificial water points may influence spatial ecology of species and ultimately the carrying capacity of an area.

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Appendix two: Edwards, S., Aschernborn, O., Gange, A. & Wiesel, I. (2015). Leopard density estimates from semi-desert commercial farmlands, south-west Namibia. *African Journal of Ecology*, DOI: 10.1111/aje.12235

African Journal of Ecology

Note and record

Leopard density estimates from semi-desert commercial farmlands, south-west Namibia

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Introduction

Protected areas are acknowledged as largely inadequate for the conservation of many carnivores (Kent & Hill, 2013). As a result, nonprotected areas such as farmland are increasingly recognized as important habitats for numerous species (Smith *et al.*, 2011). In some areas, carnivore density has been found to be higher outside of protected areas; for example, leopard density was significantly higher on farmland in north-central Namibia than the bordering Waterberg Plateau Park (Stein *et al.*, 2011a).

Farmlands in southern Namibia represent an unknown area on carnivore distribution maps and have the potential to be suitable habitat for leopards, given the artificially high density of water sources and herbivore abundance. However, at the same time, they are largely unsafe environments due to conflict with humans (Henschel *et al.*, 2008). We used camera traps to produce the first leopard density estimates for commercial farmlands in southern Namibia. Additionally, to examine the efficiency of questionnaires for assessing population status, we asked farmers to estimate leopard numbers on their land for comparison.

Materials and methods

The study was conducted across five commercial farmlands (Fig. 1) bordering the eastern boundaries of the Tsau//Khaeb (Sperrgebiet) or Namib-Naukluft National Parks, Karas region, southern Namibia. Main farming activities were livestock production of either sheep *Ovis aries*, cattle *Bos taurus* or game (oryx *Oryx gazella* and springbok *Antidorcas marsupalis*). Density of artificial water points differed between the two sites (north = 1.85 per 100 km^2, south = 5.44 per 100 km^2). During the study, farmers were asked to estimate the number of leopards on their property.

Fifty-one camera trap stations were set up at natural and artificial water sources (north n = 2, south n = 13), and along game trails and roads (north n = 19, south n = 17) spaced 3.5–4 km apart. The number of traps were proportional to study site size. Stations at water consisted of a Scoutguard SG560V (HCO Outdoors, Norcross, GA, U.S.A.) mounted in a wire cage. Scoutguards were programmed to take one photograph per trigger with a minute delay at normal sensitivity. Stations along roads consisted of two Reconyx HC600 (Reconyx Inc, Holeman, WI, U.S.A.) opposite each other. Reconyx took five photographs per trigger, with no delay and medium sensitivity.

Following recommendations of Karanth & Nichols (1998), a survey length of 60 days (29th May–28th July 2013) was used, which should meet the demographic closure assumption. Adult leopard images were identified to individual using pelage patterns. Images where identity could not be confirmed were discarded (north n = 2, south n = 3). Individual capture histories were constructed, using each day as a sampling period in a standard X-matrix format, and entered into programme CAPTURE (Rexstadt & Burnham, 1991). Density was estimated by placing a buffer with radius equal to the half mean maximum distance moved (1/2MMDM) by recaptured individuals to calculate the area covered by camera traps.

Results

A total of 28 identifiable leopard images were captured across the two sites (Table 1). Three adult individuals were detected at the northern sites, whilst five individuals were recorded in the south, not all individuals were recaptured. CAPTURE suggested the best models to be heterogeneity

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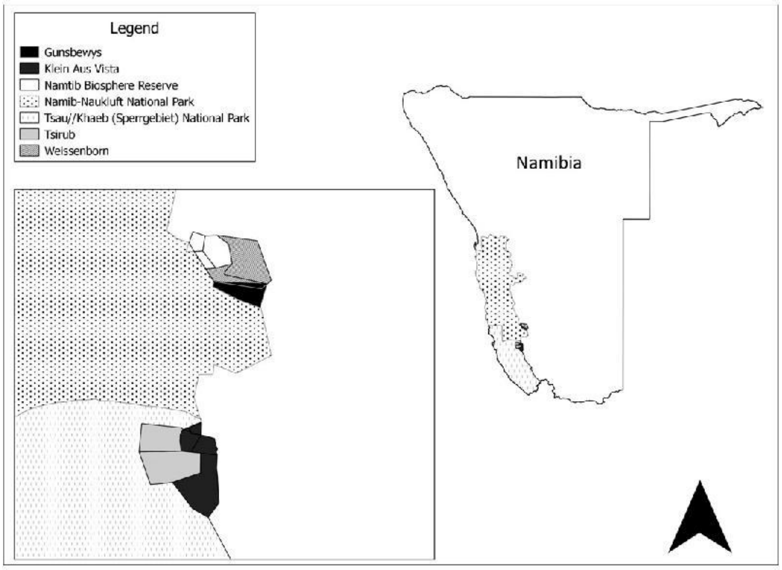

Fig 1 Location of study sites in southern Namibia

Table 1 Leopard density estimates from commercial farmlands, south-west Namibia

Site	No. leopards captured	No. recaptures	Mean capture frequency[a]	Range capture frequency[a]	Model	Abundance (SE)	95% CI	1/2MMDM (km)	Total area km^{-2}	Density (No. adults per 100 km^2)	Density – min. No. alive (No. per 100 km^2)
North	3	7	29	12–60	Mh	4 (1.15)	4–11	4.3	428.92	0.9	0.70
South	5	13	31.11	8.57–60	Mo	5 (0.41)	5–5	6.88	852.01	0.59	0.59

[a]Frequency of capture refers to the mean number of camera traps nights per event for each individual.

(Mh) for the northern sites and the null model (Mo) for the southern sites, and estimated four (SE = 1.15, 95% CI 4–11) and five (SE = 0.41, 95% CI 5–5) at the northern and southern sites, respectively. 1/2MMDM varied between the two sites; at the northern sites, a distance of 4.3 km covered a total of 428.92 km^2 producing a density of 0.9 leopards per 100 km^2, whilst a 1/2MMDM of 6.88 km at the southern sites covered an area of 852.01 km^2 producing a density of 0.59 leopards per 100 km^2. Accuracy of farmer estimates of leopard numbers compared to the number generated by camera trap data varied between farmers (Fig. 2).

Discussion

A mean leopard density of 1.2 leopards per 100 km^2 is categorized as low in Namibia (Stein *et al.*, 2011b), and our results from both sites are even lower. This is not surprising given that sub-Saharan leopard density is positively correlated with rainfall (Martin & de Meulenaer,

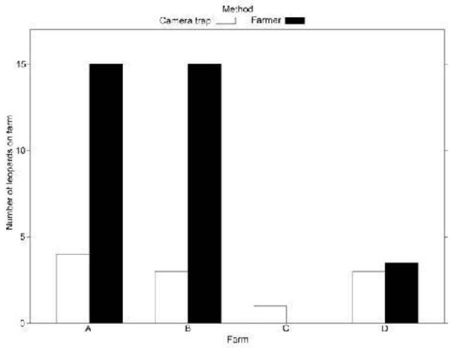

Fig 2 Comparison of leopard numbers from camera trap and farmers, commercial farmlands, south-west Namibia. The fifth farmer could not estimate leopard numbers on his land

1988), with arid conditions producing low-density populations with large home ranges (Mizutani & Jewell, 1998). Our results are similar to density estimates from other arid areas: 1.0 per 100 km^2 on commercial farmlands north-central Namibia (Stein *et al.*, 2011a), 1.3 per 100 km^2 in the Kalahari (Bothma & Le Riche, 1984) and 1.5 per 100 km^2 north-eastern Namibia (Stander *et al.*, 1997).

Foster & Harmsen (2012) noted small sample sizes and limited recaptures are associated with low precision. The northern estimate showed relatively wide 95% confidence intervals of 4–11 individuals, which using the lower and upper limits would produce density estimates in both the low- and medium-density categories of Stein *et al.* (2011b). Such a range could be due to the fact not all individuals were recaptured. As an alternative Foster & Harmsen (2012) suggest reporting the minimum number alive, which would produce lower density estimates for the northern sites (0.70 per 100 km^2), although the southern estimate would remain the same.

Differences in density estimates between sites may have reflected methodological differences. As the northern site was smaller and used less camera traps, less area was covered meaning the smaller 1/2MMDM calculated and higher density could reflect methodological differences between the study sites. Additionally, due to the lower water density in the north, less water points were monitored than in the south; here, capture frequency at water points was much higher at water (12.59), than on trails (0.82).

Questionnaires are a commonly used tool for assessing population status and human–wildlife conflict; however, concerns exist regarding the usefulness of this practice over deliberate overinflation and inaccuracy (Herrmann, Funston & Babupi, 2001). Our results show variation in the accuracy of farmer estimates of leopard numbers compared to numbers detected by camera trap. One farmer estimated over five times the number of leopards detected, whilst another was relatively accurate. Our results would further question the use of the questionnaire in lieu of field work, and the suitability of using such data gained in management practices.

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Appendix three: Edwards, S. (2014). Carnivore attendance at two cattle carcasses on a commercial farm, southern Namibia. Roan, October, 31–33.

Carnivore attendance at two cattle carcasses on a commercial farm, southern Namibia

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Introduction

For commercial farmers, dead domestic livestock represent a source of economic loss whilst for carnivores they are highly clumped, rich food sources. In southern Namibia most human-wildlife conflict is focused around actual or perceived livestock predation by carnivores. Commercial farmlands in southern Namibia are generally large with farmers only checking on livestock every two to five days, meaning cause of death is not always known, especially by the time carnivores have consumed part of or the entire carcass.

During early 2014, two fresh adult cattle carcasses, not killed by carnivores, were monitored by camera trap as part of a larger human-wildlife conflict study by the Brown Hyena Research Project. The study took place on Namtib Biosphere Reserve, a 164km^2, predator friendly, commercial farm approximately 70km north of Aus, southern Namibia.

Whilst it was already known which carnivore species occurred from an 18 month camera trapping survey across the entire farm, the question was which of these species would visit the carcasses? This is important to know as these are often the species blamed for the death of livestock after their spoor is detected and potentially killed in retaliation. Additionally dietary analysis showing domestic livestock in the diet of species known to scavenge from carcasses must take into consideration possibility it was scavenged rather than predated upon.

Methods

Two adult female cattle carcasses were located and monitored; the first carcass(carcass one) was found 19th February 2014 approximately 1.7km from the only artificial water trough provided for cattle. The cow was found early morning and had not yet been consumed by carnivores. The carcass was monitored until 28th April, when a second fresh carcass, also not yet consumed by carnivores was found approximately 1.3km from the first carcass. The second carcass was monitored until 1st June 2014. Cause of death of both animals was unclear; visual inspection showed the animals were in good condition with no obvious wounds or signs of disease. Carcasses were monitored using a Bushnell X-8 Trail camera set to take photos 24 hours a day, with one firing per trigger and a minute between firings on high sensitivity.

Carcass one

Results

Five carnivore species were recorded at the carcasses; Cape fox *Vulpes chama*, bat-eared fox *Otocyon megalotis*, black-backed jackal *Canis mesomelas*, aardwolf *Proteles cristata* and spotted hyena *Crocuta crocuta*. Bat-eared fox were only recorded at the first carcass, and for each carcass a single aardwolf was recorded only once. Whilst all carnivores, with the exception of aardwolf and bat-eared fox, were recorded eating from the carcasses, spotted hyena and bat-eared foxes were also seen rolling and rubbing against the carcass. Cattle, horse, Cape hare, porcupine and kudu were also recorded at the carcasses. Group size of carnivores varied between visits; spotted hyena ranged from one to four individuals, jackals from one to three individuals, Cape fox one to two individuals and bat-eared fox one to four individuals. Jackal and spotted hyena were the only species seen together at the carcasses. It should be noted that although lappet-faced vultures were occasionally captured on camera trap at the farm's water trough, no vultures were recorded at either carcass.

Spotted hyena rolling on ground next to carcass

Spotted hyena and jackal at the carcass

Timings of species visits

The proportions of visits per two hour time period were calculated to show when peaks in activity occurred for each carnivore species (Figure 1a & b). As expected, carnivore activity occurred mainly at night; at both carcasses jackal activity peaked at 00:00-01:59 h, whilst spotted hyena activity peaked at 04:00-05:59 h at carcass one whilst two peaks at 20:00-21:59 h and 00:00-01:59 h were seen at carcass two. Cape fox activity at both carcasses was highest around 03:00. Although jackals were present at both carcasses from day one, neither carcass was opened until spotted hyena arrived on day five for carcass one and day three for carcass two. Cape fox did not arrive at carcass one until day 36 and at carcass two until day 13 (Figure 2a & b). Spotted hyena are the only species recorded with natural markings allowing for individual recognition, therefore the amount of time spent by individuals or groups at the carcasses can be calculated for spotted hyena only. At carcass one, spotted hyenas visited nine times spending an average of 27 minutes at the carcass (range 4-105 minutes). In contrast at carcass two spotted hyena visited 27 times spending a mean of 22 minutes (range 3-94 minutes). In general time spent at carcass per visit decreased through time.

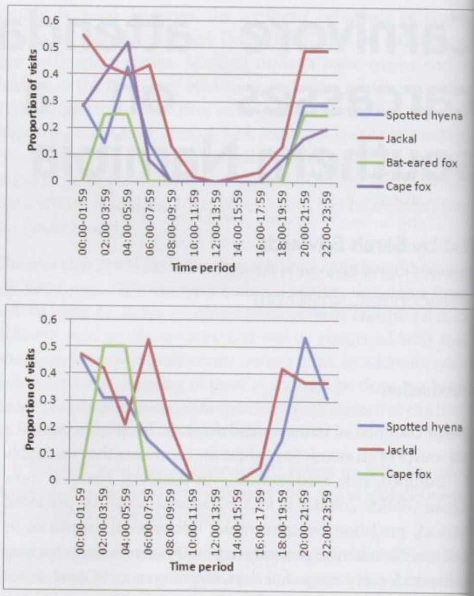

Figure 1: The proportion of visits per two hour time period illustratin the peaks in scavenging activity for each carnivore species for carcas one (Top) and carcass two (Bottom).

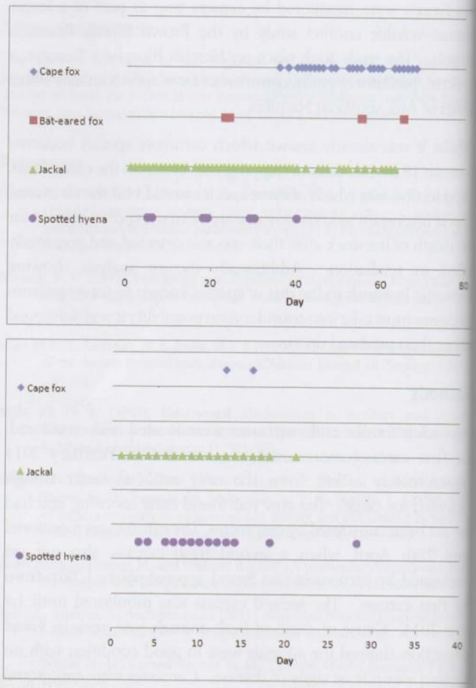

Figure 2: Presence and feeding activity of carnivore species in relatio to age of carcass (i.e. days old) for carcass one (Top) and carcass tw (Bottom).

Discussion

As large and clumped food resources, it is not surprising that the carcasses were visited repeatedly by carnivores. Jackals were the most frequently recorded species at both carcasses, although it could not be seen if this was repeated visits by a few individuals or many different individuals visiting. Due to their highly insectivorous diets neither aardwolf or bat-eared fox were expected at the carcasses, however neither species was actually recorded consuming the meat. Cape fox was not seen at the carcasses until much later than either spotted hyena or jackal, when most of the meat had been consumed. As both these species are larger and dominant over Cape fox, it is possible Cape fox was avoiding direct competition at the carcass. Alternatively Cape fox could be consuming maggots present on the carcass, rather than the meat itself. Jackal and spotted hyena were seen together at both carcasses on many occasions; no evidence of aggressive behaviour between the two species was observed from camera trap.

Both spotted hyenas and bat-eared foxes were recorded rubbing against the carcass and rolling on the ground next to the carcass. This rolling or scent rubbing behaviour is common in spotted hyena, particularly in the presence of carrion, faeces and vomit, and is believed to help transfer such odours from the environment to the animal (Rieger, 1979, cited by Drea *et al.* 2002). In a captive experiment by Drea et al. (2002), spotted hyenas which rolled in carrion odours, received more attention from conspecifics in the form of allogrooming. As both bat-eared fox and spotted hyenas are social species, it is likely the rolling behaviour observed at the carcasses was being used to confer social benefits. As bat-eared fox were not recorded eating from the carcass, it is possible this behaviour is the primary reason for visiting a carcass.

This study has demonstrated domestic livestock may be seen in the diet of carnivores as through scavenging rather than predation, even in those species not traditionally known as scavengers, i.e. Cape fox. Therefore dietary studies, particularly those focusing on human-wildlife conflict should consider this possibility.

With several species visiting carcasses repeatedly, most edible parts are consumed quickly meaning it would be difficult for a farmer to ascertain cause of death after just a day or two. With such frequent visits from carnivores, in particular jackal and spotted hyena, a large amount of spoor around the carcass was visible. Detection of such spoor or direct observation of these species at the carcass could lead to false conclusions regarding the cause of death of the animal.

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Appendix four: Questionnaire administered to farmers as part of Chapter seven

Human-wildlife conflict on commercial farmland bordering the Sperrgebiet and Namib-Naukluft National Parks

1. Farm name..(Leave blank if you prefer)
2. Farm size...
3. Number of water troughs.....................................
4. What percentage of the farm is mountain?...........
5. Type and number of livestock farmed:

Cattle	Sheep	Goats	Horses	Donkey	Poultry	Oryx	Springbok	Kudu

6. Type and number (if known) of wild game present on farm:

Oryx	Springbok	Ostrich	Steenbok	Klipspringer	Kudu	Zebra

7. Species and number (if known) of carnivores present on the farm and population status, i.e. increasing/decreasing/stable

Species	Number on farm	Population status
Spotted hyena		
Brown hyena		
Leopard		
Cheetah		
Black-backed jackal		
Caracal		
African wild cat		
Aardwolf		
Bat-eared fox		
Cape fox		
Honey badger		

8. Please detail any problems you have had with the following carnivores, detailing type of livestock killed, number of livestock killed, time of year and methods used to solve the problem.
   a. Spotted hyena

   b. Brown hyena

c. Leopard

d. Cheetah

e. Jackal

f. Caracal

9. Have you ever experienced problems with Cape fox, aardwolf, bat-eared fox, African wild cat and honey badger, such as livestock predation or digging holes? If so please detail problems and species

10. Please write in the table below which carnivore species you think are high, medium and low risk to your livestock.

Livestock	Low risk carnivores	Medium risk carnivores	High risk carnivores

11. Would you like the see the following species populations remain stable, increase or decrease (please tick)? And what is your attitude towards each species, i.e. tolerate, tolerate until cause a problem, shoot, trap etc.

Species	Increase	Remain stable	Decrease	Attitude
Spotted hyena				
Brown hyena				
Leopard				
Cheetah				
Jackal				
Caracal				
African wild cat				
Aardwolf				
Bat-eared fox				
Cape fox				
Honey badger				

12. Which mitigation methods do you currently use to protect livestock from predation? For example kraaling, livestock guarding dogs, guard donkeys etc.

13. How often do you check on livestock?..
14. What percentage of your livestock would you find acceptable to loose to carnivores per year?..
15. Where on the farm and at what time of day and year does livestock predation most often?

16. What causes of livestock loss have you experience? (Please tick)

Cause	Cattle	Calves	Sheep	Goats	Horses	Donkeys	Chicken	Game
Stock theft								

Poisonous plants								
Disease								
Carnivores								
Domestic dogs								
Veld injuries								
Calving problems								

17. Have you ever had carnivores killed by domestic dogs? If yes which species was responsible?

18. Do you experience water pipe damage? If yes which species are responsible and what mitigation methods do you use?

19. Do you experience problems with baboons? If yes please detail

20. How important is carnivore conservation to you? Please highlight/make bold 1=lowest, 5=highest

    1 2 3 4 5

Thank you for taking the time to fill in this questionnaire, the data you provide is highly valuable and very much appreciated.

Appendix five: Edwards, S., Gange, A. C. & Wiesel, I. (2015). An oasis in the desert: The potential of water sources as camera trap sites in arid environments for surveying a carnivore guild. *Journal of Arid Environments*

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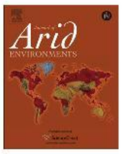

An oasis in the desert: The potential of water sources as camera trap sites in arid environments for surveying a carnivore guild

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ABSTRACT

Discussions regarding the importance of accounting for detection probability have long been present in ecological literature. Various studies have demonstrated the influence of survey design on detection probabilities, and whilst the placement of camera traps along roads is a commonly used survey design, it has shown to be biased towards certain species. In arid environments, water sources have the potential to be efficient sites for camera trap placement. We compared the influence of a water source camera trap survey design on the detection probabilities of a guild of seven carnivore species, in comparison detection probabilities from camera traps along roads, on arid, commercial farmland in southern Namibia. Results showed detection probabilities for all species to be higher at water, with the water source design producing shorter latencies of detections and higher naive occupancy estimates for most species. However, for species with unique markings, the water source design produced lower proportions of images suitable for individual identification. As detection probabilities of all species were influenced in a positive manner, we suggest placing camera traps at water sources in arid environments to be an effective survey design. However, for surveys requiring individual identification, placing camera traps along roads may be more suitable.

1. Introduction

Within the field of ecology, the issue of imperfect and varying detection probability remains a central theme of discussion (Sollmann et al., 2013), particularly pertaining to the use of relative abundance indices. Whilst statistically sound methods have been developed for those species with unique natural markings (Karanth and Nichols, 1998), relative abundance indices are still frequently used for those species without such markings, which often comprise the majority of species detected during a survey (Carbone et al., 2008). The use of relative abundance comparisons across species, space and time is particularly controversial, as such comparisons rely on the assumption of constant probability of detection (Kellner and Swihart, 2014). However, detection probability has been shown to vary with a number of factors including local density, seasonal or behavioural patterns, amount of area surveyed (Bailey et al., 2004), and survey design (Sollmann et al., 2013), meaning the assumption is unlikely to hold true (O'Connell et al., 2012), but is rarely accounted for (Kellner and Swihart, 2014). This issue has most recently been highlighted by Hayward et al. (2015) as one of the key problems facing the debate regarding the conservation use of dingoes *Canis dingo* in Australia. Hayward et al. (2015) suggest that conflicting results regarding the species' role in mesopredator suppression may be a merely an artefact of sampling methods used and failure to account for detection probability.

A number of previous studies have highlighted the importance of accounting for detection probability in multi-species surveys, by demonstrating how survey design can be biased towards particular species. Weckel et al. (2006) found both paca *Agouti paca* and armadillo *Dasypus novincinctus* had higher detection probabilities away from forest trails in Belize, whilst Harmsen et al. (2010) found off-trail camera traps failed to detect puma *Puma concolor*, ocelots *Leopardus pardalis* and white-lipped peccary *Tayassu pecari*, which were detected by trail traps in Belize. Even within a single guild, differential responses to survey design have been shown, for example Bischof et al. (2014) found species-specific differences in

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site-specific factors influencing detectability when surveying snow leopards *Panthera uncia*, stone marten *Martes foina* and red fox *Vulpes vulpes*. Additionally, in a study of puma and jaguar *Panthera onca*, two relatively similar species, Harmsen et al. (2010) showed camera traps placed on trails were biased towards puma captures, warning comparisons between relative abundances of the two species are likely to be invalid. In such circumstances, without accounting for the variation in detection probability, it may be difficult to tell if the variation seen between species capture rates is due to differences in abundance or detection probabilities (Foster and Harmsen, 2012).

Survey designs seek to maximise detection probabilities which in turn confers the benefits of higher precision estimates of abundance parameters (White et al., 1982; Karanth and Nichols, 2002; Lukacs and Burnham, 2005), and a decrease in the number of survey days, or sampling periods needed to obtain reliable data (Mackenzie and Royle, 2005; Rovero et al., 2010). However, when there is variation in the influence of the survey design on detection probabilities between species, selecting a single survey design can be problematic. Nevertheless, such an approach is likely to be the most cost effective method of surveying multiple species in a single area. Mann et al. (2014) examined the influence of camera trap placement on the detection probabilities of a range of mammals in the Little Karoo and found detection probabilities in relation to distance from roads to show extensive variation between species, suggesting camera traps placed on roads are effective for surveying carnivores, but not their prey, in an arid environment.

Many previous carnivore surveys have focused survey efforts on roads and trails, either when using camera traps (e.g. Rios-Uzeda et al., 2007), or sign surveys (e.g. Melville et al., 2006). Such an approach has been suggested to be particularly effective as roads and trails often act as natural funnels through vegetation, directing animal movement through an area (Kelly et al., 2012). Other studies have successfully used baits and lures to increase carnivore detection probabilities (Dillon and Kelly, 2007), for example Thorn et al. (2009) found a fish lure significantly increased encounter rate for brown hyenas *Hyaena brunnea*, whilst du Preez et al. (2014) found bait to significantly increase capture rate for leopards *Panthera pardus*. Previous studies have also used camera traps to produce suitable images for individual identification, for example Ngoprasert et al. (2012) used baits to encourage both Asiatic black bears *Ursus thibetanus* and sun bears *Helarctos malayanus* to expose the chest area to camera trap to show the chest markings needed for individual recognition, usually not seen when bears walk past camera traps.

The use of baits in surveys is however, debated, with concerns being raised regarding violations of the geographic closure assumption of capture–recapture surveys if the bait causes permanent immigration or emigration onto and off the trapping grid, as well as differences in individual levels of habituation through time (Balme et al., 2014). Gerber et al. (2011) examined the effects of baited camera traps on Malagasy civet *Fossa fossana* and found baits not to affect immigration or emigration, abundance or density estimates, but did increase precision of these estimates. However, for large African carnivores, the use of baits has also been suggested to raise ethical concerns as it potentially increases individual vulnerability to trophy hunting, which often uses baits (Balme et al., 2014).

Permanent water sources in an arid environment are rare and attractive to a number of species, therefore it may be considered a natural bait, without the problems associated with more traditional baits introduced into the environment for the duration of a survey only. A recent study by Edwards et al. (2015) showed evidence of temporal, rather than spatial partitioning to be the main mechanism promoting the avoidance of dominant competitors within a carnivore guild at water sources in an arid environment. In contrast, a large body of literature exists suggesting the preferential use of roads by apex predators and the avoidance of them by mesopredators in the presence of apex predators (Hayward and Marlow, 2014). Therefore, in arid environments, water sources have the potential to represent ideal locations for camera trap placement for carnivore surveys, yet the influence of such camera trap placement so far remains untested with regard to its influence on detection probabilities for multiple guild members.

This study examined the influence of camera trap placement on detection probabilities for a guild of eleven carnivore species across two commercial farmlands in southern Namibia, to investigate the potential of this survey design for multiple carnivore species. Detection probabilities produced by camera traps placed at water sources were compared to those produced by cameras placed along roads. Latency until first detection, naive occupancy estimates and species inventories produced by the two camera trap survey designs were also compared. As water is likely to be attractive to numerous carnivore species, and there being no vegetation funnel that may force carnivores to move through the site along roads, it was hypothesised the water source camera trap design would produce higher detection probabilities and naive occupancy estimates as well as shorter latencies until first detection, and a higher diversity of carnivore species inventoried. Additionally, as identifying individuals for species with unique natural markings is a fundamental aspect of density estimation, the proportion of photos where individual identification could be made was compared between the two survey designs. Here is was hypothesised the road camera trap survey design would produce higher proportions of photos for individual identification as animals are more likely to pass perpendicularly in front of road camera traps, whereas at water animals may approach from any angle.

2. Methods

2.1. Study site

The study was conducted across two neighbouring commercial farmlands; Tsirub and Klein Aus Vista (KAV), bordering the Tsau// Khaeb (Sperrgebiet) National Park, Karas region, southern Namibia. A full description of study sites can be found in Edwards et al. (2015).

2.2. Methodology

Two camera trap survey designs were compared, one with camera traps located at water sources, and another with camera traps placed along unfenced farm roads. A total of 12 Scoutguard SG560 V (HCO Outdoors, Norcross, GA, USA)camera traps were placed at water points (Tsirub $n = 7$, KAV $n = 5$), eleven being artificial water troughs and one being a permanent, natural spring on KAV. Scoutguards were programmed to take one photo per trigger, with a minute delay between triggers and set to be active 24 h per day. A full description of camera traps placed at water sources can be found in Edwards et al. (2015). A total of nine Reconyx HC600 (Reconyx Inc, Holeman, Wisconsin, USA) camera traps (Tsirub $n = 5$, KAV $n = 4$) were placed along farm roads connecting the water sources monitored by the water point camera traps, with the mean distance from water source camera traps to the nearest road camera trap being 1.79 km (range 0.45–4.27 km). Reconyx camera traps were programmed to be active 24 h a day, to take five photos at a time with no delay between triggers and at medium sensitivity. All camera traps within each survey design were spaced 3.5–4 km apart, a distance which was considered to be spatially independent. Camera traps from the road survey design any particular species. However, it is of importance that the proportions of images suitable for individual identification were lower from the water source camera trap survey design. For studies requiring identification of individuals, such as density estimations, it is therefore recommended the road survey design is used to ensure a sufficient numbers of identifiable images are obtained.

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Similarly, Srbek-Araujo and Chiarello (2005) found camera traps placed along trails to under-represent small mammal (<1 kg) diversity in neotropical Brazilian forests. As camera traps were positioned approximately 40 cm from ground level, they should have been well able to detect bat-eared fox and Cape fox with mean shoulder heights of 30 cm and 31.5 cm respectively (Walker, 1996). However, these species were both detected by water source camera traps, suggesting small body size was not the reason for non-detection. Carnivores at water sources tended to stop and drink in front of camera traps, whereas carnivores along roads walked past camera traps, therefore a combination of small body size and fast walking speed past the camera traps may explain why Cape fox and bat-eared fox were missed by road camera traps. Alternatively, the avoidance of roads by mesocarnivores in the presence of apex predators is a well documented phenomenon (Hayward and Marlow, 2014) and might explain the results seen, as well as offering as an explanation as to why all mesocarnivore detection probabilities were lower for roads than water. However, road kills of species such as brown hyena (Wiesel, 2010), Cape fox, bat-eared fox, black-backed jackal and African wild cat (Bullock et al, 2011) are relatively common, suggesting these species do commonly make use of roads even when apex carnivores are present. This information again may suggest a combination of small body size and walking speed as an explanation as to such species are not detected along roads.

Differences in detection probability have previously been seen between camera trap brands and models (Kelly and Holub, 2008), and in this study two different brands were used for the two survey designs; Reconyx were used on roads, whilst Scoutguards were used at water points. Cove and Jackson (2011) found differences in detection probability for bobcats between Reconyx and Moultrie camera traps in Missouri, with Reconyx detection probability being twice as high as Moultrie (0.23 and 0.11 respectively). Such a difference was suggested to result from the Moultrie's white flash scaring off bobcats before a photo was triggered, compared to the infra-red flash from the Reconyx. Wegge et al. (2004) also found tigers *Panthera tigris* to become trap-shy over time, believing individuals became scared of the white flash and learnt to avoid camera traps. In this study both brands of camera trap used infra-red, however differences in advertised trigger speeds, the amount of time passing between the camera trap detecting a passing target and capturing an image (Rovero et al., 2013), exist. The Reconyx HC600 advertises a trigger speed of 0.20 s, whilst the Scoutguard 560 V specifies a trigger time of 1.2 s. Such a difference in trigger speed could be expected to result in lower detection probabilities for camera traps placed at water, however the opposite result was seen. This may imply the trigger speed is less important at sites where animals are stationary in front of a camera trap, in comparison to those sites where animals are walking past camera traps.

In addition to the lower detection probabilities seen for all carnivore species in this study, camera traps placed along roads may be associated with problems such as sex biases. Balme et al. (2009) found male leopards to use man-made roads more frequently than females, whilst Salom-Perez et al. (2007) found sex differences in road use for jaguar, with females avoiding man-made trails. Such biases could have important consequences when estimating trophy hunting quotas, which are often calculated as taking a specific percentage of the male population, and should therefore be based on sound information (Spong et al., 2000). Leopard was the only species captured where male and female can easily be identified from photographs, however small sample sizes (see Edwards et al. *in press*) meant differences in detection probabilities between the sexes could not be analysed statistically. Therefore it would be of interest to examine sex biases in artificial water source use by carnivores in arid environments, to ensure water source camera trap survey designs do not produce sex biases similar to those seen for other species on roads.

Carnivore species are expected to differ in their dependence on water, which may in turn affect response to survey design, however information regarding the water requirements of African carnivores is scant. Sliwa (1996) suggested aardwolves to be generally independent of surface water, being able to obtain sufficient moisture from their diet of termites. This species was rarely detected on either road or water camera traps across the study site, and was therefore believed to occur at low density. Brown hyena are also believed to be independent of fresh drinking water (Wiesel, 2015), although this species regularly visited water troughs throughout the study area, suggesting the species will make use of such resources when available. Therefore, as species known to be independent of fresh drinking water were either captured too infrequently to include in analysis, or frequented water sources anyway, reaching conclusions regarding the effect of survey design on species independent of water is difficult and is a potential area of future research.

Examination of camera trap images suitable for individual identification showed for all three species where individual identification was possible, brown hyena, leopard and African wild cat, road camera traps produced higher proportions of suitable photos. Garrote et al. (2012) found baited camera traps produced a higher proportion of images suitable for identification than unbaited traps for Iberian lynx *Lynx pardinus*, suggesting this is a result of lynx spending more time in front of camera traps with bait. Similarly, du Preez et al. (2014) suggested leopards to spend more time in front of baited traps whilst eating thus increasing the number of images captured which improve the accuracy of identification through multiple views of the same individual. Additionally, Garrote et al. (2012) hypothesised baits caused animals to spend more time in front of traps to overcome problems with slow trigger speeds.

Whilst carnivores are likely to spend more time in front of camera traps placed at water as they stop to drink, in comparison to road camera traps, often the angle of approach to the water trough may mean the camera triggers whilst the animal is still far from the trap, or a face on shot is obtained, not suitable for identification. In comparison, road camera traps are positioned perpendicularly to roads meaning carnivores pass in front of camera traps, and are usually captured so that the whole flank of the animal is in view and when used in pairs with each trap on one side of a road, images of both the left and right hand side of the animal can be obtained. Therefore, for species where individual identification is needed for density estimation, camera traps placed along roads may provide a better survey design than traps placed at water sources. However, it is also worth trialling the use of the 'burst' setting many camera traps offer, i.e. where multiple photos are taken from a single trigger, or having no delay between triggers, which may result in more suitable photos for individual identification.

In arid environments, where carnivores often occur at low densities (Hayward et al., 2007), low sample sizes are often expected, and therefore any survey design which increases probability of detection, is likely to aid researchers. The results of this study would suggest placing camera traps at water points in arid environments when surveying a guild of sympatric carnivores to be extremely effective. Such an approach was only possible here given that there were a number of water points distributed throughout the study area, for sites where water points occur at a lower density with larger distances between them, this approach would not be possible, and further research would be warranted on camera trap survey designs in such environments. Particularly encouraging has been the fact that this survey design influenced the detection probabilities of all carnivore guild members in a positive manner and therefore was not considered to be biased towards or against

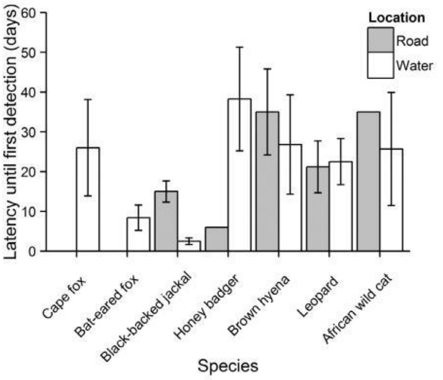

Fig. 1. Mean latency until first detection (days) (±S.E.) for carnivores detected by camera traps, for both road and water source camera trap survey designs.

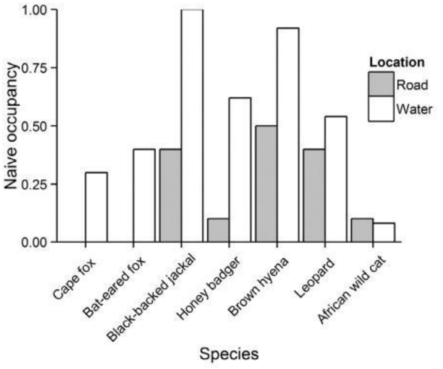

Fig. 2. Naive occupancy estimates (proportion of camera traps to detect species) for both water source and road survey designs.

photographs suitable from individual identification, i.e. where the strip or rosette pattern was clearly visible, was higher from road camera traps than those placed at water sources. A proportion of 0.6 ($n = 6$) photos from road camera traps were suitable for identification, compared to 0.13 ($n = 3$) photos from water source camera traps for brown hyena, which was not significantly different (Fisher's exact test, $P = 0.07$). Leopard showed no significant differences in the proportions of suitable photos between the two survey designs (Fisher's exact, $P = 0.41$), all photos from road camera traps were suitable for individual identification, compared to 0.61 obtained from water source camera traps. A proportion of 0.67 African wild cat images from road camera traps were suitable for individual identification compared to 0.15 from water source camera traps, which was not significantly different (Fisher's exact test, $P = 0.19$).

4. Discussion

Camera traps have long been acknowledged as being an effective and efficient method of surveying elusive and nocturnal carnivores (Karanth, 1995), with more recent studies examining the effect of camera trap placement on data collected (e.g. Mann et al., 2014). The results of this study highlight the effect of fine-scale camera trap placement on detection probability for a guild of seven sympatric carnivore species in an arid environment. That detection probabilities for all species were higher from camera traps placed at water, and for some species significantly so, in comparison to those produced by camera traps placed along roads, would suggest such a design to be suitable for multiple carnivore species in an arid environment. This finding is also supported by the shorter latency until detection for all species, with the exception of honey badger and leopard, and higher naive occupancy estimates for all species except African wild cat at water sources. Additionally, neither Cape fox nor bat-eared fox were detected by any camera traps from the road survey design, suggesting road camera trap placement may not be suitable for such species. However, as proportions of images suitable for individual identification for species with unique natural markings were higher from the road survey design, although it should be noted this was not significantly so, it would suggest road camera placement to be more suitable where identification of individuals is required.

Higher mean detection probabilities, lower latencies until first detection and higher naive occupancy estimates were seen for the water point survey design for most species, suggesting this to be a more effective and efficient method for surveying carnivores in arid environments than cameras placed along roads. High detection probabilities are desirable as they give rise to more precise estimates of abundance (Karanth and Nichols, 2002), whilst shorter latencies until first detection decrease the time needed to record species present in an area. Previous studies have found probability of detection to differ between camera traps placed on and off road, for example both leopard cat *Leopardus bengalensis* and common palm civet *Paradoxurus hermaphroditus* in Borneo (Sollmann et al., 2013) were found to have higher detection probabilities on-road in comparison to off-road. That carnivores may have higher detection probabilities on roads in environments where vegetation may restrict movement, is expected, as in such environments roads have been suggested to act as natural funnels through an area (Kelly et al., 2012). Heilbrun et al. (2006) believed their high photographic success rate of bobcats *Lynx rufus* in comparison to previous studies, was due to dense vegetation funnelling bobcats onto roads where camera traps were placed, and hypothesised such a survey design would be not be as successful in habitats with low vegetation density.

In the study site, vegetation density was low, with *Stipogrostis* grass species dominating much of the area (S. Edwards, pers. obs.), therefore such vegetation was not expected to hinder animal movement, therefore no vegetation funnel existed along roads. Such a factor may explain why this survey design was not as efficient as the water source survey design. In contrast Mann et al. (2014) found carnivore detection probability to be higher on roads than directly adjacent to roads in the arid Little Karoo. However, Mann et al. (2014) compared on and off road trap placement, whilst this study compares road and water source placements. In arid environments water is a rare resource, and even on farmlands where water is provided through artificial means, occurs at low density (5.44 troughs/100 km^2 for the study area). As a result, water is expected to be an attractant for a large number of species in the area thus explaining the water camera trap survey design was more successful in this arid environment.

The probability of detecting an animal is thought to correlate with body size, with larger bodied species being associated with higher detection probabilities (Tobler et al., 2008; Rowcliffe et al., 2013). Therefore it might not be surprising that the two smallest species as determined by shoulder heights, Cape fox and bat-eared fox, were the only species not detected by road camera traps.

were interspaced between those from the water source survey. In order to try and ensure carnivore populations were demographically closed during the study period, a survey period of 65 days was used, following the recommendations of Karanth and Nichols (1998). Additionally, a dry winter period was used, with no rainfall (29th May - 3rd August 2013), resulting in no changes to surface water availability during the study (S. Edwards, pers. obs.).

2.3. Data analysis

Carnivore camera trap images were identified and classed into independent events as described in Edwards et al. (2015). Whilst an occupancy approach may have been more suitable for such a study, the low samples sizes of some carnivore species meant models showed a poor fit to the data, therefore a comparison of relative abundance indices was used. Relative abundance indices for each species were calculated (Edwards et al., 2015), and were viewed as analogous to detection probabilities following Harmsen et al. (2010) and Mann et al. (2014). Mann–Whitney U tests were used to test for significant differences between detection probabilities produced by the water source survey design and the road survey design. Spearman's rank correlation tests were used to test for an association between detection probability and distance from water for road camera traps. Additionally for each species and camera trap survey design, latency until first detection, defined as the number of days from initial deployment until a species was first detected (Foresman and Pearson, 1998), was calculated for all positive camera traps, i.e. those which detected the species, along with the naive occupancy; the proportion of camera traps where the species was detected (MacKenzie et al., 2006). Mann–Whitney U tests were also used to test for significant differences in latencies until first detection for the water source survey design and the road survey design. All data analyses were conducted using R 3.1.1 (R Development Core Team, 2014).

For those species having individually unique markings, with sufficient sample sizes, camera trap images were examined to determine if individual identification could be made based on the clarity of markings. The proportion of images where identification could be made was then calculated from the total number of images from each survey design. As road camera traps were set to take five images per trigger with no delay between triggers, and water camera traps set to take one image per trigger, only the first image per trigger was used from road camera traps. Fisher's exact tests were conducted to examine for significant differences in the proportions of images where identification was possible for each survey design.

3. Results

Ten carnivore species were recorded over 1676 trap nights, totalling 1106 independent events (Table 1). Species detected were Cape fox *Vulpes chama* ($n = 66$), bat-eared fox *Otocyon megalotis* ($n = 26$), black-backed jackal *Canis mesomelas* ($n = 894$), honey badger *Mellivora capensis* ($n = 10$), aardwolf *Proteles cristatus* ($n = 3$), spotted hyena ($n = 3$), brown hyena ($n = 41$), leopard ($n = 33$), cheetah *Acinonyx jubatus* ($n = 1$) and African wild cat *Felis lybica* ($n = 30$). Due to low sample sizes, aardwolf, spotted hyena and cheetah were excluded from analysis. Not every species was detected by both camera trap survey designs; neither Cape fox nor bat-eared fox were detected by camera traps placed at roads.

Table 1
Total numbers of independent events by survey design for carnivore species.

Species	# of independent events	
	Water	Roads
Cape fox	66	0
Bat-eared fox	26	0
Black-backed jackal	867	27
Honey badger	8	2
Aardwolf	1	2
Spotted hyena	3	0
Brown hyena	33	8
Leopard	23	10
Cheetah	1	0
African wild cat	27	3

3.1. Detection probabilities

Mean detection probabilities were highest from the water source survey design for all species (Table 2), with Mann–Whitney U tests showing detection probability to be significantly higher from the water source survey design for black-backed jackal ($W = 100$, $P = <0.001$), honey badger ($W = 74$, $P = 0.03$) and brown hyena ($W = 77$, $P = 0.03$). Spearman's rank correlation tests showed no association between detection probability and distance of road camera traps from water for any species.

3.2. Latency until first detection

Mean latency until first detection was significantly shorter for the water source camera trap survey design for black-backed jackal ($W = 0$, $P = 0.006$) only. Mann–Whitney U tests could not be performed for honey badger and African wild cat, as for both species only one road camera trap detected the species. All other species had shorter latencies at water in comparison to roads (Fig. 1), although not significantly so, with the exceptions of honey badger and leopard, although significant differences were not seen for these species.

3.3. Naive occupancy

Naive occupancy estimates were higher for the water source survey design for all species, with the exception of African wild cat, where a difference of just 0.02 was seen (Fig. 2). The biggest difference between naive occupancy estimates for the two survey designs was seen for black-backed jackal, where naive occupancy from the water source survey design was 1.0, whilst naive occupancy from the road survey design was 0.4.

3.4. Individual identification

The three species having sufficient sample sizes and unique natural markings allowing individual identification, brown hyena, leopard and African wild cat, all showed the proportions of

Table 2
Mean detection probabilities for carnivore species from water and road camera trap survey designs, species with significant differences between detection probabilities produced by the two survey designs highlighted in bold.

Species	Mean detection probability (mean number of independent events/100 trap nights) (S.E)	
	Water	Roads
Cape fox	6.02 (5.68)	0
Bat-eared fox	4.90 (0.3)	0
Black-backed jackal	**123.13 (33.74)**	**3.87 (2.52)**
Honey badger	**2 (0.70)**	**0.27 (0.27)**
Brown hyena	**5.73 (1.54)**	**1.49 (0.58)**
Leopard	3.01 (1.05)	1.63 (0.77)
African wild cat	3.77 (2.37)	0.48 (0.37)

Appendix six: Amendments to the results of Chapter four, following Bonferroni corrections applied, as discussed during the viva.

During the viva the issue was raised regarding the use of Bonferroni corrections to the P values of the temporal and spatial resource partitioning. A Bonferroni correction is used when multiple tests are performed on several dependent or independent variables simultaneously within a single data set. It is used to decrease the chances of obtaining false negatives (type one errors) as the chances of obtaining a significant result, naturally increase as the number of tests increases (Zar 1999). To perform a Bonferroni correction, the critical significant P value (which in this thesis 0.05) is divided by the number of tests being performed, to give the new, corrected, critical P value (Zar 1999). For example, if 15 tests were being performed simultaneously on a single data set, the new critical P value would be 0.05/15 = 0.003.

Bonferroni correction was applied to all tests where multiple species pairs were tested within Chapter four, a summary of the changes to the results are given below.

Table 4.2, this showed the results of the Mardia-Watson-Wheeler tests to examine for significant differences between activity patterns of species pairs. The following species pairs no longer show significant differences:

Tsirub; Black-backed jackal and Cape fox

African wild cat and black-backed jackal

Bat-eared fox and honey badger

KAV; Honey badger and leopard

NBR: No changes to results

Generally, these changes to the individual results make very little difference to the results section as a whole. It was suggested within the discussion section of the chapter, the lack of resource partitioning between species pairs involving African wild cat, may have been due to their low density throughout the southern sites. Honey badger were also rarely recorded, having sample sizes of 34 independent samples on Tsirub and 12 on Klein Aus

Vista, which may mean their low density may negate the need for partitioning with other species.

Table 4.3, which summarised the results of the Wilcoxon tests for a significant difference in the number of days each species pair were recorded at the same water point, differed significantly than the number of days expected by chance, did not change following Bonferroni corrections.

Table 4.5, which summarised the results of the Spearman's rank correlations for assessing the degree of spatial partitioning within the carnivore guild; only black-backed jackal and bat-eared fox no longer showed evidence of spatial partitioning. Again, this new result did not change the results of the chapter, as most carnivores were observed displaying temporal, rather than spatial partitioning.

Table 4.9, which summarised the results of the Spearman's rank correlations for spatial overlap between carnivores and herbivores; these results did not change.