M.Sc. Dissertation

Resource conflicts between humans and the African wild dog (*Lycaon pictus*)

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Declaration

I hereby declare that this dissertation is my own unaided work. It is being submitted for the degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other university.

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Abstract

The African wild dog (*Lycaon pictus*) is one of South Africa's most endangered carnivores. The species has suffered massive range shrinkages in the past few decades and population numbers have dropped significantly. Along with other factors responsible for its decline, one of the most notable threats to the African wild dog is conflict with humans. These carnivores are often persecuted by farmers for their alleged depredation of livestock and captive-bred game species, although doubt exists as to whether wild dogs are the avid depredators as suggested. My research therefore aimed to investigate the conflict between people and African wild dog, focussing on livestock depredation. Due to heterogeneous farming landscapes, the history and location of protected areas and the endangered status of the African wild dog, South Africa provides many opportunities to study this particular type of human-carnivore conflict. Firstly, I conducted a meta-analysis of human-carnivore conflict using published literature about African wild dog depredation of livestock and game and compared these to other African carnivores as well as non-African carnivores. Results indicated that African wild dog were less avid depredators than other African species such as lion (*Panthera leo)* and spotted hyena (*Crocuta crocuta*). Also evident was that high carnivore and livestock densities, coupled with poor communities with poor livestock husbandry practices, make people and carnivores in developing regions more vulnerable to human-carnivore conflicts. Secondly, I assessed actual African wild dog occurrence in relation to the location of farms, livestock density and several other anthropogenic and natural landscape features. This was achieved using GPS data from four collared African wild dog individuals from packs residing in the northeastern part of South Africa and resource selection functions. Results from these analyses suggested that, whilst African wild dog may occur in close proximity to farms, they established home ranges in areas of low livestock density and few farms, indicating predictive avoidance of areas where mortality may occur. Major roads were highlighted as a vulnerability for the African wild dog, whilst nature reserves and vegetation were also important predictors of wild dog occurrence. Other anthropogenic and natural landscape features varied in importance in determining wild dog occurrence. Knowledge about how the African wild dog selects its resources will enable us to identify vulnerabilities for these carnivores as well as areas where they are likely to occur, aiding in conservation planning. Though African wild dog have historically been reported to kill livestock such goats and cattle, my study seems to indicate that these carnivores are not avid stock-killers. Given the precarious survival status of the African wild dog and the food security needs of people in a developing region strongly suggests the need for cooperation of farmers and the education of communities to aid the recovery of this uniquely African carnivore.

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Chapter 1

Introduction

Rationale

Agricultural land use makes up large parts of the Earth's terrestrial landscape and while it contributes to human livelihoods and food security, it destroys natural habitat and thus has negative repercussions for biodiversity and wildlife conservation efforts (Tscharntke *et al.* 2005). Agricultural landscapes are mosaics of different cultivated products for human consumption or use (Bennett *et al.* 2006). These mosaics can consist of tree plantations, pastures, cultivated crops and other horticultural activities interspersed with roads, human settlements, streams and wetlands and some natural vegetation patches (Bennett *et al.* 2006). The semi-natural or natural vegetation patches within the mosaics are excluded from human land-use and can include small forests, trees scattered throughout a pasture or human settlement, native grassland areas and dense vegetation along roads, waterways and agricultural field boundaries (Bennett 1990, Luck & Daily 2003). In human-altered areas, such as agricultural sites, even small remnant natural areas or woodlands can provide important refuges for native wildlife (Soga *et al.* 2014). These refuges can provide important resources, such as shelter and food, for a variety of different species, from invertebrates, such as bumblebees (*Bombus* spp, McFrederick & LeBuhn 2006), small mammals (Milstead *et al.* 2007), large mammals such as elephants (*Loxodonta africana*, Hoare 1999), and carnivores (Markovchick-Nicholls *et al.* 2008).

Historically, the objectives of the agriculture sector seemed irreconcilable with that of wildlife conservation, as land set aside for conservation was deemed wasteful or at the cost of local communities' livelihood needs (West *et al*. 2006, DeGeorges & Reilly 2008). An estimated 50% of reserves and protected areas worldwide have been founded in areas traditionally occupied by indigenous people (MacKenzie 1997). Within Africa, thousands of people were evicted from settlements when protected areas were established (DeGeorges & Reilly 2008) and subsequently relocated to densely populated and impoverished communities bordering the reserves and protected areas (Anthony 2007). Most of these communities still exist today and the inhabitants often exploit the bordering natural areas for firewood, food and medicine (McNeely *et al.* 1995, Anthony 2007), conflicting with wildlife park authorities and laws (Rangarajan 2003). Due to the proximity to protected areas, wildlife may occur in agricultural areas bordering reserves (Found 2016), but are often viewed as "pests" to agricultural production and subsequently indiscriminately eradicated (Atwood & Breck 2012).

Human-wildlife conflict is a global issue (Treves & Karanth 2003), although conflict incidents differ between regions due to resident wildlife species and variations in farming practices (Treves 2009). In most countries today, most conflict events with wildlife are characterised by mammalian carnivore species and commercial farmers (Naughton-Treves *et al.* 2003). Mammalian carnivores (hereafter carnivores), especially the larger-bodied ones (≥ 40 kg as described in Wallach *et al.* (2015), present scientists and reserve managers with one of the most difficult conservation challenges. Large areas are required to conserve carnivores (Maddox 2003). These same areas are often needed to fulfil the livelihood needs of people, including activities such as farming and mining (Wang & Macdonald 2006). These aforementioned activities are generally damaging to the environment and can ultimately cause the disappearance of large bodied carnivores from these sites (Ray *et al.* 2005). Coupled with ever-growing human populations are habitat modifications and a growing demand for ecological services and natural resources, such as timber and areas for the pasture of livestock (Hollar 2011). Agricultural areas will cause added pressure on the environment since demands for bioenergy feedstocks and food resources increase, resulting in the loss of more grasslands and other habitats (Dale *et al.* 2011; Wright & Wimberly 2013).

These global expansions of anthropogenic influences have unsurprisingly increased the occurrence and intensity of human-carnivore conflicts (Treves & Karanth 2003). Human-carnivore conflicts are defined as a perceived negative interaction between carnivores and humans, resulting in injury or loss to humans, often instigating retaliation (Madden 2004). Human-carnivore conflicts not only have disadvantageous impacts on people and their livelihoods, but the management of so-called "problem animals" can be detrimental to conservation efforts (Atwood & Breck 2012). For example, the snow leopard (*Panthera uncia)* is listed as Endangered by the IUCN (The International Union for Conservation of Nature) and their populations are still decreasing (IUCN 2016). Extensive conservation efforts and monetary inputs, such as educating rural villages about husbandry practices and raising awareness for conservation, aim to increase snow leopard population numbers (McCarthy& Chapron 2003), but they are often still persecuted for livestock depredation (Bagchi & Mishra 2006).

Anthropogenic activities and retaliatory killings have been suggested as the primary driver of several large carnivore declines, including the African lion (*Panthera leo*), tiger (*Panthera tigris*) and Mexican wolf (*Canis lupus baileyii*) (Michalski *et al.* 2006). Livestock predation by different carnivore species is a major concern and cause of conflict for farmers globally (Van Niekerk 2010), with only some examples including coyote (*Canis latrans)* depredating sheep (*Ovis aries*) in California, USA (Timm & Connolly 2001), golden jackal (*Canis aureus*) killing cattle and calves (*Bos taurus*) in Israel (Yom-Tov *et al.* 1995) and brown bear (*Ursus arctos*) and grey wolf (*Canis lupis*) killing sheep and goats (*Capra aegagrus hircus)* in Slovakia (Rigg 2004). In Africa, major livestock losses have been attributed to carnivores, with caracal (*Caracal caracal*) and black-backed jackal (*Canis mesomelas*) depredating sheep in South Africa (Thorn *et al.* 2013), spotted hyena (*Crocuta crocuta*) killing horses (*Equus caballus*) in Ethiopia (Abay *et al.* 2011), lion depredating cattle in Cameroon (Tumenta *et al.* 2013) and wild dog killing goats in Kenya (Woodroffe *et al.*

2005a). Regardless of location or livestock targeted, it is clear that livestock depredation by carnivores is a common problem, and that the factors that both initiate and mitigate this behaviour must be investigated.

Livestock farming in SA

Due to low viability of crop production stemming from adverse climatic conditions (Blignaut *et al.* 2009), animal agriculture is the most important and primary income generator in South Africa for both rural and commercial farming in different climatic zones (Shackleton *et al.* 2001). Livestock agriculture is one of the largest and fastest-growing sectors in South Africa, with different livestock subsectors consisting of dairy farming, beef farming, sheep and goat farming, poultry farming and game ranching (commercial only) (Goldblatt 2010). Livestock production across South Africa is not homogenous (Cousins 2008), with both rural-based and commercial production contributing significantly to household food security (Livestock Development Strategy for South Africa 2006). In sub- Saharan Africa, 41% of all agricultural land consists of small or very small subsistence agricultural lands, whilst only 12% consist of large and very large commercial agricultural lands (Samberg *et al.* 2016). When compared with commercial farms, these smallholder farms contribute more food calories toward direct human consumption at a local scale (Samberg *et al.* 2016).

Despite the numerous subsistence farms contributing to produced calories, the success of the South African livestock sector in relation to gross domestic product (GDP) is ascribed to commercial farming and livestock intensification to increase production numbers and turnover rate (Livestock Development Strategy for South Africa 2006). The total production of livestock food products (excluding non-food products such as wool or fertiliser) from commercial agricultural systems comprises and average of 4 million tons per annum (Goldblatt 2010). South Africa produces 85% of all its beef requirements, with extensive cattle ranches occurring mostly in the Free State, Kwazulu-Natal and Limpopo Provinces, with herds mainly comprised of the indigenous Afrikaner or Nguni cattle breeds (Reist-Marti *et al.* 2003). These two breeds are popular due to their tick resistance, high fertility, low inter-calf periods and the production of tender meat (Strydom *et al.* 2000). Sheep farming is concentrated in the interior Cape regions and the Free State Province, whilst goats are common throughout many Provinces (Snowder & Duckett 2003). The Dorper sheep and the Boer goat are both hardy, locally developed breeds, and are responsible for most of South Africa's mutton and goat products (Malan 2000, Snowder & Duckett 2003), while Merino sheep and Angora goats are used primarily for textile products (Visser *et al.* 2009). Poultry production in South Africa is the most intensive producer of food products when compared to the other meat-producing livestock sectors, with an annual poultry meat production of 960,000 tons, with 768,000 tons consisting of broiler chickens (Dyubele *et al.* 2010). The remainder consists of ducks, geese, turkey and ostrich meat (Dyubele *et al.* 2010). Game ranching is an increasingly prevalent commercial farming venture in

South Africa, because many farmers find it more profitable than livestock farming (Bothma 2005). In addition to income derived from sport hunting, stud breeding and tourism, breeding of rare colour morphs has also become a popular income generator due to rapidly escalating sale prices (Bothma 2005). The dichotomy between subsistence and commercial farming systems, coupled with the need for food security in a developing country may make South African farmers especially vulnerable to conflict with carnivores when livestock and game species are depredated.

African wild dog and its decline

The wild dog, also known as the African painted dog, is a crepuscular carnivore found in sub-Saharan Africa (Woodroffe *et al.* 2005b). It is characterised by large ears, a long muzzle and distinctive black, brown and white coat markings that are not only unique to each individual, but also bilaterally asymmetrical on the body (Woodroffe *et al.* 2005b). Wild dogs weigh an average of 20-30 kg, are 60-75 cm tall and have an average lifespan of 11 years in nature (Estes 1991). Wild dogs are habitat generalists (Whittington *et al.* 2011) but as with many other carnivores are possibly influenced or restricted by human-altered landscape features (Jenkins *et al.* 2015).

Wild dogs are obligate group-living, forming permanent packs and adhering to a hierarchical, cooperative social structure among both sexes (Estes 1991). A pack generally comprises of the alpha pair, 4-8 adults, 5-11 pups and 2-6 yearlings (Woodroffe & Ginsberg 1997). The alpha pair usually consists of the oldest female in the pack and a prime aged male (aged between 4-6 years), as the older male is usurped and forced into a more subordinate position by the younger, stronger and more fertile male (Creel & Creel 2002). In wild dogs, unlike most other group-living carnivores such as wolves, males remain in their packs of birth, while long distance dispersal occurs primarily by small groups of related juvenile females that join existing packs (Creel & Creel 2002) or form new packs with unrelated males (Girman *et al.* 2001). Female dispersal is therefore important for the genetic variation within wild dog populations (Girman *et al.* 2001). The longest dispersal distance of a wild dog individual was recently found to be 476 km^2, between Northern Tuli Game Reserve and Hwange National Park in Zimbabwe (Davies-Mostert *et al.* 2012).

Wild dogs are obligate cooperative breeders (Van Den Berghe *et al.* 2012), and other pack members help rear the pups of the alpha pair (McNutt & Silk 2008). The alpha female can produce a litter of 2-22 pups, although litter size is influenced by maternal age and pack size, with older females in larger packs having and successfully rearing more pups than younger females in smaller packs (McNutt & Silk 2008). Pup survival is possibly due to older females having more experience in raising pups, and larger packs having more helpers and more frequent, successful hunts (McNutt & Silk 2008). Despite this, the average survival rate for a litter of pups, as calculated from a study in northern Botswana, is often less than 50% (McNutt & Silk 2008). Juveniles from a previous year’s litter bring back food for the mother in the den, guarding the pups while the pack is away hunting and defending them against possible predators (Creel & Creel 2002). Dens are often established in empty termite mounds that have previously been excavated by other animals, such as aardvark (*Orycteropus afer*), and pups are confined to the den for the first three months of life (Mbizah *et al.* 2014). Throughout the rest of the year, wild dogs have large home ranges of 423-1318 km^2, but they change their usual wide ranging behaviour during the denning period for den defence and pup food provisioning (Creel & Creel 2002), with home ranges averaging 50-260 km^2 (Mbizah *et al.* 2014). An individual wild dog can cover an average area of 10 km^2 daily (Davies-Mostert *et al.* 2012). Wild dog packs mostly hunt medium sized antelope like impala (*Aepyceros melampus*) and Thompson's gazelle (*Eudorcas thomsonii*) by approaching silently and then chasing the prey down at an average speed of 66 km per hour over an average distance of 6 km (Estes & Goddard 1967). Prey is continuously bitten on the belly, rump and legs until it falls down, and is then consumed quickly by the pack (Kingdon 1988).

Despite extensive conservation efforts and protection under the South African National Environmental Management: Biodiversity Act (NEMA 2004), wild dog populations have been declining dramatically in the past century, and today the species is classified as Endangered by the IUCN Red List of Threatened Species (Woodroffe & Sillero-Zubiri 2012, IUCN 2016). Even whilst being well protected by conservation actions and legislation, wild dogs are found at low population densities of 2-27 individuals per 1000 km^2 across a variety of different sub-Saharan ecosystems (Davies-Mostert *et al.* 2009), having suffered major range shrinkages in the past century (Figure 1.1). Recent population numbers in protected areas are estimated at only 300-500 individuals (Dr Kelly Marnewick in litt) with one of the few viable, free ranging populations occurring in the Kruger National Park (Lindsey *et al.* 2004b). It is uncertain what the population numbers might be outside of protected areas. One reason for this decline is the interspecific competition (Creel *et al.* 2004) and direct killing of adults and pups by larger carnivores (Creel 2001), with 47% of adult and 20% of pup deaths being caused by lion (Sillero-Zubiri 2004). Additional reasons for decline include kleptoparasitism of their kills by lion and hyena (Fanshawe & Fitzgibbon 1993), and deadly infectious diseases such as rabies and canine distemper (Fanshawe *et al.* 1991), with rabies contributing to the extinction of wild dogs in the Serengeti ecosystem from 1990-1991 (Woodroffe & Ginsberg 1997). In 2016, the Lower Sabie wild dog pack in Kruger National Park, a pack of 13 individuals, was wiped out due to the canine distemper virus (Dale Hes in litt). However, shrinking habitats and conflict with humans have been ascribed as the major reasons for the population decline of the wild dog, with government-sanctioned killings lasting up until the late 20^{th} century (Creel *et al.* 2004). Today, persecution is still an ongoing problem (Swarner 2004), with 26% of a population of 196 studied wild dogs in the Laikipia District in Northern Kenya dying due to shooting and poisoning by farmers (Woodroffe *et al.* 2005b). Mortality on roads carrying heavy traffic is another danger to these species, with nine wild dogs killed on roads in the Greater Mapungubwe Transfrontier Conservation Area within a three-month period in 2012 (Collinson *et al.* 2015).

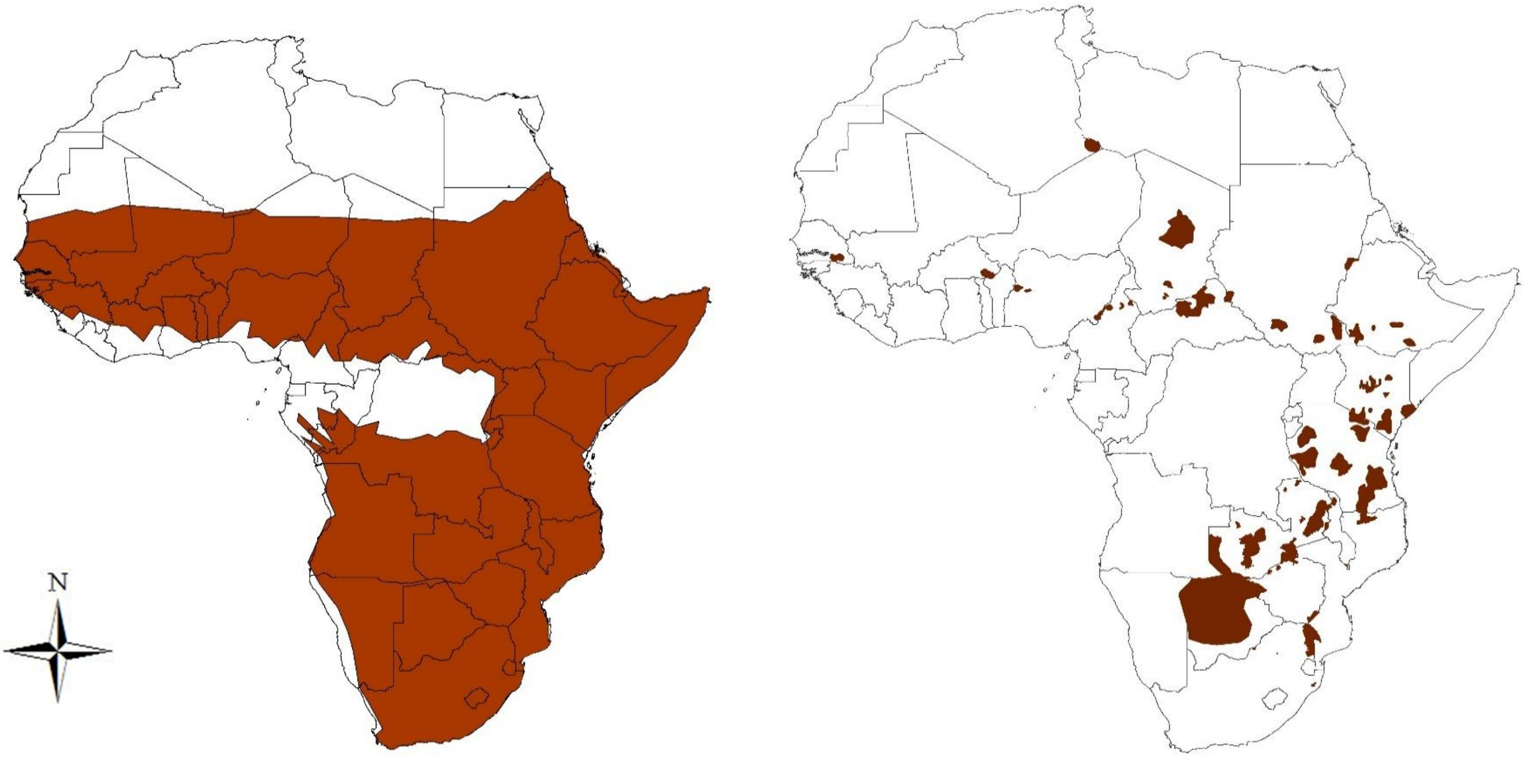

Figure 1.1. Published historical (left) and current (right) geographical distribution of the African wild dog throughout Africa. Both distributions of African wild dog were estimated and compiled by the IUCN SSC range-wide conservation planning process for Cheetah and African wild dog. The current geographic range comprises only areas of known residence. Wild dogs have been virtually eradicated from large regions of their former ranges in North and West Africa, with the largest populations remaining in southern Africa, especially Botswana, Tanzania, western Zimbabwe and the Kruger National Park. Data for the historical map were obtained from http://cheetahandwilddog.org/prosa.html, and data for the current map was obtained from the IUCN, with permission to download granted by the IUCN at 2016-11-20 14:10:01 UTC.

Historically, wild dogs have not garnered public sympathy compared to species that are considered more charismatic and iconic, such as leopard (*Panthera pardus*) or lion (Lindsey *et al.* 2005). Similarly, myths, superstitions and negative perceptions surrounding wild dogs remain prevalent in modern times, leading to at least 15 consumptive uses for wild dog body parts in traditional medicine (Page 2014), posing a risk for the continued survival of these animals even in protected areas (Mbizah *et al.* 2014).

The aim of this dissertation was to investigate human-wildlife conflict with regards to the African wild dog (*Lycaon pictus*) in a global and regional context and to assess the home range characteristics and resource selection of these carnivores to ascertain predictors of their occurrence and their vulnerability to persecution by people.

Dissertation layout

This dissertation comprises of four chapters. In addition to this introductory chapter (Chapter 1), there are two data chapters (Chapters 2-3) and a general discussion chapter (Chapter 4). Chapter 2 consists of a meta-analysis of published literature on human-carnivore conflict at a global scale, focussing on African wild dogs and other local and global mammalian carnivores as livestock depredators. Chapter 3 investigates human-carnivore relating to African wild dog at a regional scale, focussing on the predictors of their depredation by assessing their use of resources in the environment to determine predictors of their occurrence, depredation potential and to assess their vulnerability. The two data chapters each include an abstract, introduction, methods, results and discussion sections. A supplementary section is appended to Chapter 3 and a reference section is provided at the end of this dissertation. Tables and figures are numbered in sequence for each chapter. Throughout this dissertation, I endeavoured to avoid repetition of information between chapters, although some overlap in content may occur.

Chapter 2

A meta-analysis of human-carnivore conflict: South African and global perspectives

Abstract

Human-carnivore conflict is a global problem and stems from growing human populations, increased demand for natural resources and land to graze livestock. Carnivores often depredate livestock, leading to their persecution. This is detrimental to conservation efforts, especially that of endangered species such as the African wild dog. I therefore conducted a meta-analysis of scientific literature to assess human-wild dog conflict in southern Africa with those of other carnivores both locally and globally to compare common patterns of human-carnivore conflicts, including the 1) livestock and game depredated, the 2) morphology, behavioural and ecological correlates of carnivores involved in depredation; and the farmer type (commercial vs subsistence) experiencing depredation. Specific focus was placed on general patters of depredation events globally and locally, community vulnerabilities and reaction to depredation, and carnivore species involved in livestock attacks. Institute for Scientific Information scientific publications and other literature from scientific databases relating to quantifiable human-carnivore conflicts were sourced from 1982-2015. This resulted in 77 publications, reporting 33 species of carnivores (seven publications on African wild dog), depredating 13 livestock types and game from 26 commercial and 51 subsistence communities globally. High carnivore and livestock densities, coupled with poor communities with poor livestock husbandry practices, make developing regions more vulnerable to human-carnivore conflicts. This will contribute to risk of persecution of carnivores, particularly the endangered African wild dog. In addition, livestock are more vulnerable to depredation from nocturnal carnivores, whilst other carnivore morphologies and behaviors, such as body size, hunting tactics and sociality reportedly did not affect the likelihood of livestock depredation. I conclude that the African wild dog is equally damaging as a livestock depredator when compared to other carnivores in a global context, but is less damaging than other species, such as spotted hyena and lion, in an African context.

Keywords: African wild dog, carnivores, conflict, depredation, livestock, meta-analysis

Introduction

Vulnerability to depredation and mitigation methods

Human-carnivore conflict is influenced by biological, sociological and socio-economic factors, and people from different economical classes, cultures, beliefs and attitudes can be affected differently by livestock depredation (Atwood & Breck 2012). Subsistence agriculture, practiced mostly in developing regions, such as Africa, Asia and India, is defined by self-sufficient farming of crops and animals (Ellis & Biggs 2001), but farmers seldom have surplus stock to sell (Waters 2006). Subsistence farmers often struggle to produce agricultural products due to poverty (Morton 2007) and other difficulties such as theft (Tinsley 2003), droughts or floods (Suarez *et al.* 2008), poor soil quality (Lal 2004) and depredation of livestock by carnivores (Namgail *et al.* 2007). The depredation of livestock, coupled with these other stressors, intensifies human-carnivore conflict and the persecution of carnivores (Datiko & Bekele 2013). Commercial farming involves the production of crops and livestock for the market (Walford 2002), and is characterised by the use of specialised tools and machines (Van Huylenbroeck *et al.* 2007) and intensive livestock husbandry practices, including selective and cross-breeding (Simm *et al.* 2005), inoculations (Hutchison *et al.* 2005) and specialised nutritional supplements (Arriaga *et al.* 2009). Due to these large monetary inputs by commercial farmers, depredation of livestock is perceived as massive financial loss (Sillero-Zubiri *et al.* 2001), often leading to the indiscriminate killing of carnivores (Schumann *et al.* 2008) and thus aggravating human-carnivore conflict.

The perceived or monetary value of the livestock killed adds to the magnitude and type of retaliation initiated by livestock depredation (Namgail *et al.* 2007). Cattle tend not only to have a higher monetary value than smaller livestock, but also hold cultural value for many people, being a centre of identity and a symbol of wealth and respect, for example in the Maasai culture, thus eliciting a strong emotional response when killed by predators (Kolowski & Holekamp 2006). In Kenya, cattle are considered as live "savings" that are available to be converted into money when needed and the farmer owning the most cattle in a community is considered a good leader, as he is able to help other families in crises (Ouma *et al.* 2003). Goats, like cattle, are a similarly important social currency in most African countries, as they are used in the practice of paying a bride price (known as lobola), are exchanged to or given as loans to relatives and used in ceremonies or religious rites (Braker *et al.* 2002). Poor husbandry practices may contribute to human-carnivore conflict by allowing carnivores easy access to livestock (Ogada *et al.* 2003). For example, carnivores can access livestock when there is insufficient livestock guarding, such as the use of inexperienced herders or children tasked with guarding (Ikanda & Packer 2008) and grazing livestock in dangerous locations known to contain carnivores (Bhattarai & Fischer 2014).

Farmers invariably attempt to mitigate losses to carnivores by either acting preventatively or reactively (Carter *et al.* 2012). Preventative measures include the use of deterrents and repellents (Follmann *et al.* 1980). Deterrents and repellents include physical barriers, projectiles, visual and acoustic repellents, explosives and chemicals, all aimed at discouraging carnivore presence, to stop near approach and attack (Smith *et al.* 2000). Deterrents can include the use of chemical substances, such as lithium-chloride baits for aversive conditioning (Gustavson *et al.* 1974) or painting ear tags and protection collars of livestock with pungent chemicals (Landa & Tømmeras 1997). Visual and acoustic repellents include frightening stimuli to prevent a predator from entering areas where livestock are kept, examples of which include crackers (Koehler *et al.* 1990), alarm calls (LeFranc *et al.* 1987), gas exploders (Bomford & O'Brien 1990), fladry barriers (Musiani *et al.* 2003) and guard dogs (Marker *et al.* 2005), while physical barriers include structures such as bomas and corrals (Ogada *et al.* 2003) or electric fences to safeguard livestock (Karhu & Anderson 2006). Projectile repellents are utilised on carnivores that have already moved into an area and been detected (Smith *et al.* 2000), such as anti-riot rubber bullets (Stenhouse 1982), ferret soft-slugs (Clarkson 1989) and rock-throwing (Smith *et al.* 2000). The efficacy of many of these methods is low or short-lived, as some are too expensive for long-term use, require constant human presence and/or predators become habituated to adverse stimuli (Smith *et al.* 2000), and can often only be afforded by commercial farmers.

Farmers may resort to pre-emptive killing of carnivores as a preventative measure or retaliatory killing when livestock are killed or if preventative measures fail (Carter *et al.* 2012). Reactive measures include the use of lethal substances or mechanisms that deliberately remove carnivores to protect livestock (Treves & Naughton-Treves 2005). Examples include steel-jawed or serrated-tooth traps (Fisher *et al.* 2015), poisoned bait carcasses (Berger 2006), staked pitfall traps, and hunting (Daly 2006). Although considered as the cheapest and most effective method of reducing depredation, lethal control is commonly nonselective and kills non-target species (Rochlitz *et al.* 2010), is energy intensive and often has the unintended consequence of an influx of other replacement carnivore species or individuals (Crooks & Soulé 1999, Ritchie & Johnson 2009). The implementation of both preventative and retaliatory practices to control depredation by carnivores are also dependent on economic factors, since (poorer) subsistence farmers are unable to afford economically costly preventative measures (Thirgood *et al.* 2005), in addition to paying for the replacement of livestock lost to carnivores (Wang & Macdonald 2006). For example, between 1988-1996, rural villagers living in the Nanda Devi Biosphere Reserve located in India lost US$ 29,272 in sheep and goats to Persian leopards (*Panthera pardus saxicolor*) (Rao *et al.* 2002). Similarly, livestock predated by snow leopards (*Panthera uncia*) resulted in 25% loss annually of the average per capita income of villagers in Nepal (Oli *et al.* 1994). In Web Valley, Ethiopia, pastoralists suffered a financial loss of US$ 13,054 over three years, with depredation on cattle, sheep and goats by spotted hyena and African leopard (*Panthera pardus pardus*) (Atickem et al 2010). In Namibia, subsistence farmers lost an annual US$ 78 per household to depredating carnivores (Jones & Barnes 2006).

Morphological and ecological predictors of attack

Carnivore species differ in their activity patterns, hunting techniques and sociality, each contributing to or easing human-carnivore conflict (Ray *et al.* 2005). Daily activity patterns vary from exclusively nocturnal species (e.g. caracal (*Caracal caracal*)), through crepuscular (e.g. African wild dog) to diurnal species (e.g. cheetah (*Acinonyx jubatus*); Gehrt *et al.* 2010). Carnivores employ different hunting strategies, depending on their morphology, behaviour and type of prey they hunt (Maddox 2003). Three main types of hunting techniques are utilised, namely ambush (sit-and-wait) run-down and opportunistic (Gehrt *et al.* 2010). Ambush hunting includes stalking prey, followed by a short rush or chase of the prey, whereas run-down hunting involves long-distance chases to tire out prey (Rigg 2004). Opportunistic carnivores generally do not employ a strict hunting mode (Jaksić 1989), but rather select prey in the same relative abundance as is available in the environment, feeding on anything encountered and caught (Delibes-Mateos *et al.* 2008). The red fox (*Vuples vulpes)* feeds mostly on European wild rabbit (*Oryctolagus cuniculus*) when it is abundant in the environment, but shifts its diet to other prey when rabbit abundance is low, typical of an opportunistic feeder (Bartel & Knowlton 2005, Delibes-Mateos *et al.* 2008).

Predator behaviour following prey capture may add to their vulnerability to human-carnivore conflict (Buchholz 2007). For example, lion are more likely to stay and defend livestock carcasses (which invariably lead to confrontations that get them killed), while spotted hyena are more wary of humans and often flee kill sites where possible (Patterson *et al.* 2004). Leopard (*Panthera pardus*) are secretive and hide their kills and themselves thoroughly (Patterson *et al.* 2004). A large proportion of the felid family are solitary except during the breeding season, and most of the canid family display varying levels of group-living, from monogamous pair-bonds in black-backed jackal (*Canis mesomelas*) to packs as occurs in grey wolf (Gehrt *et al.* 2010) and African wild dog (*Lycaon pictus*) (Estes 1991). Additional group members may offer increased protection against other carnivores (McNutt 1996), increased hunting efficiency (Treves & Karanth 2003) and alloparental care for offspring (Ray *et al.* 2005). Larger groups have greater food requirements (Gehrt *et al.* 2010). Greater food requirements possibly make social, pack-living carnivores, such as the African wild dog, more likely to experience conflicts with humans, although this hypothesis is yet to be tested.

African wild dog- human conflicts

The African wild dog (hereafter wild dog) is one of the world's most endangered large carnivores, extirpated from 64% of its historical range (Fanshawe et al., 1997). Conflict with humans coupled with habitat losses have been ascribed as the major reasons for the population decline of wild dog

(Woodroffe & Ginsberg 1999), with government-sanctioned killings lasting up until the late 20th century (Creel *et al.* 2004). Today, persecution is still an ongoing problem (Swarner 2004), with 26% of a population of 196 studied wild dogs in the Laikipia District in Northern Kenya dying due to shooting and poisoning by farmers (Woodroffe *et al.* 2005b). In addition to myths and superstitions that still remain prevalent, wild dogs are often blamed for livestock depredation and income loss by farmers (Lindsey *et al.* 2004a, Woodroffe *et al.* 2005). Wild dogs have also been ranked as the least favourite carnivore by South African ranchers, even when compared to other species known to be avid depredators such as black-backed jackal (*Canis mesomelas*) (Lindsey *et al.* 2005). Moreover, wild dogs are often blamed for the depredation of expensive trophy game, such as the golden wildebeest, also known as the kings wildebeest, a colour variant of the blue wildebeest (*Connochaetes taurinus*), leading to their extensive persecution (Mbizah *et al.* 2014). This particular type of conflict is especially prevalent in southern Africa, where the hunting industry is thriving, with about 12000 game farms in South Africa generating approximately R7 billion through annual biltong (dried, cured meat) and trophy hunt sales (Van der Merwe *et al.* 2014).

South African auction sales for wildlife species grew from US$ 5.9 million to US$ 95.2 million in only ten years (Dry 2014). In 2014, a 4.5 year old bull golden wildebeest could fetch a staggering market price of US$ 6552 (ZAR 90,000), compared to a blue wildebeest of the same size that would cost only US$ 400 (ZAR 5,493) (Dry 2014). It is therefore no surprise that the negative attitudes of wildlife ranchers originate from the perception that potential income is lost when wild dogs predate on wildlife on game farms, or that the mere presence of these carnivores causes trophy animals to hide or flee, impairing hunting for humans (Fanshawe *et al.* 1991). These numerous negative perceptions may not reflect the true impact of wild dogs, since studies in Zimbabwe have shown that fewer than half of livestock attacks can be attributed to wild dogs (Rasmussen 1999). A study conducted in southwestern Kenya showed that wild dog kills annually were made up of 67% Thompsons gazelle, 24% impala and 9% blue wildebeest, with no livestock killed, as reported by local Maasai herdsmen, even though a pack often encountered unattended, free-roaming cattle while hunting (Fuller & Kat 1990).

The aim of this study was to compare common patterns of human-carnivore conflicts relating to wild dog in southern Africa with those of other carnivores both locally and globally to assess the impact of wild dog depredation on livestock in a local and global context. I conducted a meta-analysis of published scientific literature, and focussed on four different aspects. 1) Globally map human-carnivore conflicts as extracted from publications to assess conflict incidents compared to livestock and carnivore densities. 2) Investigate the types of livestock depredated most frequently. 3) Examine the opportunities of depredation (such as unattended livestock or poor husbandry techniques) and the type and grade of retaliation by farmers (preventative or reactive). 4) Ascertain the African and non-African carnivore species involved in depredation events in order to ascertain which carnivore species characteristics predicted livestock depredation.

Materials and Methods

Metadata sourcing and review

A systematic review of global and local human-carnivore conflict from 1982-2015 in order to examine depredation events historically and currently and was performed by following the guidelines and search methods outlined by Kent (2001). I used 1982 as the starting date, because this was the earliest published paper found in the literature. I considered human-carnivore conflict as the negative interactions that arise between humans and wildlife resulting in loss or injury of livestock and consequently human livelihoods (Madden 2004). Various search engines and bibliographic databases namely, Google Scholar, JSTOR, Web of Science, ScienceDirect, Springer, BioOne and Wiley Online Library were searched for published Institute for Scientific Information (ISI) and other publications including technical reports, dissertations and theses containing information on human-carnivore conflicts both in South Africa and globally. Publications from these databases were all accessible from the University of the Witwatersrand Library Online resources. Web searches for relevant literature were focused by employing logical operators and modifiers (Kent 2001), using key phrases such as “livestock depredation”, “carnivores AND livestock”, “farming loss to carnivores” and “carnivore-human conflict”. Before publications were downloaded, the abstract and result sections were searched for quantifiable information regarding carnivore species involved in the attacks and numbers of livestock types depredated by predator species. Publications that did not state any of the aforementioned information were discarded. Alternatively, when a publication listed only total livestock numbers depredated by carnivore species without differentiating between different livestock types lost to predators, it was still downloaded but could only be included in the farm type, opportunity of depredation and retaliation analysis. I acquired additional publications by cross-referencing the reference lists of each publication.

Relevant papers were downloaded and information extracted about area of conflict, Global Positioning System (GPS) coordinates in decimal degrees of reported study site, livestock types targeted by predators and carnivore species involved in depredation events. Additionally, I investigated farm types involved in depredations, opportunity of depredation and retaliation. I explain these categories in detail, below.

Mapping of conflict localities

Maps were created of human-carnivore conflict localities globally, along with maps of global livestock densities and carnivore richness. GPS coordinates were obtained from publications for each study site and converted to longitude and latitude for use in ArcMap (ArcGIS for desktop Version 10.1, Environmental Systems Research Institute (ESRI) Development Team). To obtain GPS coordinates for publications that did not list the coordinates, the reported study site was searched by its name in Google maps (https://maps.google.com/) and the approximate centre of the site used to obtain the longitude and latitude. For mapping, each publication was considered as one human-carnivore incident, even if the publication reported multiple carnivore species involved in different livestock type depredations, as often only one set of GPS coordinates were given per study site and not per carnivore depredation event in that study site. All coordinates, study site information and total depredation numbers per study site were saved in Microsoft Excel 2013, and imported into ArcMap. The basemap "Dark Grey Canvas" was added directly from ArcGIS online (a desktop tool in ArcMap, but also obtainable from: http://www.esri.com/software/arcgis/arcgisonline) in order to plot the longitudes and latitudes for continents.

Subsequently, I downloaded global predicted livestock densities for cattle, goats, sheep and poultry from the Food and Agriculture Organisation (FAO) of the United Nations (available from: http://www.fao.org/Ag/againfo/resources/en/glw/GLW_dens.html) because these are the most common livestock types kept globally for meat and other livestock products (Robinson *et al.* 2014). The GIS files of these maps are free to download through the FAO's GeoNetwork data repository and are corrected for unsuitability and adjusted using the most recently available (2005) observed totals of each livestock type to create livestock density maps. This meant that the most complete, available livestock population numbers were collected at a regional level and converted to livestock population densities (Robinson & Pozzi 2011). These densities were then adjusted according to satellite-derived land cover and vegetation indices that showed sufficient grazing, as well as areas unsuitable for livestock farming, such as steep elevations and urbanised areas (Robinson & Pozzi 2011). These adjusted densities are therefore accurate in showing where livestock would actually occur versus which areas would be unsuitable, and therefore unlikely, to house livestock. The GIS files for cattle, goats, sheep and poultry were imported into ArcMap and the coordinates of human-carnivore incidents overlaid on each livestock density map to show depredation incidents relative to livestock densities. Lastly, I downloaded the GIS file for a carnivore richness map form Biodiversity Mapping (http://www.biodiversitymapping.org) showing the global distribution of native, extant carnivore species at a 10 km^2 resolution. The map was compiled by Jenkins *et al.* (2013) based on data from the IUCN July 2013 update, free for academic use. This map was imported into ArcMap and the coordinates of human-carnivore incidents overlaid to show incidents relative to carnivore richness. Maps were then visually compared to investigate where depredation incidents took place, which continents suffered more incidents (by number of GPS dots) and whether depredation was linked to livestock densities and/or carnivore richness.

Livestock types depredated

In 1993, about 3831 different breeds of livestock existed across the world (Hall & Ruane 1993), and that number has since risen to over 8000 breeds and 40 species kept on different farms globally (Yaro *et al.* 2016). For the purpose of this study, I did not differentiate between different livestock breeds, since they were often not distinguished in the literature. I therefore defined livestock using common names (Table 2.1). Since depredation by carnivores were often reported as single events, I considered each livestock type separately.

Table 2.1. Common livestock types and other vulnerable animals depredated by carnivores globally, as listed in publications, with short descriptions, uses and average weights as listed by Porter *et al.* (2016).

Livestock common name	**Scientific name**	**Description and use**	**Average Weight (Kg)**
Calf	*Bos taurus*	Used in farming for meat production (veal) or reared to supplement the cattle herd.	28
Camel	*Camelus spp*	Used in farming for milk, meat, hair for textile goods and working animals	589
Cattle	*Bos taurus*	Most common type of large domesticated livestock. Used in meat and dairy production, leather goods and as draught animals.	1088
Domestic dog	*Canis familiaris*	Often used in agriculture as livestock guarding or herding animals or to guard property.	45
Donkey	*Equus africanus asinus*	Most often used as draft animals in agriculture.	499
Dzo	*Bos grunniens* × *Bos taurus*	A hybrid between cattle and yak. Is thought to be stronger and more "hardworking" than either cattle or yak.	839
Game	varied	Refers to non-domesticated animals that are kept on farms in natural conditions for either trophy or sport hunting and the meat industry. Most common species kept in South Africa are the blue wildebeest (*Connochaetes taurinus*).	131 (wildebeest) 138 (reindeer)
Goat	*Capra aegagrus hircus*	One of the oldest domesticated species. Used in the production of meat, milk, cheese, and textile products.	140
Horse	*Equus caballus*	Used in leisure activities, as transport animals and as draft animals. Also used for meat for both human and animal consumption.	997
Lamb	*Ovis aries or Capra aegagrus hircus*	Used to supplement the herd, meat production and raised for meat and wool/ textile products.	4
Pig	*Sus scrofa domesticus*	Most commonly used for meat production.	358
Poultry: include Chicken, Duck, Turkey	*Gallus domesticus, Anas Platyrhynchos, Meleagris*	Refers to domesticated fowl of different types typically from the order Galliformes, used in the production of feathers, eggs and meat. Chickens are the most commonly kept.	2
Sheep	*Ovis aries*	Typically used for the production of wool and meat	130
Shoat	*Ovis aries* or *Capra aegagrus hircus*	Term used when publications did not distinguish between sheep and goats because these animals are often kept in mixed herds.	135
Yak	*Bos grunniens*	A long-haired domestic bovid adapted to high-altitude areas. Used in the production of meat, milk, textile products and as draft animals.	589

Farm type, opportunity for depredation& retaliation

I recorded the farm types (either subsistence or commercial) experiencing the carnivore attacks, chance of livestock depredation and retaliation by farmers. When farm types were not explicitly stated in a publication, it was assumed that a farm was commercial if the total livestock stated in the publication was ≥ 200 head of livestock and subsistence if it kept < 200, using farm classifications by Galanopoulos *et al.* (2006). I defined the ease of predator access to livestock leading to a predation event (here opportunity of depredation) by characterising the reasons stated in publications for the depredation of livestock into a high and a low category (Table 2.2). I defined retaliation as what type of action a farmer took after or before a depredation event occurred. Retaliation ranged from non-violent to violent measures (Table 2.3).

Table 2.2. Self-defined classification for chance of livestock depredation. Categories were created using events mentioned in publications, where the opportunities of possible predation were either low or high. Events stated in publications for the Low category indicate possible reasons of depredation, whereas events stated in publications for the High category were given as definitive reasons for livestock depredation.

Opportunity of depredation	**Criteria for classification**
Low	No or few guard dogs used Juvenile herders tasked with guarding Poor corralling practices No livestock safeguarding at night Livestock left to wander
High	Livestock grazed in dangerous (predator rich) locations such as in/alongside reserves or national parks Vulnerable animals such as sickly/ young animals Natural or anthropogenic reasons for a decrease in the numbers of the native wild herbivores cause an increase in livestock depredation (decline in prey) Increased predation events due to seasonal increases in livestock densities such as during lambing/ calving/ foaling times (seasonal)

Table 2.3. Self-defined types of retaliation by subsistence and commercial farmers involved in carnivore-human conflicts, graded from 0 (none stated) to 3 (reactive). Criteria for classifications were created using events mentioned in publications relating to action taken against depredating carnivores.

Retaliation	Grade of retaliation	Criteria for classification
None stated	0	Publication did not list whether action was taken against a livestock depredating carnivore
None	1	No action was taken by farmers due to: Compensation schemes paying for killed livestock Strict conservation legislation, offenders are known to be prosecuted
Preventative	2	Carnivore attacks were forestalled by: Livestock intensification – better corralling practices, better trained/ more guard dogs, more herdsmen Herdsmen shouting and waving sticks to scare off carnivores before predation took place The use of deterrents or repellents (visual, acoustic or chemical)
Reactive	3	Carnivores were persecuted for killing livestock by: Poison Shot with a firearm Poaching (when protected carnivores are killed illegally) Lethal traps (steel-jawed, staked pitfall, wire snares) Hunted with large hunting dogs

Assessment of human-carnivore conflicts and reported depredators

In order to investigate which livestock types were targeted most frequently by which species of carnivore, the number and types of livestock kills per carnivore species per year were extracted from each of the publications. In the instances where publications listed only grand totals and percentages of livestock depredated by carnivore, the values per carnivore species were calculated using the formula:

$$Number\ depredated\ per\ carnivore = \frac{\%\ per\ carnivore}{100} \times total\ livestock\ depredated$$

I created a list of the morphological, behavioural and ecological characteristics of the main carnivore species depredating on livestock (Table 2.4). Carnivores were classified by body weight as small (2-19 kg), medium (20-49 kg) and large (> 50 kg) using a modification of defining categories used by Macdonald (2001) (Table 2.4). Feral dogs were classified as having a variable average weight, because of the range in weights by breed composition of packs. Carnivore sociality was defined as solitary (occurs alone throughout the year except during mating season), social (forms loose-knit groups or monogamous pair bonds) or highly social (forms packs/prides with distinct hierarchies). I also considered activity period (diurnal, crepuscular and nocturnal) and hunting mode (run-down, ambush and opportunistic). To obtain a standard estimate of loss (hereafter livestock mass equivalency), I calculated per kilogram loss of livestock and game animals depredated by different carnivore species per livestock type per publication using the following formula:

$$Livestock\ mass\ equivalency = \frac{n\ depredated}{140} \times average\ livestock\ weight$$

Where 140 is the mass of a standard-sized livestock type in kilograms (goat). Weights for young animals (calves and lambs) were taken as the average weight at birth, weights for dzo (*Bos grunniens* × *Bos taurus*) were calculated by averaging the weight of cattle (*Bos tuarus*) and yak (*Bos grunniens*) and weights for shoats were taken as the average of sheep (*Ovis aries*) and goat (*Capra aegagrus hircus*) weights. The average weight of a broiler chicken (*Gallus domesticus*) was used for poultry weight (Robinson *et al.* 2014). As types of African game depredated were not specified in publications, I took the average weight of a more commonly kept game type in South Africa, blue wildebeest (*Connochaetes taurinus*), that is hunted for both meat and trophies (Hoffman & Wiklund 2006).

Table 2.4. Carnivore species involved in livestock attacks by common name, species name, their predator codes (used in analyses and graphs), activity pattern, body size, sociality and hunting mode. Body size was defined as small (S), medium (M) and large (L).

Carnivore common name	Scientific name	Predator codes	Activity period	Body size	Sociality	Hunting mode
African leopard	*Panthera pardus*	AL	Nocturnal	M	Solitary	Opportunistic
African wildcat	*Felis silvestris lybica*	AW	Nocturnal	S	Solitary	Ambush
African wild dog	*Lycaon pictus*	AWD	Crepuscular	M	Highly social	Run down
American grey wolf	*Canis lupus*	AG	Nocturnal	M	Highly social	Run down
Asian black bear	*Ursus thibetanus*	AB	Diurnal	L	Solitary	Opportunistic
Asian grey wolf	*Canis lupus*	AS	Nocturnal	M	Highly social	Run down
Black-backed jackal	*Canis mesomelas*	BB	Crepuscular	S	Social	Opportunistic
Caracal	*Caracal*	CA	Nocturnal	S	Solitary	Ambush
Cheetah	*Acinonyx jubatus*	CH	Diurnal	M	Solitary	Run down
Coyote	*Canis latrans*	CO	Crepuscular	S	Social	Opportunistic
Dhole	*Cuon alpinus*	DH	Diurnal	S	Highly social	Run down
Eurasian brown bear	*Ursus arctos*	EB	Nocturnal	L	Solitary	Opportunistic
Eurasian lynx	*Lynx*	EL	Crepuscular	M	Solitary	Ambush
European grey wolf	*Canis lupus*	EG	Nocturnal	M	Highly social	Run down
Feral dog	*Canis lupus familiaris*	FD	Diurnal	Variable	Social	Opportunistic
Golden jackal	*Canis aureus*	GJ	Crepuscular	S	Social	Opportunistic
Grizzly bear	*Ursus arctos ssp*	GB	Nocturnal	L	Solitary	Opportunistic
Himalayan brown bear	*Ursus arctos isabellinus*	HB	Nocturnal	L	Solitary	Opportunistic
Himalayan wolf	*Canis himalayensis*	HW	Nocturnal	L	Solitary	Opportunistic
Iberian lynx	*Lynx pardinus*	IL	Nocturnal	S	Solitary	Ambush
Iberian wolf	*Canis lupus signatus*	IW	Nocturnal	M	Highly social	Run down
Jaguar	*Panthera onca*	JA	Nocturnal	L	Solitary	Ambush
Lion (African)	*Panthera leo*	LI	Nocturnal	L	Highly social	Ambush
Mountain lion	*Puma concolor*	ML	Nocturnal	L	Solitary	Ambush
Persian leopard	*Panthera pardus saxicolor*	PL	Nocturnal	M	Solitary	Ambush
Red fox	*Vulpes*	RF	Crepuscular	S	Social	Opportunistic
Serval	*Leptailurus serval*	SE	Nocturnal	S	Solitary	Ambush
Side-striped jackal	*Canis adustus*	SS	Nocturnal	S	Social	Opportunistic
Snow leopard	*Panthera uncia*	SL	Crepuscular	L	Solitary	Ambush
Spotted hyena	*Crocuta*	SH	Nocturnal	L	Social	Opportunistic
Tibetan wolf	*Canis lupus chanco*	TW	Diurnal	M	Social	Opportunistic
Tiger	*Panthera tigris*	TI	Nocturnal	L	Solitary	Ambush

Statistical analysis

All statistical analyses for were performed using RStudio Desktop software (Version 0.99.902, R Studio Development Core Team. 2010). Data were first tested for normality using the Shapiro-Wilk Normality test. Next, mixed effects logistic regression were performed using the package lme4 (Bates *et al.* 2015) on the data. Linear mixed effect regression models (denoted lmer) were created for datasets, as these types of models account for both fixed and random effects (Bolker *et al.* 2009). I ran three sets of analyses. I first analysed livestock vulnerability and losses incurred by depredation using livestock type (fixed effect) depredated by livestock mass equivalency (response variable) by region of depredation (random effect). Next, in order to analyse the predictors of livestock attack and the type and grade of retaliation by farmers, another linear mixed effect regression model was created using the total number of livestock depredated per publication (response variable), farm types, grade of retaliation (GOR) and opportunity for depredation (OFD) (fixed effects) and region of depredation (random effect), also testing for interactions between farm type and GOR and farm type and OFD. Finally, I investigated the 33 different carnivore species implicated in livestock and game attacks by predator type, predator body size class, activity period, sociality and hunting mode (all fixed effects) by livestock mass equivalency (response variable). The regions of the depredation incidents were again included as a random effect in both models. I used the Differences of Least Squares Means (difflsmeans) to conduct posthoc tests for models. All significance levels were set to $\alpha = 0.05$ and the Wald Chi-Squared statistic was used to report p-values for all features tested. Boxplots and bar graphs were created for data visualisation using the package ggplot2 (Wickham 2009).

Results

General findings

A total of 77 publications reported quantifiable human-carnivore conflicts by 33 carnivore species relating to livestock and game from 1982-2015. Of these, 52 publications distinguished between different types of livestock numbers depredated per carnivore, while 25 only provided totals of livestock depredated per carnivore species without mentioning different livestock types. Only two publications provided numbers depredated for game, one from Africa (Thorn *et al.* 2012) and one from North America (Treves *et al.* 2002), while 15 publications reported depredation of domestic dogs by carnivores. Because domestic dogs are not valued as livestock, they were not included in analyses. The percentages of depredated livestock types (calculated as the number of times a livestock type was reported per publication) ranged from mostly cattle (79%) and sheep (71%) to goat (58%), horse (37%), donkey (28%), poultry (20%), pig (14%), yak (15%), shoat (7%), dzo (2%) and camel (2%). Several carnivores were involved in livestock attacks, most notably six species of wolf, four of bear, three of leopard, three of jackal, two of lynx, one species of lion, spotted hyena and wild dog.

Conflict localities

Different publications on human-carnivore conflicts ($n = 77$) reported livestock depredation events that occurred on six continents by a variety of different mammalian carnivore species, with only seven publications reporting depredation by wild dog (Figure 2.1). Africa showed the highest number of depredation events ($n = 29$), with Asia reporting the second highest ($n = 24$) and Europe the third highest (n = 10) (Figure 2.2). Publications reported that North America experienced the third lowest (n = 9), South America the second lowest (n = 4) and Australia reported only one depredation event (Figure 2.2). North Africa reportedly experienced the highest total number of livestock losses, with 7845 livestock animals depredated by carnivores in the past 33 years. Asia reported the second highest number of livestock losses with 4214 livestock animals depredated and southern Africa was third highest with 3949 livestock animals depredated. North America reported a loss of 1931 livestock animals and Europe 1774 livestock animals. Australia reported the second lowest number of livestock lost with 330 livestock animals depredated and South America was lowest with 148 livestock animals reported. Africa reportedly suffered the highest number of high-grade livestock depredation incidents than other regions, with between 1015-3346 livestock depredated in four depredation events (Figure 2.2).

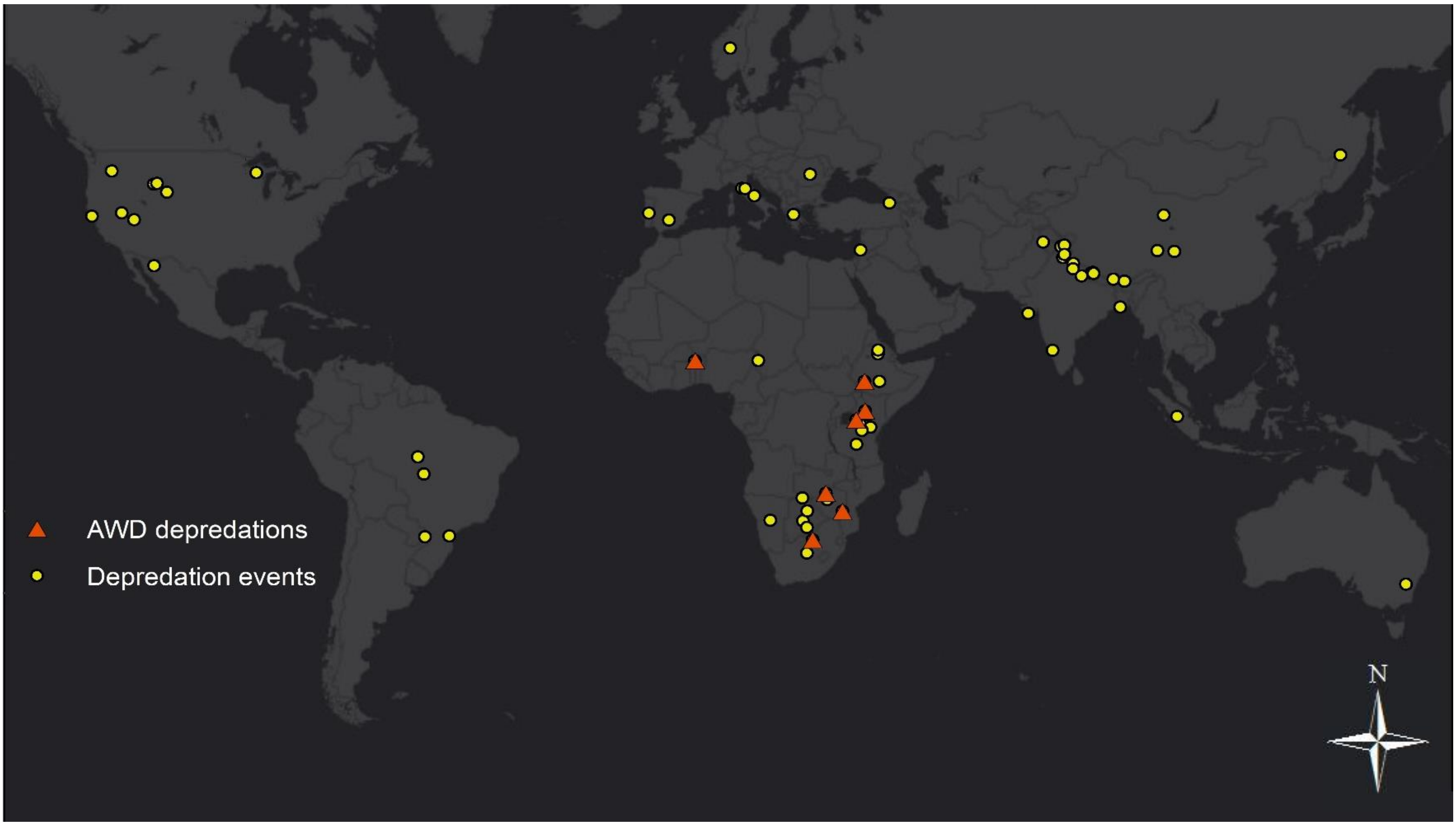

Figure 2.1. GPS points showing global livestock depredation events by African wild dog (AWD) and other mammalian carnivores as reported by 77 publications dated 1982-2015.

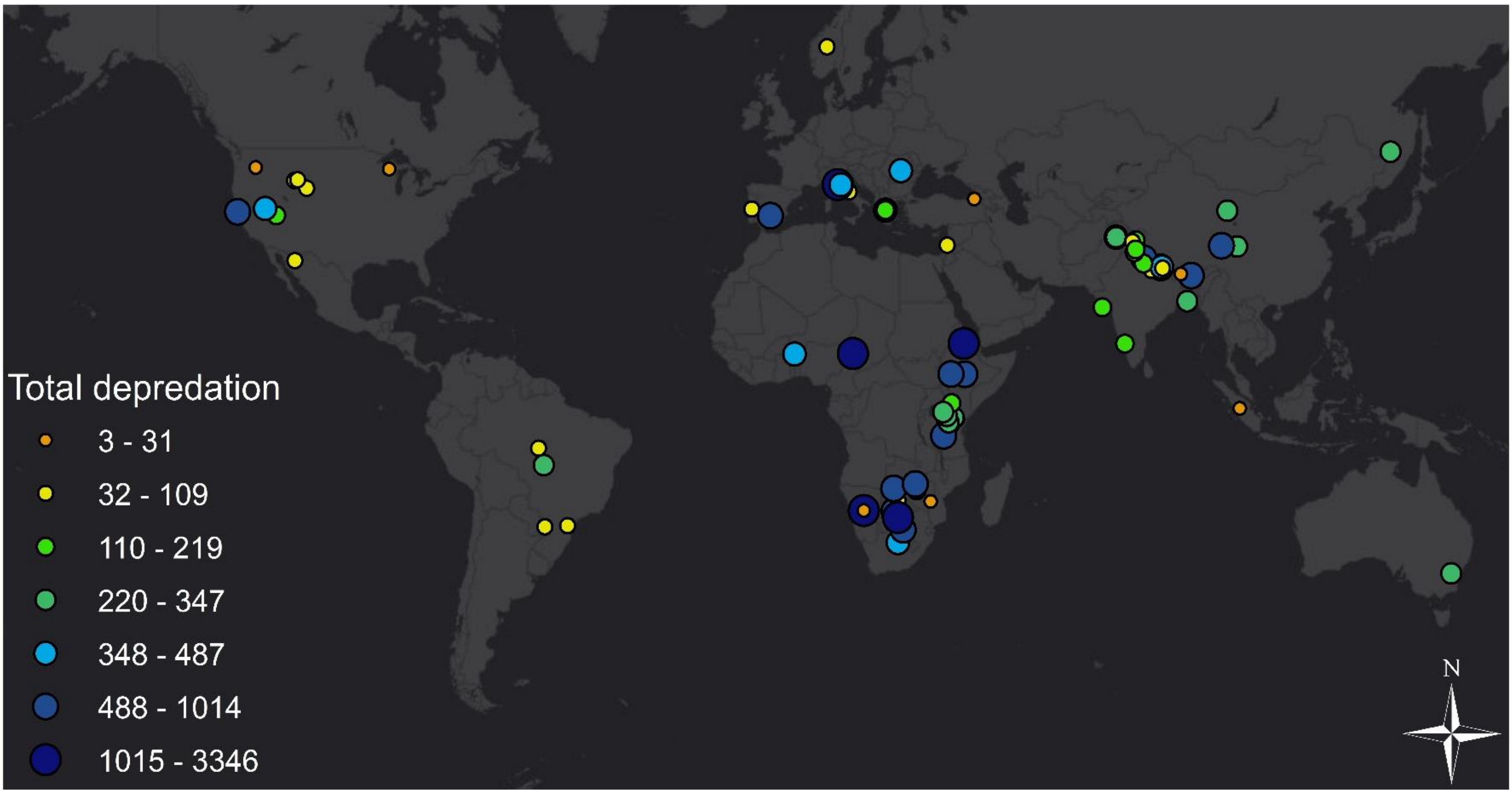

Figure 2.2. GPS points showing global livestock depredation events graded from low to high numbers of livestock depredated as reported by 77 publications dated 1982-2015.

Cattle were reported as the heaviest livestock type depredated and are the second most popular livestock types kept by farmers, numbering at 1.4 billion globally (Food and Agriculture Organisation of the united nation statistics 2011). Cattle occur in high densities per km^2 throughout Europe, India, North America, South America and South Africa (Figure 2.3a). Goats were reportedly the second highest depredated livestock type, and high densities of goats are kept in the poorer regions such as India and Africa (Figure 2.3b). High densities of sheep are found throughout Europe, Asia and southern Africa, and occur in especially high densities in Australia (Figure 2.3c). Although reported as the fourth highest depredated livestock type, poultry is the world's most populous livestock type, with 19 billion chickens worldwide (The Economist Online 2011), with the highest densities occurring in Asia (Figure 2.3d). Unsurprisingly, most of the livestock depredation incidents fell within the high livestock density areas.

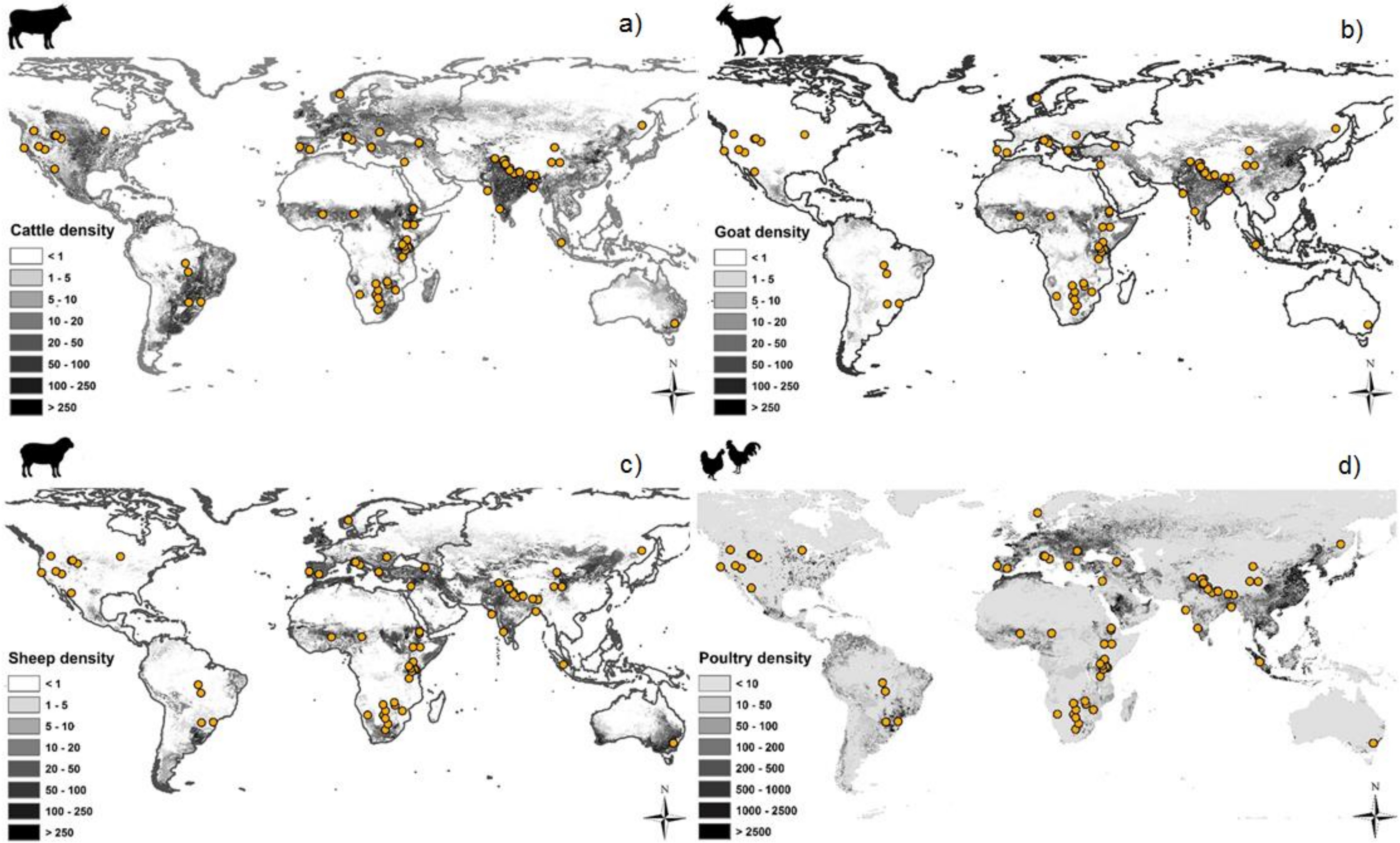

Figure 2.3. Global livestock density maps downloaded and modified from the FAO, a) cattle density, b) goat density, c) sheep density and d) poultry density. Yellow circles are GPS points that represent carnivore depredation events from publications dated1982-2015. Dark grey areas indicate high livestock densities per km^2, while light areas indicate low livestock densities per km^2 (Robinson *et al.* 2014).

In Africa and Asia, there are higher numbers of carnivore species per 10 km^2 than on any of the other continents, with Australia having no large native carnivore species (Figure 2.4). Europe, North America and South America have low densities of carnivores (Figure 2.4). For all other regions excluding Africa and parts of Asia, depredation incidents occurred outside of areas of high carnivore richness, while in Africa and Indonesia, all depredation incidents occurred within the high species richness areas (Figure 2.4).

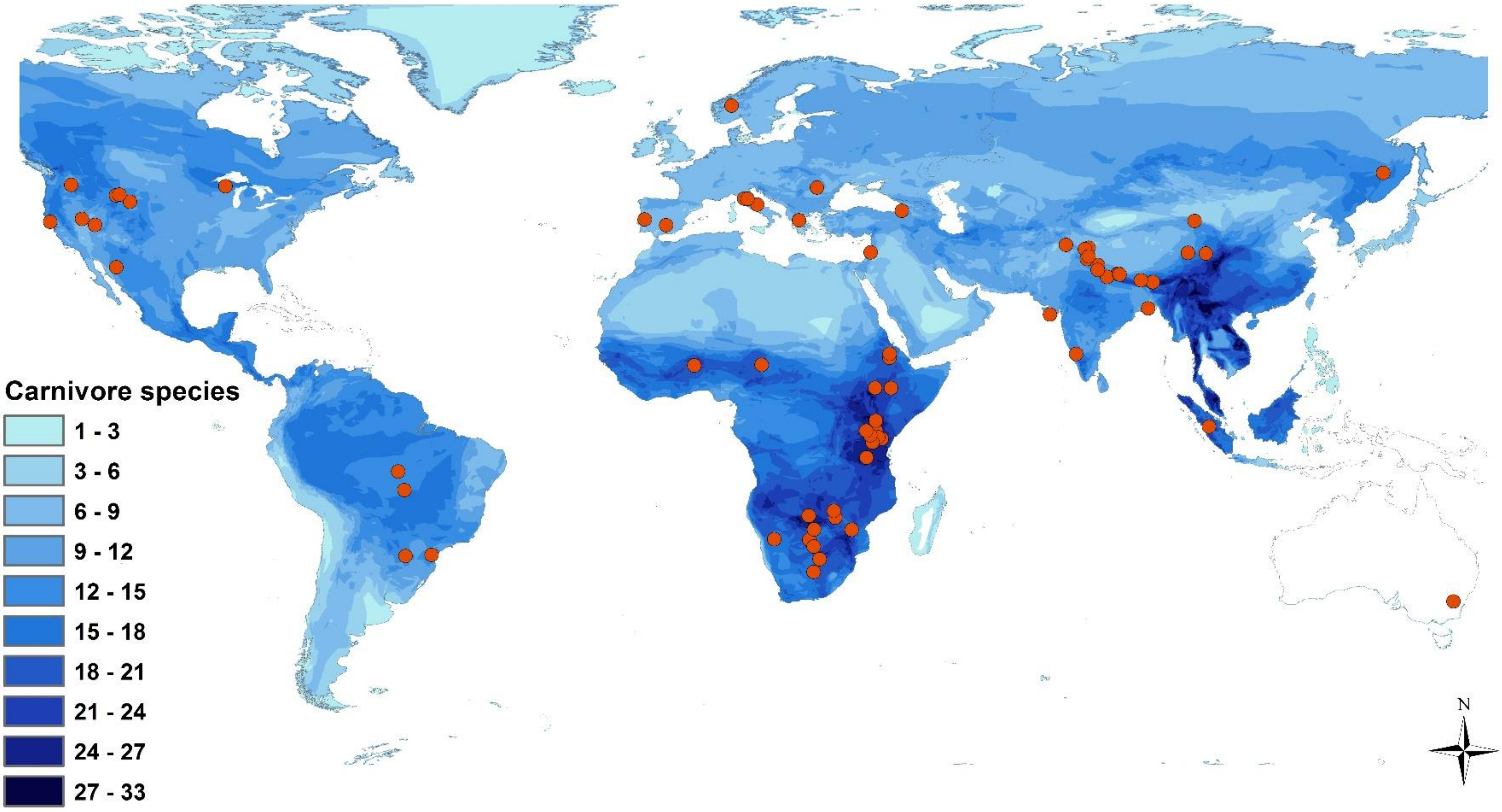

Figure 2.4.Global carnivore richness per 10 km^2. Dark blue areas indicate a high number of different carnivore species per 10 km^2. Orange circles represent GPS points of depredation events as extracted form publications dated 1982-2015. The map represents only extant, native species. Carnivore species that were introduced to continents, such as dingos (Australia), were ignored. Map data were obtained and modified from BiodiversityMapping.org and are based on data from the IUCN 2013 update (Jenkins *et al.* 2013).

Livestock depredated

From the 77 publications downloaded, 20,164 livestock individuals were reported as depredated globally, constituting 7294 tons of livestock lost to carnivores from 1982-2015. From publications, Africa reportedly experienced the most depredation, constituting 60% of the world's mass lost in livestock compared to the combined loss of 40% in other continents. Thirteen livestock types were the targets of depredation by carnivores, along with game, with sheep ranking as the highest number of depredated livestock type (by individual head count) globally with 5442 individuals depredated. Goats were second highest with 3794 individuals depredated. Cattle were third with 3460 individuals depredated and poultry fourth with 2119 individuals depredated. In terms of total mass of livestock lost, cattle, the heaviest livestock type, constituted 51% of tons lost globally. Mass lost in goats were second highest with 15% of tons lost, and sheep third with 12% of tons. Livestock type was a significant predictor of livestock individuals depredated (χ^2 (13) =242.68, p < 0.001), with cattle constituting the highest amount of mass lost and calves, lambs and poultry constituting the lowest mass lost (Figure 2.5) .

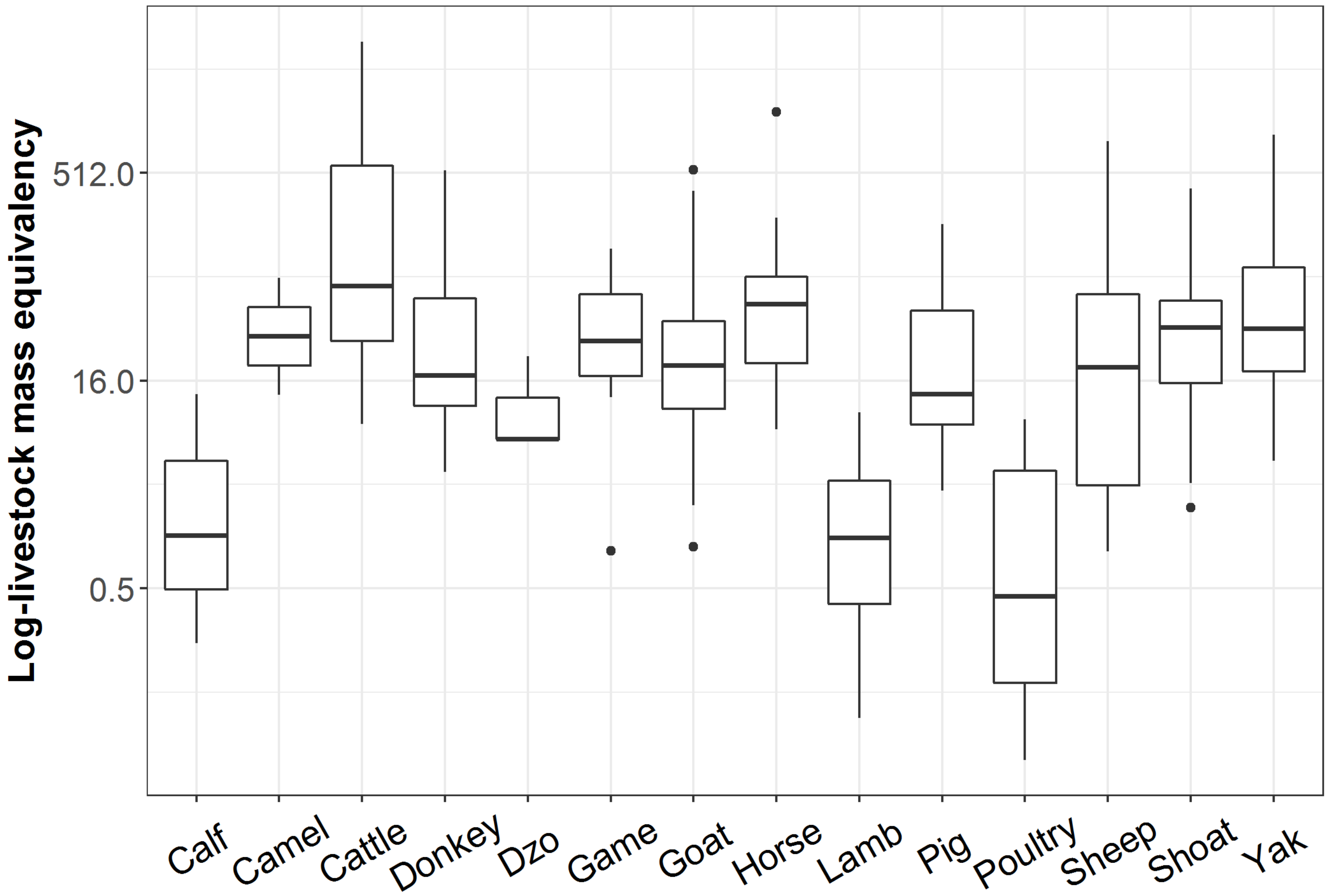

Figure 2.5. Different livestock types and game depredated by carnivores globally by logged livestock mass equivalency values and 95% CI. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Information was extracted and modified from 77 scientific publications concerning human-carnivore conflicts, from 1982-2015.

Farm type, opportunity for depredation& retaliation

Of 77 publications downloaded, results did not indicate a difference in the number of livestock lost to carnivore depredation by subsistence (number of publications, *n* = 51) and commercial (*n* = 26) farmers (Table 2.5). Grade of retaliation did not differ in the 77 publications, nor did the opportunity for depredation (Table 2.5), indicating that these factors do not explain why some livestock types are depredated more than others. Studies involving commercial farmers most frequently failed to state whether or not they retaliated, with only a small number specifically stating grades of retaliation (Table 2.5). Studies involving subsistence farmers stated more frequently that they practiced no retaliation with few stating the use of other grades of retaliation (Table 2.5). It is possible that subsistence farmers are more likely to offer predators a high chance of encountering livestock, thus resulting in higher levels of depredation, as the statistical test showed a trend toward significance (Table 2.5).

Table 2.5. Results of Linear mixed effect regression model comparing farm type (commercial or subsistence), grade of retaliation (GOR) and opportunity for depredation(OFD) and the interactions between farm types and other factors (shown by :) for farms involved in human-carnivore conflict worldwide, as extracted from 77 publications dating between 1982-2015. GOR was defined as none stated (0), none (1), preventative (2) and reactive (3). OFD was defined as high and low. Bolded values denote statistical significance and values that show a trend toward significance are indicated with an asterisk (*).

Comparisons and interactions	**Outcome**	**Factor**	**Estimate**	**Std. Error**	***P*-value**
Commercial vs Subsistence farmers	No difference	/	0.05	0.17	0.761
Different categories of GOR	No difference	/	0.05	0.62	0.933
Different categories of OFD	No difference	/	-0.13	0.62	0.824
GOR : Subsistence farmers	No difference	0	0.45	0.80	0.569
GOR : Subsistence farmers	Difference	1	1.02	0.42	**0.018**
GOR : Subsistence farmers	No difference	2	0.47	0.60	0.429
GOR : Subsistence farmers	No difference	3	0.39	0.56	0.488
GOR : Commercial farmers	Difference	0	-0.67	0.34	**0.047**
GOR : Commercial farmers	No difference	1	-0.55	0.56	0.330
GOR : Commercial farmers	No difference	2	-0.59	0.56	0.296
GOR : Commercial farmers	No difference	3	-0.05	0.17	0.761
OFD : Subsistence farmers	No difference	High	0.63	0.36	0.082 *
OFD : Subsistence farmers	No difference	Low	-0.26	0.29	0.372
OFD : Commercial farmers	No difference	High	0.31	0.46	0.497
OFD : Commercial farmers	No difference	Low	0.26	0.29	0.372

From 77 publications, southern Africa reported greater losses in average livestock mass equivalency (total summed livestock mass equivalency per region / number of depredation incidents per region) than northern Africa (Figure 2.6). Wild dog were reportedly only involved in four depredation incidents in southern Africa and seven incidents in northern Africa. North and South America reported fewer livestock mass losses than other regions, whilst Australia reported the highest average livestock mass lost in only one depredation incident (Figure 2.6).

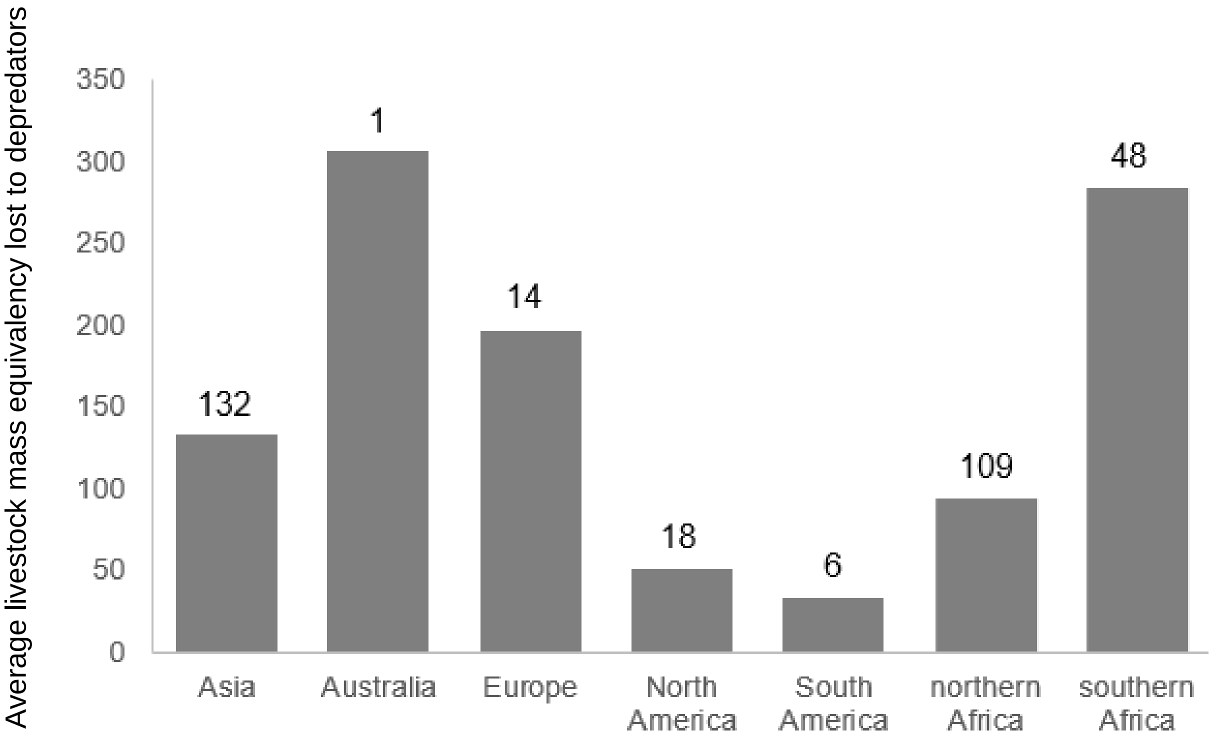

Figure 2.6. Average livestock mass per number of depredation incidents (numbers above bars) lost due to carnivore depredation globally per region affected. Information was extracted and modified from 77 scientific publications concerning human-carnivore conflicts from 1982-2015.

Carnivores involved in depredation events

From 77 publications, African carnivore species contributed 49% (*n* = 349) to global predation incidents. As reported in seven publications, wild dogs were involved in 12 livestock depredation incidents, accounting for 3% of global livestock depredation, and were responsible for only 1% of local livestock mass lost. Fourteen publications quantified 56 spotted hyena incidents, accounting for 16% of global livestock depredation and 46% of local livestock mass lost. Lions were involved in 36 incidents reported in 10 publications, accounting for 10% of global livestock depredation and for 33% of local livestock mass lost. African leopards were implicated in 23 predation incidents in eight publications, and accounted for 6% of global predation and 6% of local livestock mass lost. Predator species was a significant predictor of livestock depredation (χ^2 (32) = 90.39, $p < 0.001$), with different species causing different amounts of damage in terms of livestock mass lost to depredation (Figure 2.6). African carnivore species were not reported to be worse livestock depredators when compared to carnivore species on other continents (χ^2 (1) = 4.60, p= 0.110), with African species causing similar amounts of livestock mass lost to depredation than non-African species (Figure 2.7).

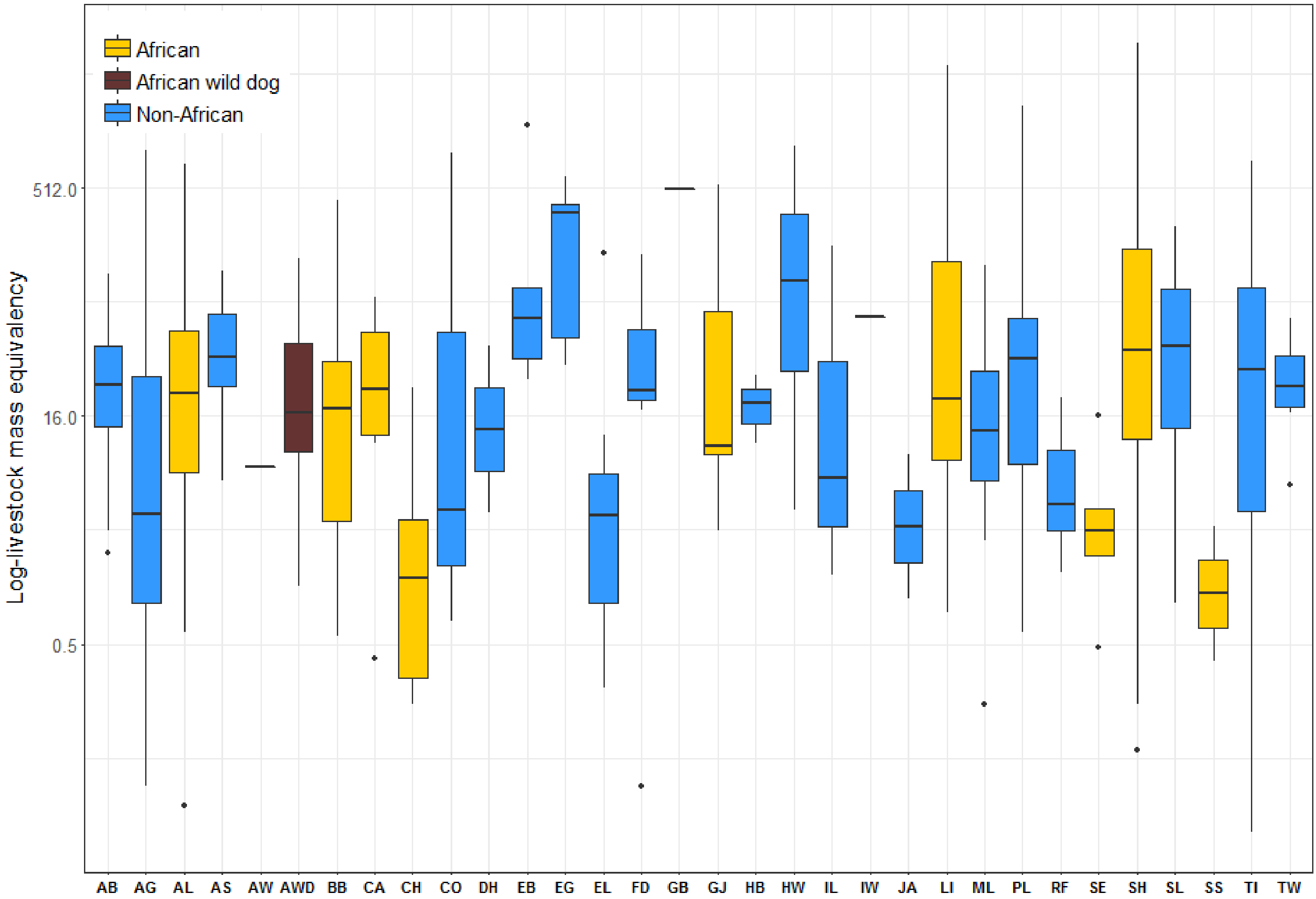

Figure 2.7. Different carnivore species (by predator code) involved in livestock and game depredation incidents globally by logged livestock mass equivalency values and 95% CI. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots) and bars without boxes show small sample sizes. Information was extracted and modified from 77 scientific publications concerning human-carnivore conflicts from 1982-2015. Coloured boxes show African carnivore species (in yellow), non-African species (in blue) and African wild dog (in dark brown) as a standalone for comparison.

When compared amongst themselves, African carnivores were responsible for different amounts of livestock mass lost due to depredation (χ^2 (10) = 21.24, p = 0.019), and wild dog (AWD) caused less livestock mass losses than lion (LI) and spotted hyena (SH) (Figure 2.8). Wild dog were reported to depredate cattle (number of times reported depredated, *n* = 2) and goats (*n* = 3) and caused higher losses in livestock mass for goats than cattle (Figure 2.3). Wild dog were also reported to depredate game (*n* = 1), sheep (*n* = 1) and shoats (*n* = 1), although mass lost due to wild dog depredation for these three types of animals was negligible (Figure 2.8). Spotted hyena depredated more types of livestock, and were the only species to target camels and horses (Figure 2.8). Lion and spotted hyena were jointly responsible for more mass lost for donkeys and pigs (Figure 2.8). Cheetah depredated only goats, and caused the least amount of mass loss of all the African carnivores (Figure 2.8).

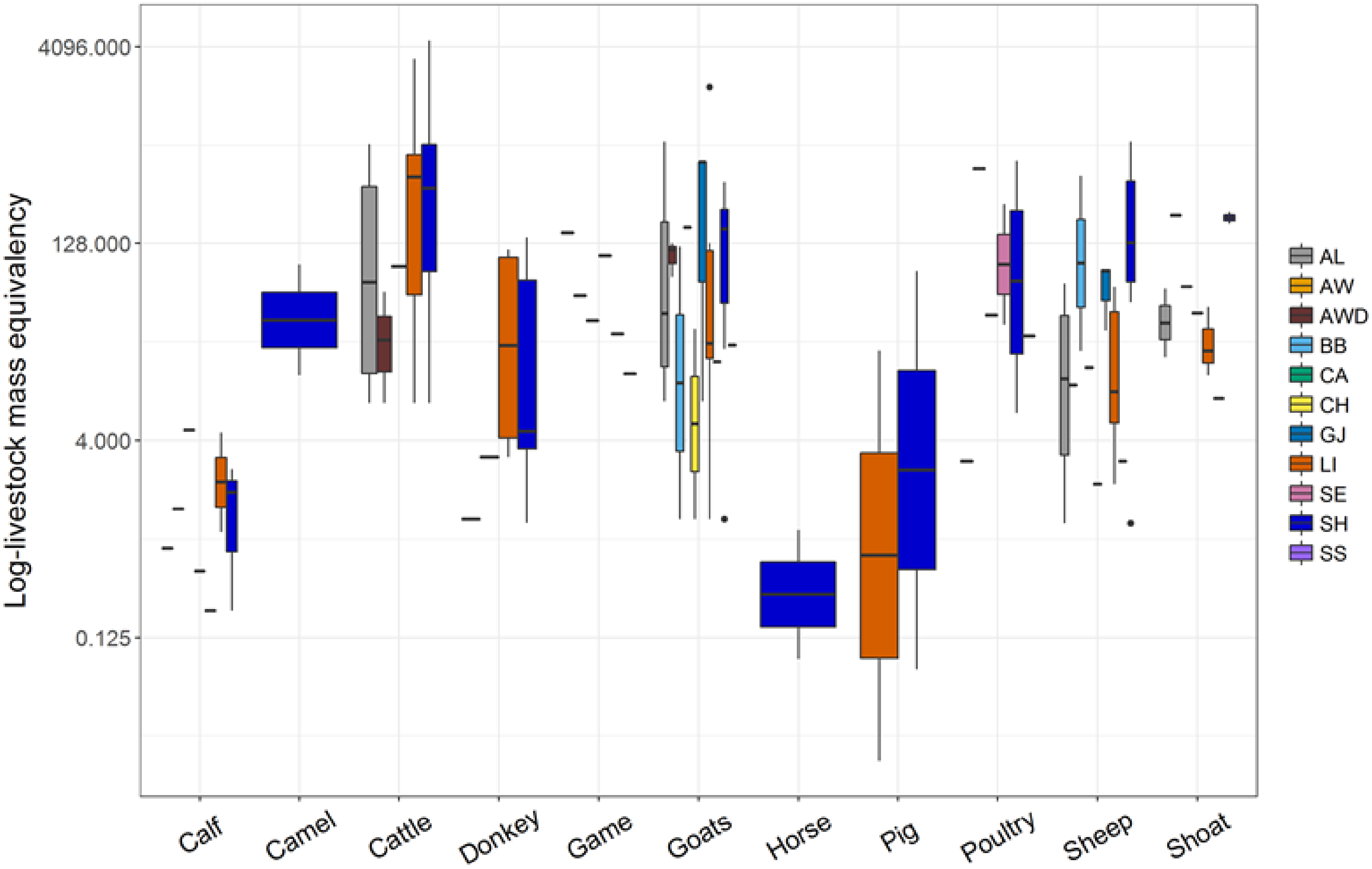

Figure 2.8. Different African carnivore species (by predator code) involved in livestock and game depredation incidents in southern and northern Africa by logged livestock mass equivalency values and 95% CI. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots) and bars without boxes show small sample sizes. Information was extracted and modified from 77 scientific publications concerning human-carnivore conflicts from 1982-2015. Variable box widths are due to differing sample sizes and coloured boxes represent different carnivore species by predator code. Wild dogs shown in the dark brown colour, and are reported only in the cattle and goats depredation categories.

Carnivore body size was not a predictor of livestock depredation (χ^2 (3) = 4.19, p = 0.241), with carnivores of medium body size (including wild dog) causing similar amounts of livestock mass losses compared to carnivores with large or small body sizes (Figure 2.9). Feral dogs (with variable body sizes) caused negligible amounts of livestock mass losses (Figure 2.9).

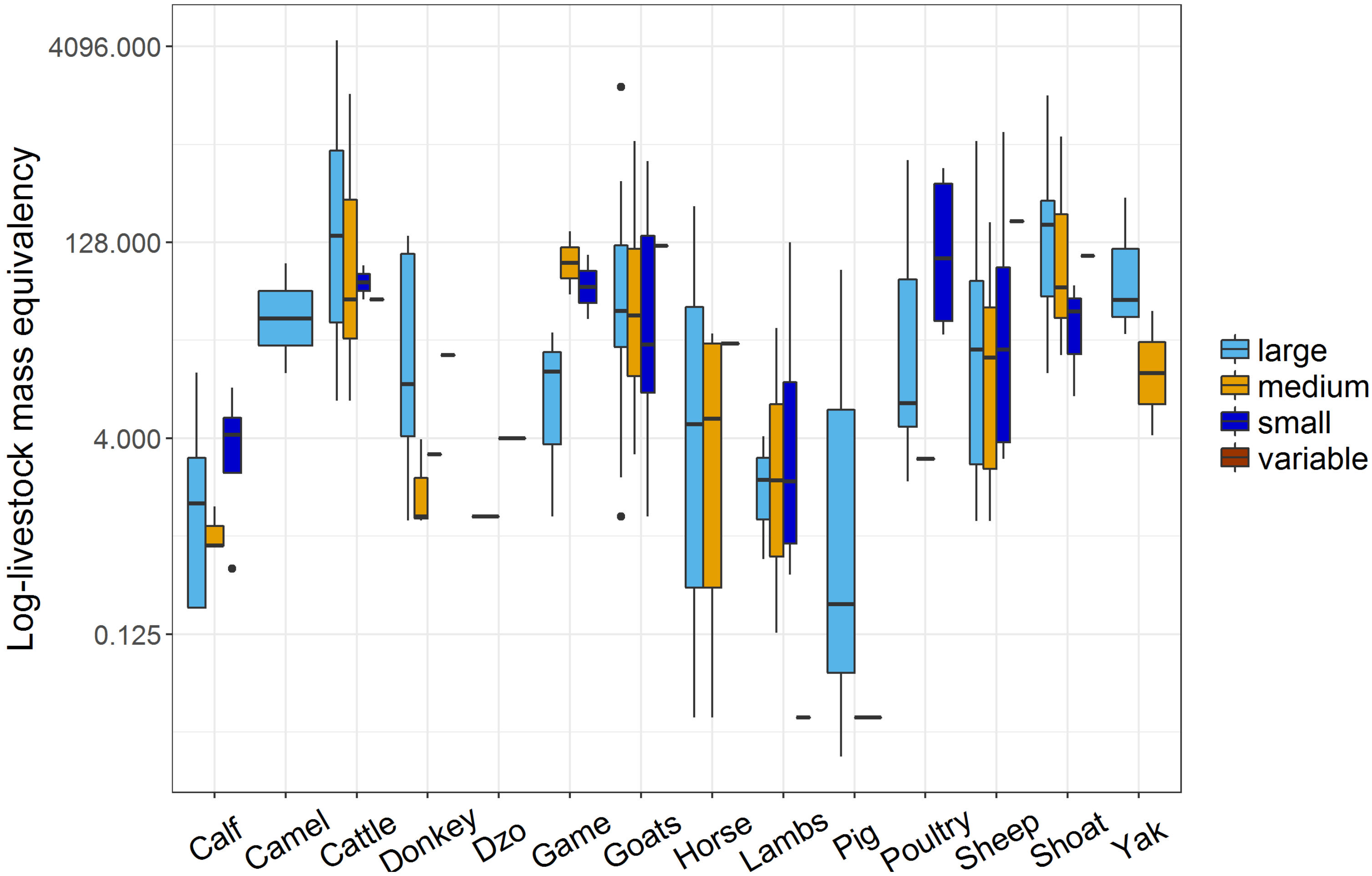

Figure 2.9. Carnivores with different body sizes involved in global livestock and game depredation incidents by logged livestock mass equivalency values and 95% CI. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots) and bars without boxes show small sample sizes. Information was extracted and modified from 77 scientific publications concerning human-carnivore conflicts from 1982-2015. Variable box widths are due to differing sample sizes. Coloured boxes represent large (light blue), medium (golden yellow), small (dark blue) and variable (dark brown) body sizes. Wild dogs fall within the medium body size category.

Carnivore activity period was a significant predictor of livestock depredation (χ^2 (2) = 6.14, p = 0.046), with diurnal carnivores (such as dhole and cheetah) causing less livestock mass losses than nocturnal carnivores (such as spotted hyena and leopard) (Figure 2.10). Wild dog (with a crepuscular activity period) caused similar levels of livestock mass losses compared to carnivores of diurnal and nocturnal activity periods (Figure 2.10).

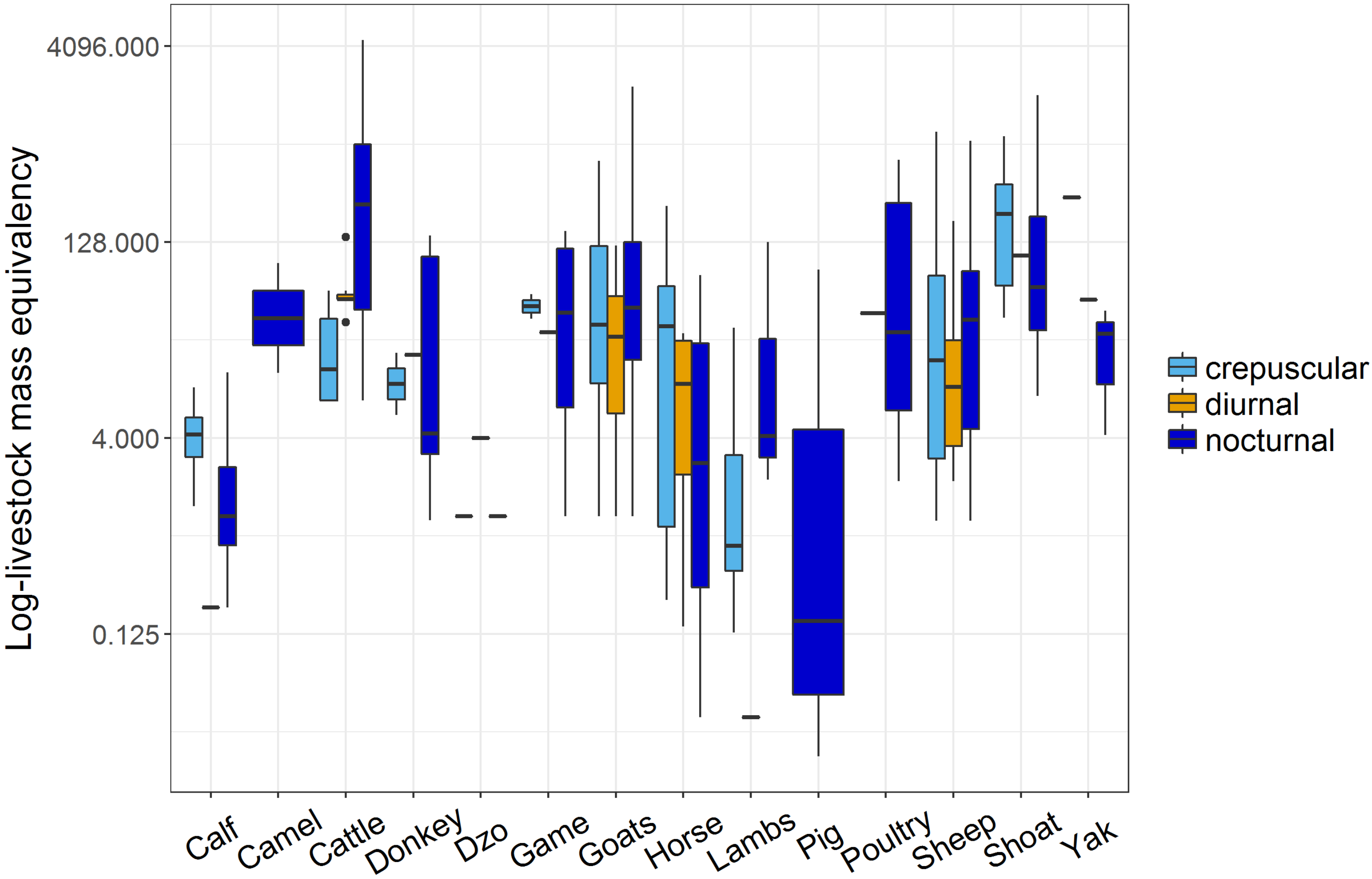

Figure 2.10. Carnivores with different activity periods involved in global livestock and game depredation incidents by logged livestock mass equivalency values and 95% CI. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots) and bars without boxes show small sample sizes. Information was extracted and modified from 77 scientific publications concerning human-carnivore conflicts dating from 1982-2015. Variable box widths are due to differing sample sizes. Coloured boxes represent crepuscular (light blue), diurnal (golden yellow) and nocturnal (dark blue) activity periods. Wild dogs fall within the crepuscular activity period category.

Sociality was not a predictor of livestock depredation (χ^2 (2) = 3.47, p = 0.176), with highly social carnivores (such as wild dog) causing similar amounts of livestock mass losses compared to social (such as black-backed jackal) and solitary (such as leopard) carnivores (Figure 2.11). Social carnivores reportedly targeted fewer livestock types than either highly social or solitary carnivores (Figure 2.11).

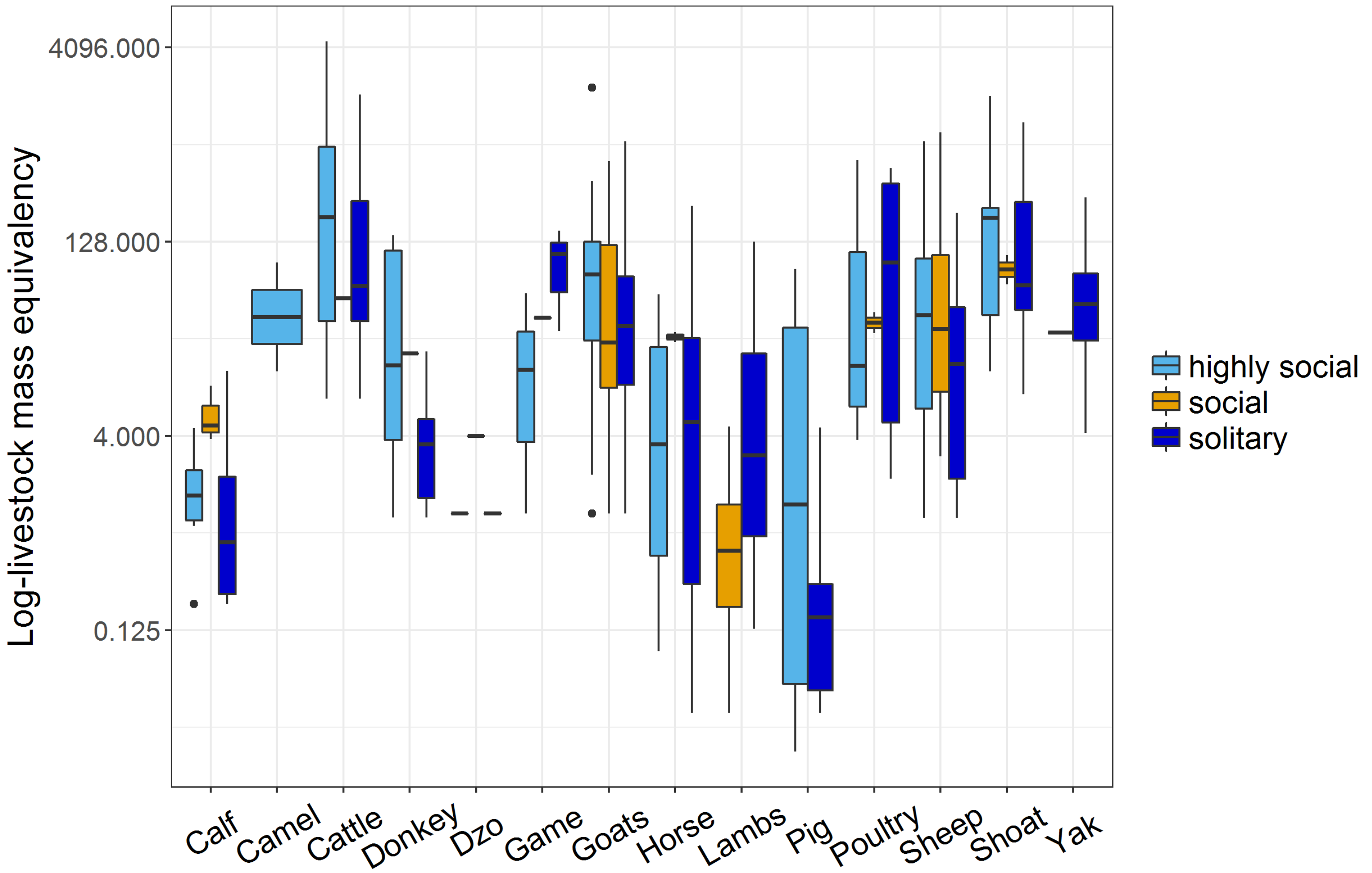

Figure 2.11. Carnivores with different social organisations (sociality) involved in global livestock and game depredation incidents by logged livestock mass equivalency values and 95% CI. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots) and bars without boxes show small sample sizes. Information was extracted and modified from 77 scientific publications concerning human-carnivore conflicts from 1982-2015. Variable box widths are due to differing sample sizes. Coloured boxes represent highly social (light blue), social (golden yellow) and solitary (dark blue) social organisations. Wild dogs fall within the highly social category.

Hunting mode was not a significant predictor of livestock depredation (χ^2 (2) = 1.12, p = 0.545), with run down hunters (such as the wild dog) causing equal livestock mass losses compared to ambush hunters (such as lion) or opportunistic hunters (such as golden jackal) (Figure 2.12). Run down hunters reportedly targeted fewer livestock types (n = 8) than either ambush or opportunistic carnivores (Figure 2.12).

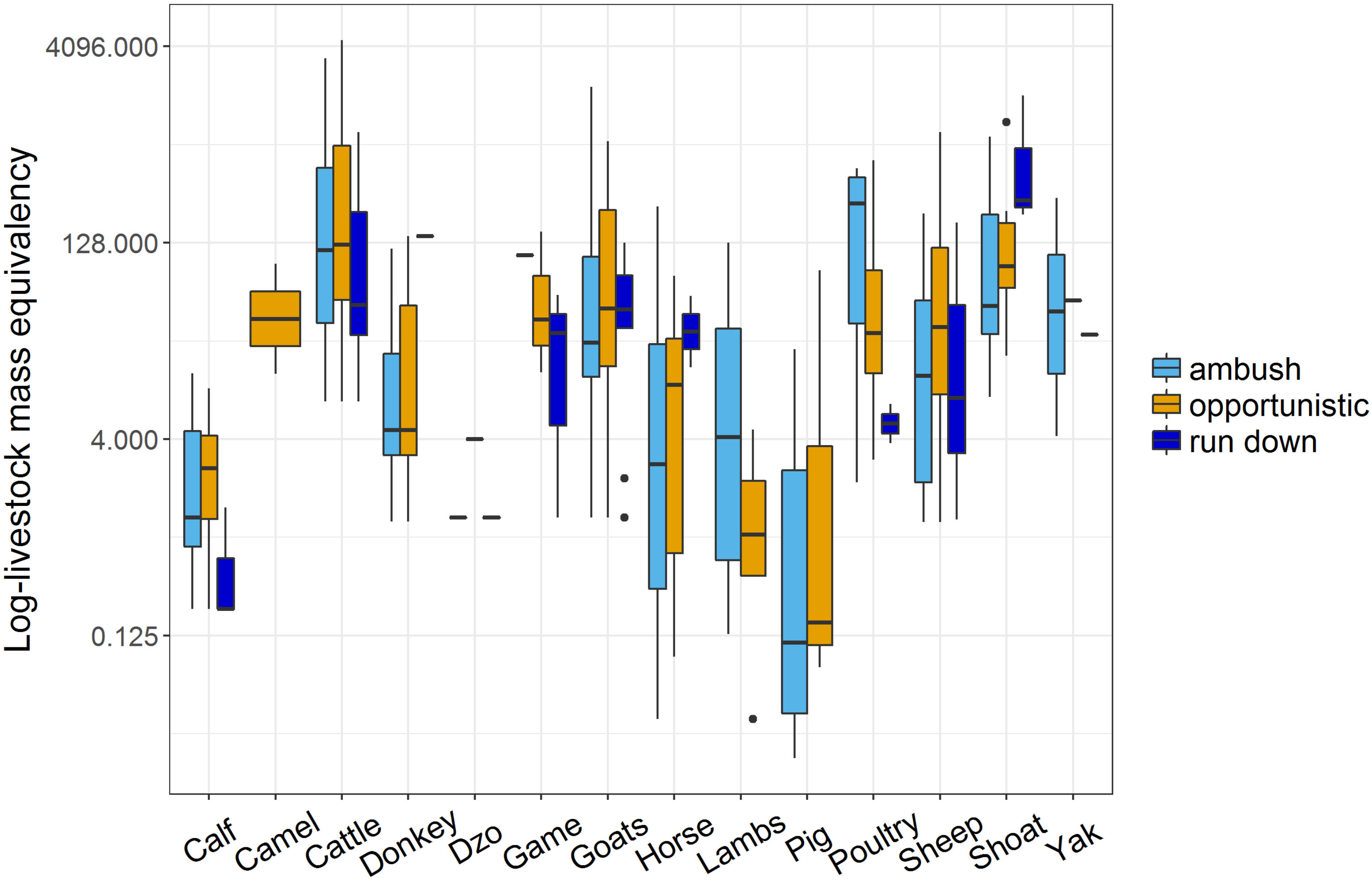

Figure 2.12. Carnivores that employ different hunting modes involved in global livestock and game depredation incidents by logged livestock mass equivalency values and 95% CI. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots) and bars without boxes show small sample sizes. Information was extracted and modified from 77 scientific publications concerning human-carnivore conflicts dating from 1982-2015. Variable box widths are due to differing sample sizes. Coloured boxes represent highly carnivores that employ ambush (light blue), opportunistic (golden yellow) and run down (dark blue) hunting tactics. Wild dogs fall within the highly run down hunting category.

Discussion

This meta-analysis aimed to assess common patterns of human-carnivore conflicts relating to wild dog in southern Africa with those of other carnivores both locally and globally, to compare the impact of wild dog depredation on livestock in a local and global context. I specifically focussed on mapping depredation events from publications to assess depredation incidents compared to livestock and carnivore densities. I examined whether commercial or subsistence farming practices and certain husbandry techniques elicited depredation, and investigated the types of livestock targeted and the mass lost due to depredation. I investigated the carnivore species involved in depredations and compared wild dog to African and non-African carnivores. I also considered whether body size and species-typical behaviours and ecology were predictors of depredation.

Human-carnivore conflict is a historical and current global problem for livestock farmers (Treves & Karanth 2003). The global farming community reported a loss of 7294 tons of livestock by 33 different carnivore species, including wild dog, from 1982 to 2015. Africa and Asia experienced the highest number of depredation incidents, possibly because these two continents house some of the highest densities of livestock per km^2 (100-250 individuals, Robinson *et al.* 2014), as well as the highest carnivore richness per $10km^2$ (24-33 individuals, Jenkins *et al.* 2013). Specifically, Africa experienced the highest number of high-grade depredation incidents, with higher numbers of livestock depredated per incident than other regions, especially when compared to first world regions such as North America. Not surprisingly, Africa is the continent with one of the highest number of persecutions of carnivores due to depredation incidents (Ripple *et al.* 2014). Livestock is still an exponentially growing subsector of agriculture in developing regions such as Africa and Asia (Thornton 2010) and coupled with high carnivore densities and growing and expanding human populations (Hollar 2011), this may create widespread opportunities for depredation events and therefore human-carnivore conflicts.

Southern Africa was one of the regions that experienced the highest number of average mass lost per depredation incident. As mentioned previously, farmers in poorer, developing areas often do not have the funds to pay for expensive livestock safeguarding devices or practices (Smith *et al.* 2000), and would therefore be more vulnerable to livestock depredation. Conversely, North America suffered fewer losses in mass of livestock to depredators. In addition to having more funds and technologically advanced methods available to safeguard livestock (Beschta & Ripple 2009), the USA and Europe have historically hunted native carnivores to extirpation (Ripple *et al.* 2014), explaining why these continents have low carnivore densities per 10 km^2. For example, the grey wolf's overall range has decreased by a third, having been hunted and extirpated from most of its former range throughout Western Europe and the United States of America (Ripple *et al.* 2014). Hunting has also reduced mountain lion distributions throughout the USA, extirpating them from most of their former ranges (Laliberte & Ripple 2004).

Culling carnivores should however not be viewed as a solution for regions housing high densities of livestock and carnivores such as southern Africa. Carnivore culling would not only be detrimental to conservation efforts on endangered species (Atwood & Breck 2012) such as the wild dog, but may have the unintended consequence of an increase in population numbers of other carnivore species (Ritchie & Johnson 2009) and increases of herbivores or pest species on farms such as rodents (Miller *et al.* 2001), thus aggravating farmer losses. Population declines of grey wolf in the early 20^{th} century in Yellowstone Park lead to increases in elk abundance, that in turn lead to vegetation structure changes due to more herbivory by elk (Miller *et al.* 2012). Similarly, coyote numbers increased and their distributions expanded, which lead to increased predation on a wider variety of prey (Prugh *et al.* 2009). This released smaller prey such as rodents from coyote predation pressure, leading to increases of rodent numbers (Miller *et al.* 2012). Killing carnivores may thus aggravate conflicts instead of solving them in addition to incurring other losses from rodent and herbivore damages to crops. It should therefore be recognised that manipulating the population numbers of carnivore species in isolation leads to unexpected and cascading ecological effects that impacts not only biodiversity and the natural ecosystem, but livestock keepers and their livelihoods (Ruscoe *et al.* 2011).

Livestock type was a predictor of depredation, and of the 13 livestock types and game examined, cattle and goats were reported to constitute the highest mass lost to carnivores. Results show that cattle and goats are some of the most populous livestock types kept throughout the world, meaning high numbers of animals per km^2 and thus a greater likelihood that carnivores would encounter and depredate these livestock types. Higher stocking densities often lead to increases in livestock depredation by carnivores (Hebblewhite 2011, Suryawanshi *et al.* 2013). Goats are kept in particularly high densities in developing regions, such as Africa and India, indicating that this is an important resource for poorer communities. This could be because goats are hardy and adaptable to many climates and conditions, are easier to keep on small areas of land than larger livestock (such as cattle) and feed on a variety of plants often indelible to other livestock such as cattle or sheep (Devendra 2001). Unlike other livestock types, they require low amounts of resource inputs for moderate levels of meat and milk production and are prolific reproducers that mature and breed early (Lebbie 2004). This adds to their popularity with subsistence or rural farmers that often do not have the funds to provide additional feed or other livestock intensification practices (Tilman *et al.* 2002).

Loss of livestock to carnivores means less food available for a community (Tveraa *et al.* 2014), loss of financial security (Ouma *et al.* 2003), loss of non-food products (such as organic fertiliser, wool, feathers, hides and bones, Sansoucy 1995) and economic loss of animals that would have been sold or used to bolster herd numbers (Garrote 2013). Additionally, many African cultures regard livestock such as cattle and goats as a status symbol (Braker *et al.* 2002, Kolowski & Holekamp 2006) and loss of these animals to depredation may therefore be culturally damaging, particularly to subsistence communities. Although subsistence and commercial farms suffered similar livestock mass losses in my research, these results may not reflect true loss, because while the loss of a single cow means monetary loss for commercial farmers, it means a livelihood loss for subsistence farmers who often depend on multiple products and services from a single animal (Jeannette *et al.* 2011). Additionally, subsistence farmers do not have funds to replace livestock lost (Wang & Macdonald 2006) nor do they have funds for livestock guarding (Thirgood *et al.* 2005). This may indicate why results showed that predators possibly have a greater opportuity of encountering and depredating livestock in a community that practices subsistence farming. Publications report that subsistence farmers were more likely not to retaliate against depredators, possibly because many types of preventative and reactive methods are costly to implement and upkeep (Smith *et al.* 2000). Publications reported that commercial farmers were more likely not to state what type of retaliation they practised, perhaps fearing legal repercussions such as fines and legal repercussions (Johannesen 2006).

The order Carnivora is diverse and comprises over 280 different species (Macdonald 2001), with similar and dissimilar physiognomy, activity patterns, hunting techniques and sociality (Gehrt *et al.* 2010). These factors may be predictors of depredation and can either contribute to or ease human-carnivore conflict (Ray *et al.* 2005). In my research, 33 different carnivore species, including wild dog, were responsible for varying livestock losses globally, with no singular carnivore ranking as the worst depredator. Logically, this is due to different people in different areas experiencing different economic, social, agroecological (ecological processes that determine agricultural production) and demographic conditions (Steinfeld *et al.* 2013). Similarly, various livestock types are kept under different conditions and in different numbers and densities around the world (Thornton *et al.* 2007). Although African carnivores contributed heavily to livestock (cattle, goat and sheep) losses generally, these were comparable to carnivores from other continents. Wild dog were less avid depredators than lion or spotted hyena, as the latter targeted heavier livestock types (cattle, donkeys and pigs) than wild dog. Multiple other studies have shown that lions are often the primary depredators of cattle (Bauer & Iongh 2005, Ikanda & Packer 2008), while spotted hyenas are often accountable for shoat depredation (Manoa, & Mwaura 2016).

Published research about wild dog depredation on livestock and game species is scant, with only seven publications providing quantifiable depredation events of different livestock types. My meta-analysis of scientific literature has shown that wild dog caused more mass losses of goats, a medium-weight livestock type (140 kg, Porter *et al.* 2016), than for cattle, calves, game or sheep. One previous study on wild dog prey choice has shown that prey are chosen in a body mass range of 16-32 kg or 120-140 kg, possibly due to the smaller likelihood of being injured when hunting (Hayward *et al.* 2006b). In Kenya, wild dog depredation on livestock was uncommon where natural prey was abundant, but was high in areas where natural prey was severely depleted (Woodroffe *et al.* 2005b). Similarly, a study in Zimbabwe showed that the diet of wild dog consisted mostly of greater kudu (*Tragelaphus strepsiceros*) (22%), with only negligible numbers of livestock depredated (0.7%) (Pole 2004). Although my study showed that wild dog depredates game species kept on farms, very little evidence of this has been provided, with only a single publication quantifying game losses by wild dog (Thorn *et al.* 2012).

Because published reports, including Thorn *et al.* (2012), did not state the species of game lost to carnivores, I benchmarked game loss against blue wildebeest, which is commonly kept in South Africa for both meat and trophy hunting (Hoffman & Wiklund 2006). Although not a particularly heavy game type, the golden wildebeest, can fetch exorbitant market prices of US$ 6552 (ZAR 90000) (Dry 2014). Similarly, a standard impala (*Aepyceros melampus*) ewe fetches US$ 584 (ZAR 8000), whereas the black colour variant would fetch a staggering US$ 2555 (ZAR 35000) in comparison (Wildlife Trading 2016). The perceived value of a trophy game animals increases exponentially with either increased size or rarity (Johnson *et al.* 2010), setting a higher market price. Game ranching is one of the fastest growing industries in southern Africa, with game numbers increasing from 575 000 in 1964 (Du Toit 2007) to more than 18.6 million in 2015 (Van Hoven 2015), with private owned commercial ranches comprising approximately 17 million hectares (Taylor & Van Rooyen 2016). Not surprisingly, carnivores such as wild dog are therefore prosecuted for depredating these expensive game species (Mbizah *et al.* 2014). Hence, it is clear that further investigation is needed in order to quantify depredation incidences by wild dog to assess its contribution to game depredation.

Carnivore morphology was not a predictor of depredation, with medium-bodied carnivores causing similar livestock mass losses as small and large sized predators. Large predators, such as lion, are able to take down large prey (Emmerson & Raffaelli 2004), gorge themselves and then do not have to feed for several days, although kill frequency increases with group size (Lehmann *et al.* 2008). In contrast, small predators are commonly not able to take down prey much larger than themselves (Radloff & Du Toit 2004), but would depredate multiple numbers of smaller livestock types per depredation incident, such as the Iberian lynx depredating an average of nine lambs per predation incident (Garrote 2013). This means that small, medium and large predators may be equally damaging in terms of livestock depredation, as the loss of one cow to a large or medium predator might equate to the loss of several lambs to a smaller carnivore.

Livestock suffered fewer attacks from exclusively diurnal carnivores such as cheetah and dhole, than nocturnal carnivores such as African leopard and crepuscular carnivores such as black-backed jackal or wild dog. Nocturnal activity is an ancestral pattern of mammals (Heesy & Hall 2010). Of extant mammal species, about 44% are nocturnal, 29% are crepuscular and 26% are diurnal (Jones *et al.* 2009). Livestock are mainly diurnal with some crepuscular activity (Gregorini *et al.* 2006). This means that livestock are more vulnerable during night-time hours and, because most carnivores are nocturnal (Dong *et al.* 2011) and humans are diurnal and less vigilant at night (Walker *et al.* 2014), at a higher risk of depredation at night than during the day.

Carnivores with different social organisation (solitary, social and highly social) caused similar amounts of livestock damage, suggesting that sociality is not a predictor of livestock depredation. Highly social carnivores, such as many wolf species and wild dog, have larger home ranges and cover great distances to find food (Mladenoff *et al.* 1999), increasing the possibility of encounters with farmland and livestock (Pomilia *et al.* 2015), therefore increasing the opportunity for depredation events. Solitary carnivores, such as leopard, are cryptic and stash kills to be eaten later (Hayward *et al.* 2006a). This secretive behaviour makes leopard difficult to find (Patterson *et al.* 2004) and if they become habitual livestock killers are capable of causing large amounts of damage to livestock herds

(Wang & Macdonald 2006). Small, social carnivores such as black-backed jackal are often more abundant in agropastoralist landscape than natural areas (Sinclair *et al.* 2015), thus increasing their contact with livestock. Therefore, even though different carnivore species have different social structures, each type can equally contribute to human carnivore conflict through their species-specific behaviours.

Different carnivore species employ different hunting strategies (Maddox 2003), namely ambush, run down and opportunistic (Gehrt *et al.* 2010). My results indicated that hunting strategy was not a predictor of livestock depredation, indicating that livestock are generally vulnerable to depredation by carnivores. Livestock in subsistence communities, such as cattle and goats, are often left to wander freely (Wang & Macdonald 2006, Hemson *et al.* 2009), and spend more than half of their time during the day feeding (Nianogo & Thomas 2004). Unlike free-living African ungulates that tend to recognise and avoid dangerous areas with dense cover (Kie 1999), livestock such as cattle can spend up to 30% of their time browsing in dense areas and goats as much as 82% (Nianogo & Thomas 2004). Livestock therefore occur closer to, and spend more time in, forest or shrubs and may therefore be at a higher risk of being predated upon by ambush predators while hindering hunting opportunities for run down carnivores. Domestic livestock lack the anti-predator behaviours that are instinctive for natural prey species, such as recognising dangerous areas or carnivores, and are therefore much easier to kill than wild prey of a similar size (Sih *et al.* 2010). These hypotheses may however not fully explain the complex interactions between predator hunting mode and livestock depredation, and require further exploration.

It must be noted that the findings of this study are from a meta-analysis of scientific literature, and may therefore be subject to a level of reporting bias. For example, a global problem with human-carnivore conflict studies is that pastoralists may often exaggerate livestock losses by carnivore depredation in the hope of receiving compensation from government or other authorities (Holmern *et al.* 2007, Namgail *et al.* 2007, Lagendijk & Gusset 2008, Gusset *et al.* 2009, Aryal *et al.* 2014). Similarly, missing livestock may be reported as depredated without having been confirmed (Rigg 2004). An additional issue faced is the frequent misidentification of depredating carnivores, especially in areas of multiple sympatric carnivore occurrences (Page 2014) and a bias for predators sighted near homesteads or farms (Gese 2004). Lastly, I acknowledge that, because the reports I sourced were only in English, reports and publications from non-English speaking areas may be underrepresented in this study.

Conclusion

This meta-analysis study of published scientific literature form 1982-2015 has shown that, in a global context, wild dog are equally damaging in terms of livestock depredated compared to carnivores from other regions, but are less damaging when compared only to other African carnivores. Many carnivores are involved in human-carnivore conflicts globally and African carnivores compared to non-African carnivores in relation to mass of livestock lost, although lion and spotted hyena were worse depredators than African wild dog on an African scale. Some livestock types, specifically goats, are more often depredated by most species of carnivores, while the depredation of heavier livestock such as cattle constitute the most damage in terms of livestock mass lost, and potentially greater financial loss. However, a comprehensive search of scientific literature failed to deliver literature quantifying wild dog depredation on livestock and game, and may therefore have influenced results. A review of literature indicates that carnivore activity period may be a predictor of livestock attack, while carnivore morphology, sociality and hunting mode may not be important in this regard. Reports indicate that subsistence farmers are more likely to suffer high chances of depredation occurring, and most likely do not have the funds to safeguard their livestock. A global and local comparison of conflict showed that developed regions are characterised by low carnivore densities and low depredation incidents, whereas developing regions, like southern Africa, are characterised by high carnivore densities and high livestock depredation incidents. This possibly makes developing regions more prone to human-carnivore conflict. This study has shown the importance of finding a solution to human-carnivore conflict, as effective wildlife management in the 21st century must account for the conservation needs of carnivores, particularly that of the African wild dog, as well as the sustained livelihoods of people.

Chapter 3

Spatial and temporal space use patterns and resource selection of the African wild dog pertaining to human-wildlife conflict

Abstract

For animals prone to human-carnivore conflicts, such as the endangered African wild dog, it is important to understand which features drive occurrence, as selection or avoidance of these features would influence the effectiveness of management and conservation strategies. Here, I investigated human-carnivore conflict relating to wild dog at a regional scale, particularly focussing on comparing the spatial and temporal space use patterns and resource selection of four packs of African wild dog in Limpopo and Mpumalanga Provinces, South Africa. Data were collected from one collared individual per pack occurring in the Waterberg, Skukuza, Orpen and Bluebank areas. The Waterberg and Bluebank packs occurred outside of the Kruger National Park and had access to multiple areas with farmland, whilst the Skukuza and Orpen packs occurred within the boundaries of the Kruger National Park. I ascertained wild dog home ranges and assessed their occurrence in seven anthropomorphic and natural landscape features using GIS analyses and Resource Selection Functions. The Waterberg and Orpen packs jointly displayed the largest 95% home ranges (847 km^2 and 848 km^2 respectively), whilst the Skukuza pack displayed the second largest 95% home range (490 km^2) and the Bluebank pack displayed the smallest home range (220 km^2). The Waterberg pack occurred in close proximity to the area with the highest number of game farms, hunting lodges and mixed-use (game and domestic livestock) farms and along with the Bluebank pack, occurred in close proximity to areas housing moderate to high densities of cattle and goats. However, the core home ranges of these two packs did not overlap areas of high cattle and goat densities. In addition to potential conflict with farmers, occurrence on roads with fast-moving traffic and road mortality was highlighted as a concern for three of the wild dog packs. Other anthropogenic and natural landscape features, such as agricultural landscape features and rivers varied in importance as predictors of wild dog occurrence. This study showed that whilst wild dog packs may occur in close proximity to farms and areas that house livestock, packs establish home ranges in areas with few farms and low livestock densities, pointing to avoidance of areas where human-carnivore conflict and resulting mortality may occur.

Keywords: African wild dog, human-carnivore conflict, occurrence, resource selection, space use

Introduction

Heterogeneity of resources within a habitat is an important contributor to the survival of animal species (Smith *et al.* 2013). Variation in a habitat includes environmental gradients (Flesch & Steidl 2010), natural boundaries, such as mountains (Peters *et al.* 2006), and anthropogenic modifications (Bennett *et al.* 2006). These variations in landscape structures influence the space use patterns of the animals that occupy that environment (McIntyre & Wiens 1999). Differences in movement (space use) patterns may have repercussions for an individual animal's health (Patterson *et al.* 2008), the structure and dynamics of populations and communities (Johnson *et al.* 1992), and ultimately ecosystems (Roshier *et al.* 2008). Understanding the reasons and mechanisms of animal space use is therefore essential for developing management strategies for conservation (Festa-Bianchet & Apollonio 2003).

The definition of animal space use patterns differ to that of dispersal, as the animal does not move away from its home range to occupy a different habitat, but remains and travels between different areas within the home range (Bastille-Rousseau *et al.* 2016). Space use may be classified at several different temporal and spatial scales (Yackulic *et al.* 2011). Space use patterns can be studied at a coarse temporal scale, such as annually, and may be classified in terms of broad strategies including migration and nomadism (Morales *et al.* 2004). At a very fine temporal scale, space use may be classified as changes between different behavioural states such as foraging, resting, grooming or interacting with objects in the environment (Singh *et al.* 2012, Bastille-Rousseau *et al.* 2016). Animals that occupy unmodified, stable or resource-rich environments tend to move on relatively small scales (Mitchell & Powell 2004). Alternatively, in altered, resource-poor or unpredictable environments, animals tend to move at broader scales to meet their short-term needs, reflecting search strategies to find widely distributed resources (Fauchald *et al.* 2000). Whether at a broad or a fine scale, an animal's space use within an environment is a result of behavioural and physiological adaptations (Horne *et al.* 2008). Factors that may affect the use of space within an area include the location of conspecifics or competitors (Wauters *et al.* 2000), the location and distribution of resources and the physiological needs of the animal (such as the need to rest) (Leone & Estevez 2008) and the tendency for site fidelity (territoriality) and the establishment of home ranges (Tweed *et al.* 2003).

Generally, two approaches are used when studying animal space use. One uses a mechanistic approach to model animal space use using diffusion-advection models based on hypothesised animal behaviours, such as the attraction to home range core areas or aversion to foreign scents (Moorcroft & Barnett 2008). The second approach uses estimates of relevant model parameters fit to observed animal location or telemetry data in order to determine resource selection (Börger *et al.* 2006). Due to the ultimate association with cover, water and food resources, resource selection is generally assessed using environmental characteristics such as vegetation type and structure (Horne *et al.* 2008).

Resource selection

All animal populations require sufficient quantities of resources, defined as a consumable factor (e.g. food, water, shelter) that leads to an increased body-growth rate, reproductive rate, and ultimately fitness (Tilman 1982). When an animal selects a resource, it does so on a continuum starting at the large scale of a geographic area, such as different species of migratory birds selecting a landscape that contains areas of forest in Ontario, Canada (Freemark & Merriam 1986). Animals then select an individual home range within that geographic area, and different habitats within the home range down to the small-scale selection of particular elements, such as feeding sites and nesting/den sites in the habitat (Manly *et al.* 2007). An animal will decide to use these different resource-filled areas within habitats, also known as patches, by interacting with the different resources that it encounters in these areas (Orians & Wittenberger 1991).

The resource selection of an animal describes the quantity of a particular resource used versus the availability of that resource in the habitat (Manly *et al.* 2007). Resource selection is influenced by multiple extrinsic factors such as time constraints, social pressures (such as population density), territoriality, competition, predation, habitat patch size and inter-patch distance (Manly *et al.* 2007). Intrinsic influences on resource selection include the body size and condition of the animal, how much energy is available for expenditure versus how energy depleted the animal is, and how far the animal is able to travel to explore patches (Boyce 2006). An animal's travel ability sets the upper limit to its ability to explore patches, but is not absolute and would be subject to internal and external factors. For example, a smaller bodied animal such as a white-footed mouse (*Peromyscus leucopus*) can travel an average distance of 422 metres a night (Merriam & Lanoue 1990), while a grey wolf (*Canis lupis*) is able to cover an average distance of 50 kilometres a day when prey is abundant (Mladenoff *et al.* 1999).

The initial decision of exploring a patch or searching for another is usually made quickly and is based on general features in the environment, such as the presence of risk, competition with other species or conspecifics, or the perceived value of available food resources (Orians & Wittenberger 1991). Animals would rather move to a different patch with poorer resources that is danger-free, than remain in a patch where the resource quality is better but has a high risk factor (Brown 1999, Le Gouar *et al.* 2012). For example, foraging grey squirrels (*Sciurus carolinensis*) avoid areas within a city park where domestic dogs (*Canis lupus familiaris*) and cats (*Felis catus*) are often found, even if those areas contain high numbers of acorns (Lima *et al.* 1985). The risk of competition or predation can therefore significantly alter an animal's spatial distribution (Broekhuis *et al.* 2013). By altering its space use, an animal may avoid potentially costly encounters with others species or conspecifics when utilising areas of low risk, called refuges, or altering their habitat use and predator-avoidance behaviours, as risk is not homogenously distributed in the landscape (Broekhuis *et al.* 2013).

Responses to risk may either be reactive, based on an animal's knowledge of real-time risk, or predictive, with animals taking preventative measures to avoid areas or habitats where previous risk encounters occurred (Valeix *et al.* 2012). These risk response behaviours are commonly seen in predator-prey interactions (Brown *et al.* 1999), as observed with elk (*Cervus canadensis*) in Yellowstone Park choosing coniferous forest over grasslands that are associated with grey wolf predation risk (Creel *et al.* 2005). Coyotes (*Canis latrans*), although more numerous than grey wolves, adjust their behaviour spatially and temporally to avoid areas used by wolves (Berger & Gese 2007). In another example, cheetah utilize the same areas as lion and hyena, but show reactive risk responses because predictive responses lead to missed kill opportunities and are therefore energetically costly (Broekhuis *et al.* 2013). The same study showed that cheetah resource selection is therefore a hierarchical process, driven primarily by resource acquisition and thereafter by risk avoidance (Broekhuis *et al.* 2013). Risk response behaviours are also observed in predator-predator (Broekhuis *et al.* 2013) as well in human-predator (Valeix *et al.* 2012) interactions. For example, in Botswana, lion (*Panthera leo*) mostly avoid cattle posts, but when they did use these areas, they avoided the times of day when humans were most active and travelled at high speeds in order to reduce time spent in these areas (Valeix *et al.* 2012).

The African wild dog (*Lyaon pictus*) is medium-sized carnivore (20 – 30 kg) occurring in a variety of different sub-Saharan ecosystems (Davies-Mostert *et al.* 2009). It is under severe threat and listed as Endangered, with populations declining due to interspecific competition (Creel 2001), kleptoparasitism (Fanshawe & Fitzgibbon 1993), deadly infectious diseases (Woodroffe & Ginsberg 1997), shrinking habitats (Creel *et al.* 2004) and conflict with humans (Swarner 2004). Space use has rarely been researched in the African wild dog, although some studies have shown that wild dogs are able to travel average distances of 8.5-10.5 kilometres daily within their territories, with minimum travel distances of 5-6 kilometres daily. (Fuller & Kat 1990, Pomilia *et al.* 2015). Wild dog packs on the hunt are capable of covering 2 kilometres in 30 minutes (Fuller & Kat 1990) and wild dogs in another study was observed to travel up to 40 kilometres in one day (Pomilia *et al.* 2015). Wild dogs have been shown to avoid human settlements, activities and livestock predictably (Woodroffe 2011). Hence, it is important to investigate whether actual space use patterns of wild dog packs reflect their supposed livestock depredating behaviour, as well as which landscape features determine their occurrence patterns. Such knowledge could contribute to conserving these carnivores. The aim of this study was therefore to assess human-carnivore conflict relating to African wild dogs at a regional scale, particularly focussing on comparing the spatial and temporal space use patterns and resource selection of four packs, two inside and two outside of Kruger National Park in South Africa. There were 2 objectives. 1) Ascertain the home ranges of the four wild dog packs, assess the size of home ranges and whether the packs inside the Kruger National Park moved out of the protected area into agricultural areas/ high livestock density areas where they would potentially be exposed to livestock and humans. 2) Assess whether the packs used areas characterised by specific landscape features (predictors of occurrence) such as vegetation types or water sources (such as rivers) and avoiding potentially dangerous areas such as major roads. I made three predictions. 1) The two packs inside of the Kruger National Park will not avoid roads as traffic on these roads is slow moving and non-lethal, whereas packs outside reserves will avoid roads with heavy traffic that has the potential to be lethal. 2) The two packs outside reserves will encounter more human-altered landscape features and would possibly avoid these areas and be found more often in natural landscapes, whereas packs inside of Kruger National Park will encounter natural areas with small, interspersed human-altered areas. 3) Packs outside of reserves are free roaming and should thus have larger home ranges than the packs inside of reserves that are restricted by wildlife fences.

Materials and Methods

Study sites

Data were collected from GPS fixes of four individuals in each of four packs. The four wild dog packs were located and collared in the Limpopo and Mpumalanga Provinces in the most northern part of South Africa (Figure 3.1, showing location only). The Skukuza and Orpen packs occurred within the Kruger National Park, and the Bluebank and Waterberg packs outside of national parks in biosphere reserves (described below; Figure 3.1). The Limpopo and Mpumalanga provinces are mostly dominated by savanna grasslands, sweet Lowveld Bushveld and Mixed Lowveld Bushveld vegetation types (Figure 3.2) and experience mainly summer rainfall, with a hot and humid climate throughout the summer months (Newbould 2003, Mucina & Rutherford 2006). Limpopo Province is ideal for cattle farming and game ranching, and many types of crops, such as tropical fruits, peanuts, tea and coffee, and there are commercial forests in the province (Mucina & Rutherford 2006). The most common agricultural activities within the Waterberg Biosphere Reserve and surrounding areas are game farming, involving the breeding and keeping of plains game, and domestic livestock production (De Klerk 2003). Due to profitability, farmers in this area often combine these two agricultural land uses (Bothma 2005). Limpopo Province also has a thriving tourism industry, with four provincial reserves, several luxury private game reserves as well as the Kruger National Park (KNP), a formally protected area (Dubin 2011). Formal protected areas such as the KNP are clearly demarcated geographic areas set out specifically for conservation purposes, where no human interference activities (such as wood or animal harvesting) are allowed by law (Pimbert & Pretty 1997).

The KNP also forms a large part of Mpumalanga's eastern side, covering an area of 20, 000 km^2, and is a popular tourist destination for wildlife viewing safaris (Kruger & Saayman 2010). More than 68% of the rest of Mpumalanga Province is used for agriculture, including forestry products, citrus, tobacco, cattle, goat, and poultry farming (Dubin 2011). The primary vegetation types in the southern half of Kruger (from Orpen downward) is thorn trees and red bush-willow veld, along with Knobthorn and Marula veld, providing ample grazing areas for herbivores (Gertenbach 1983). The park is home to several large mammals, many species of birds, antelope, amphibians (Braack 2006) and many species of reptiles and invertebrates (Kruger & Saayman 2010). The majority of the park remains fenced to stop dangerous animals from entering human inhabited areas and to keep poachers out (Kruger & Saayman 2010). However, the 150 km long fences between the park's eastern border and Mozambique were removed in 2002 in order to establish the Great Limpopo Transfrontier Park, enabling wildlife to re-establish old migratory routes, and thus ensuring their persistence (Ramutsindela 2005). Bull elephants are culprits of damaging fences, and some of the fences are old and not electrified, therefore making the fences on the western side of KNP porous to animal movements (Ferguson *et al.* 2012).

Biosphere reserves differ from formal national reserves as they promote environmental and livelihood solutions, combining the conservation of natural areas and the existing animals with the sustainable use of the land by people requiring natural resources, such as firewood and medicinal plants (Dogsé 2004). The Kruger to Canyons biosphere reserve encompasses a total size of 2.5 million hectares, which includes the Kruger National Park, the Blyde River Canyon and the Wolkberg region, which is a floral hotspot (Coetzer *et al.* 2010). The central area of the reserve lies between the Letaba and Sabie Rivers, and is made up of savanna woodlands, Afromontane forest and grassland veld types (Coetzer *et al.* 2010).

The KNP has a high number of large mammal species, such as elephant (*Loxodonta africana*), white rhinoceros (*Ceratotherium simum*), giraffe (*Giraffa camelopardalis*), predators including lion and leopard (*Panthera pardus*), antelope species such as common tsessebe (*Damaliscus lunatus*), sable (*Hippotragus niger*), and roan (*Hippotragus equinus*), along with a total of 140 endemic species of plants, birds, reptiles, invertebrates and amphibians (Coetzer *et al.* 2010). The Waterberg biosphere reserve is 417, 406 hectares in size (De Klerk 2003). Veld types in the biosphere reserve include sour bushveld, mixed bushveld, mountainous sourveld and arid sweet bushveld (De Klerk 2003). Animal species found in this region includes impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), klipspringer (*Oreotragus oreotragus*), giraffe, warthog (*Phacochoerus africanus*), white-backed vultures (*Gyps africanus*) and predators such as leopard, lion, spotted hyena (*Crocuta crocuta*) and wild dogs (De Klerk 2003).

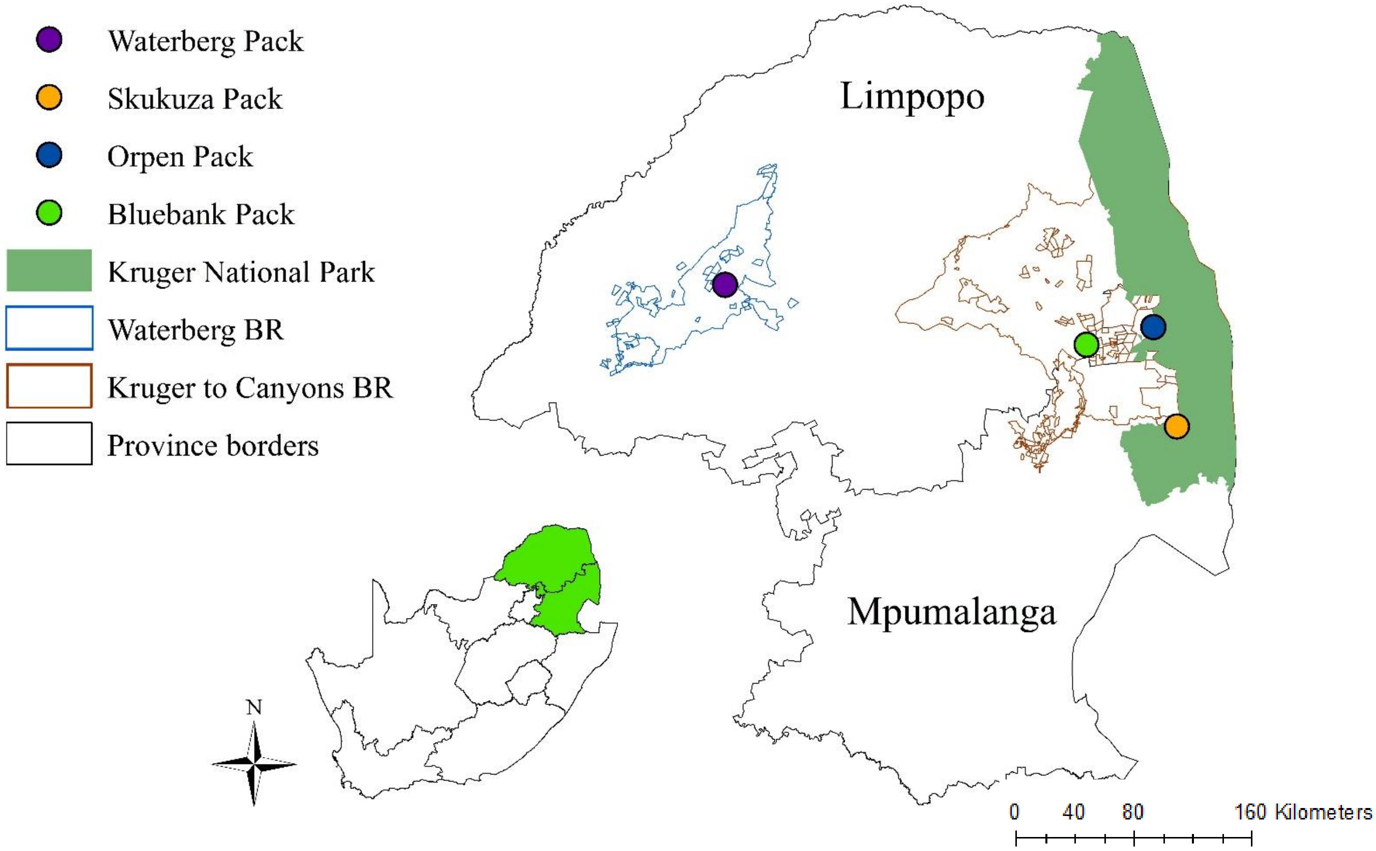

Figure 3.1. The location of four wild dog packs in the Limpopo and Mpumalanga Provinces, South Africa. Two packs, Skukuza and Orpen, were found within Kruger National Park, while the Waterberg pack were located within the Waterberg Biosphere Reserve (BR) and the Bluebank pack occurs within the Kruger to Canyons BR. A map of South Africa is inset, not to scale.

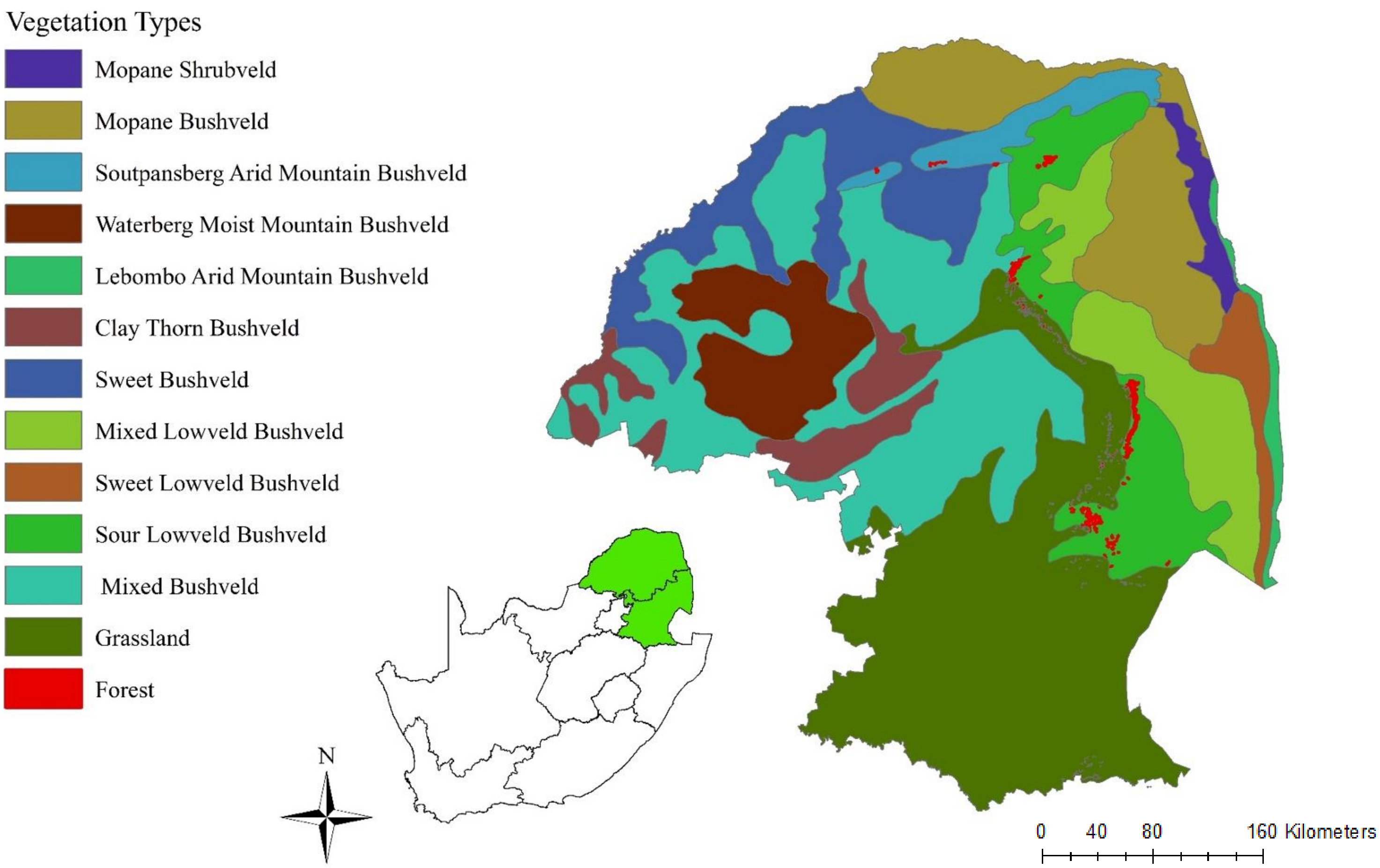

Figure 3.2. Vegetation types found in the Limpopo and Mpumalanga Provinces as used in the SAFARI 2000 project undertaken by the National Botanical Institute as imported from ArcGIS online. A map of South Africa is inset, not to scale.

Collaring and GPS tracking

Collaring of four wild dog individuals was done with the assistance of the EWT (Endangered Wildlife Trust) and the South African National Park's Veterinary Services. Individuals were selected opportunistically. A dose of 10 mg Neltrexine administered via tranquiliser dart was used to immobilise one dog per pack to fit collars and collect blood and tissues samples for analysis by others. While sedated, body condition of each individual was evaluated by examining gum and dental condition, skin health and tick loads, where a scored on a 5 point scale from poor to excellent body condition. The wild dogs were then revived after the procedure using 6.25 mg Antisedan. Two Iridium GPS collars (satellite) and two Ultra-high frequency (UHF) GPS collars were fitted to four individual wild dogs from four different packs (Table 3.1) located in Skukuza, Orpen, Waterberg and Bluebank. Wild dog packs will henceforth be referred to using their pack location. The EWT's Carnivore Conservation Programme is a registered project with the South African National Parks (SANParks) and ethical permission to collar the four individuals was granted under the memorandum of understanding between the EWT and SANParks.

Table 3.1. Collaring location and individual information of four wild dog individuals and their packs in Limpopo and Mpumalanga, South Africa.

Wild dog Pack location	Wild dog status and sex	Type of collar fitted	Age	Body condition	Adult pack size	Number of pups	Date collared	Number of days monitored	Number of occurrence fixes
Skukuza	Alpha ♀	UHF GPS	3	Average	4	5	2013/11/22	79	304
Orpen	Alpha ♂	Satellite	4	Excellent	17	15	2015/01/27	150	588
Waterberg	Alpha ♂	UHF GPS	1	Average	7	unknown	2013/11/21	110	399
Bluebank	Alpha ♂	Satellite	3	Poor	6	unknown	2014/05/03	389	1456

Sampling fixes for collars were set at 4-hour intervals per day, because this allows for an adequate sample size for a species that can travel great distances daily (Woodroffe & Ginsberg 1998), and in order to avoid autocorrelation (here defined as short sampling intervals between fixes that cause biases when estimating home ranges and other occurrence analyses) as per the guidelines of Gannon & Sikes (2007). Satellite Iridium collars (model G5C 275 D, manufactured by Sirtrack Ltd) were used to collar the Bluebank and Waterberg individuals. The collars transmitted and relayed the GPS fixes via a satellite to a central recording beacon on Earth. The fixes were then available for download directly from the Sirtrack website. GPS-UHF collars (VERTEX PLUS model, manufactured by VECTRONIC Aerospace) were used to collar the Skukuza and Waterberg individuals. The fixes were saved on a SIM (Subscriber Identity Module) card within the collar. A UHF Handheld Terminal was used to download the data from the collar SIM using the proximal download method, requiring the user to be within 1.5 to 2 km of the collared individual, depending on the landscape and surrounding vegetation. The Handheld Terminal was then plugged into a computer for data transfer, and therefore no download costs or animal immobilisation were involved. These two types of collars were used due to funding constraints at the time. Duplicate entries (fixes with identical date- time stamps) were removed and the data saved as an .xls sheet (Excel 97-2003 Workbook), later to be imported into ArcMap version 10.1 (ESRI development team).

Home range analysis with T-LoCoH

Wild dog GPS data were imported into RStudio, the projection and time formats defined and tested for autocorrelation. Wild dog home ranges and occurrence patterns were analysed using the R package T-LoCoH (Time Local Convex Hull). This package utilises a nonparametric Lagrangian method for calculating utilization distributions from GPS data by aggregating Minimum Convex Polygons (MCPs) constructed for each data point into isopleths (Lyons *et al.* 2013). I used the k-method, which identifies the k^{th} nearest neighbour for each spatial data point and then constructs a local convex hull (Getz &Wilmers 2004), and the time parameter was set to s = 0. I selected the k-method as it is simple and intuitive, selecting for the smallest values of k that created hulls with the least number of holes in the core areas (Lyons 2014). Isopleths (10%, 50%, 95% and 100%) for the Waterberg, Skukuza, Orpen and Bluebank wild dog packs were created in accordance with guidelines set out in the T-LoCoH for R Tutorial and Users Guide (Lyons 2014), and isopleth area sizes were calculated using the field calculator in ArcMap. The 95% and 50% isopleths are standardly used in home range studies as it represents the areas within the home range most used by animals (Börger *et al*. 2006). Although 10% and 100% home ranges are not commonly used, I included these in my analyses in order to include areas that are lightly used (Powell 2000). The 100% home range includes outlier points that are regarded as 'occasional sallies' (Powell 2000). However, for an endangered species like the wild dog that is still persecuted on farms, these occasional sallies could bring them into contact with farms, possibly leading to mortality. Simple calculation of MCPs, although a popular method still used today, is highly biased during home range estimation and is unable to differentiate internal space use once the simple MCP has been constructed (Burgman & Fox 2003). Kernel Density Estimators (KDE's) are more suitable for concave geometries and uses multiple epicentres of activity (as shown by GPS points) to estimate density distributions while ignoring outlying points (Kamler *et al.* 2012). KDE's show the areas within the home range that are utilised most often by an individual/pack (Hemson *et al.* 2005), but struggles to account for unused areas due to unsuitable terrain or boundaries, such as rocky outcrops (Getz *et al.* 2007).

In order to compare pack home ranges according to seasons, the available data for the four wild dog packs were partitioned into the four different seasons for South Africa (where applicable) as obtained from the South African National Weather Service (Spring: 1 September – 30 November, Summer: 1 December – 28 February, Autumn: 1 March – 31 May and Winter: 1 June- 31 August). This allowed me to investigate whether packs inside and outside of reserves changed their use of space according to seasons. Due to available data, only the Bluebank pack was monitored for all four seasons. The Orpen pack was monitored for autumn, summer and winter, the Waterberg pack was monitored for autumn, spring and summer and the Skukuza pack was monitored for spring and summer.

Resource selection

Wild dog pack occurrence in Limpopo and Mpumalanga were analysed using Resource Selection Functions. Resource Selection Functions (RSFs) are mathematical models used to estimate the probability of a resource unit being used by a species (Rogers *et al.* 2007), and is used as a proxy for habitat suitability (Boyce *et al.* 2002). The resource units (pixels of land) that are selected by animals have associated predictor resource variables for presence (such as water sources), mortality (such as major roads) or covariates of resources, such as anthropogenic landscape alteration (Boyce *et al.* 2002). The RSF analysis as well as the underlying assumptions depend on the study design. My study follows the Design 2 pattern as outlined by Manly *et al.* (2007). With this design, individual animals are identified by radio-tracking collars and their use of resources, as obtained from aerial imagery, are measured for each individual animal, although resource availability can be extrapolated to population level. Using real location data is more useful than model-created data, as inferences about resource selection are dependent on the random sampling of an animal's real-time occurrence, and not model-based occurrence that relies on the selected statistical model being correct (Manly *et al.* 2007).

Odds ratios (ORs) are used for binary data as measures of association when comparing an exposure and an outcome (Bland & Altman 2000). ORs represent the chance that a specific exposure will lead to an outcome, versus the chance of an absence of that exposure creating an outcome (Bland & Altman 2000). When OR = 1.0, the chance of either outcome occurring is equally likely (Lipsitz *et al.* 1991). When OR < 1, the chance of the outcome occurring is less likely and when OR > 1 the chance of the outcome occurring is great (Lipsitz *et al.* 1991). Hence for my study, if OR = 1.0, the odds of occurrence or non-occurrence of the wild dog pack at a feature (either natural or anthropogenic) was equal. When OR < 1, the odds of occurrence of a wild dog pack at a feature was low, and if OR > 1, the odds of occurrence at a feature was high. It must be noted that, as mentioned previously, non-occurrence may not mean absence, as the animal may have been undetected and not truly absent (Manly *et al.* 2007).

Mapping & analysis

To obtain accurate distance measurements from GPS fixes to environmental features, it is critically important to use a projected coordinate system in addition to a geographic coordinate system (usually WGS 1984) when mapping GPS points in a mapping program such as ArcMap (Maher 2013). The Universal Transverse Mercator (UTM) projection is an internationally used projection system that is highly accurate and divides the globe into 60 zones, each 6 degrees wide (Karney 2011). For this study, I used the WGS 1984 UTM Zone 36S projection for all subsequent map analyses. All terrain features, excluding livestock density and agricultural landscape features were downloaded directly from ArcGIS online (a standard tool in the ArcMap program that allows for direct import of maps without needing to access the ESRI website first). Global livestock densities, as used in Chapter 2, were downloaded from the Food and Agriculture Organisation (FAO) of the United Nations (available from: http://www.fao.org/Ag/againfo/resources/en/glw/GLW_dens.html), and clipped to the Limpopo and Mpumalanga Provinces for convenience. Due to zero raster values in areas of pack occurrence, sheep were omitted from the analyses. Farm data were obtained from a previous study by Soeraj-Pillai (2016), and I added to this file by searching farms, hunting lodges and game farms in google maps and exporting the GPS coordinates to a Microsoft Excel spreadsheet.

GPS point files saved as .xls were imported into ArcMap and converted to shapefiles (a geospatial vector data format specifically for GIS software). Home range squares (HRS) were then generated using the square polygon tool. These squares encompassed all the location points for each wild dog pack, and the HRS of each pack was saved as a separate shapefile. I then imported these shapefiles into the Geospatial Modelling Environment (GME) software (Beyer 2001, Version 0.7.2.RC2) command builder to generate random points for each home range square using the same number of points as the original number of observations for each pack at a 1:1 ratio. This random point generation method is standard approach in RSF analysis because it requires presence/available data or presence/absence data; true absence is almost impossible to quantify accurately, as the organism might have been undetected and not truly absent (Manly *et al.* 2007). The generated random points were therefore a measure of available resources for each wild dog pack within its home range, whereas the original points represent true presence at the resource within the home range (Manly *et al.* 2007). A HRS is used rather than a Minimum Convex Polygon (MCP) as per the guidelines and parameters of the GME software (Beyer 2001). HRS provides a standardized and stratified sampling design (Beyer 2001), encompass all of the location points (unlike MCP's) and allow for more "randomness" when points are generated, thus allowing for potentially more available areas of use within the home range, which would not be the case when using a MCP (Supplementary material: Figure S1).

The generated random points were then imported into ArcMap and along with the original point data and were used to conduct near, intersect and extract analyses for anthropogenic and natural features and their subclasses (Supplementary material: Table S1). Near analysis was used for all shapefiles, except for vegetation (as it represents continuous features) and determines the straight-line distance (in metres) from each location point to the closest environmental feature. Intersect analysis computes the geometric intersection of the input features where overlap occur, and was used for determining in which vegetation types the packs occurred compared to the vegetation types available in the environment. For the raster files (livestock density), I used the extract values to points tool to extract the values of the raster based on the input presence location points and random points. All output attribute tables were exported to Microsoft Excel and saved for use in Rstudio.

Statistical analysis

I performed all statistical analyses for RSF's using RStudio Desktop software (Version 0.99.902, R Studio Development Core Team. 2010). Home range data were not analysed statistically as T-LoCoH provides robust estimates of animal home ranges (Lyons 2014). RSF data sets were first tested for normality using the Shapiro-Wilk Normality test. I performed randomization (permutation) tests, logistic regression and calculated confidence intervals and odds ratios for all data sets. Firstly, random permutation tests were conducted to analyse whether presence and available data were located at significantly different distances from each of the environmental features considered here. Pairwise random sampling without replacement was performed using 1000 iterations, as per standard practice (Golland & Fischl 2003). The permutation tests calculated the mean difference between the observed and randomized data, and generated a p-value. Next, logistic regression was performed using the glmmsr package (Ogden 2016) on all environmental features for all four wild dog packs to assess whether or not a wild dog pack selected a feature. Due to occurrence within the Kruger National Park, the Skukuza and Orpen packs were not analysed for proximity to nature reserves and only results for the Waterberg and Bluebank packs (occurring outside of the KNP) were presented. A generalised linear model (denoted glm) following quasi-likelihood estimation was created for each feature, as it accounts for data that are over-dispersed and is used for grouped binary (here presence and available) data (Hardin *et al.* 2007).

Due to the nature of the outputs for intersected data in ArcMap, vegetation data did not have associated numerical values. Vegetation data were pooled according to vegetation category (Sour Lowveld Bushveld, Forest, Grassland, Mixed Lowveld Bushveld, Mopane Bushveld and Sweet Lowveld Bushveld) for each wild dog pack per different season. Counts were therefore created using the number of times a vegetation category was used by a wild dog pack per season and were then modelled using a generalised linear model. The Wald Chi-Squared statistic was used to report p-values for all features tested. Odds ratios and 95% confidence intervals were then calculated and plotted for all features per wild dog pack in order to assess the change in probability of wild dog occurrence in relation to anthropogenic and natural landscape features. I did not plot the ORs on a logarithmic scale, as is often the convention (Egger *et al.* 1997), since the arithmetic scale preserves proportionality and is therefore visually less misleading than the log scale (Rothman *et al.* 2011). All significance levels were set to $\alpha = 0.05$. Boxplots and bar plots were created for each RSF (feature and season) per pack using the package ggplot2 (Wickham 2009).

Results

Overview

Results for home ranges as calculated by T-LoCoH are given as home range isopleth sizes organised in a table. Maps were drawn to depict the locations of pack home ranges in relation to the Kruger National Park and biosphere reserves, as well as Waterberg, Skukuza and Bluebank pack home ranges in relation to agricultural landscape features and cattle and goat densities. As the Orpen pack did not occur close to agricultural landscape features or areas with any livestock densities (see below), maps for this pack are not shown. Because the poultry density map for the study sites showed only < 10 chickens per km^2 and no other densities, maps for poultry are not shown, although values are reported under the RSF results.

Results from RSFs based on proximity to environmental features were organised into three graphs per pack per feature tested: 1) presence versus available data for each of the subclass within the feature tested; 2) presence versus available data per season for the feature tested; and 3) odds-ratio for each wild dog pack occurrence per feature subclass (Supplementary material: Table S1). Comparisons were made between presence and available data for each feature subclass, between presence data for each different feature within each subclass, and between presence data per season. Seven environmental features were evaluated for each wild dog pack to assess which influenced the occurrence of wild dogs within Limpopo and Mpumalanga Provinces. Waterberg, Skukuza, Orpen and Bluebank wild dog packs are reported in sequence for each of the anthropogenic and natural landscape features tested. Occurrence at a resource or landscape feature would be indicated by close proximity to that resource or feature (< 5 km) and may then be indicative of possible mortality (for dangerous landscape features) or the importance of that resource or feature to wild dogs. Odds ratio plots with 95% CI are presented per pack for each feature subclass.

Home ranges

T-LoCoH calculated home range sizes indicated that the Waterberg and Orpen packs jointly occupied large 95% home range (generally accepted as the true home range size, Manly *et al.* 2007, Lyons 2014) isopleths of 847 km^2 and 848 km^2 respectively (Table 3.2). The Skukuza pack occupied the next largest 95% home range, with a total area of 490 km^2, and the Bluebank pack had the smallest 95% home range of 220 km^2 (Table 3.2). The Waterberg pack occurred within the Waterberg biosphere reserve (top left, Figure 3.4a), with the pack's home range spanning across multiple private nature reserves, including Pearson, Alem, Hen Nel, Belanie, Innes Mellet, Kindjie, Wyn van Staden, Les Brown and Pierre Fourie private nature reserves. The Waterberg 95% isopleth remained mostly within the biosphere reserve, although a small area of approximately 192 km^2 (22% of the total 95% isopleth) occurred outside of the biosphere reserve (top left, Figure 3.4a). The Waterberg pack's 10% home range did not overlap any reserves (top left, Figure 3.4a). The Skukuza pack's 100% home range extended slightly outside the border of KNP, comprising an area of only 2.5 km^2, with the remainder of the home range remaining completely within the borders of KNP (bottom right, Figure 3.4a). GPS fixes indicated that the Skukuza pack made few excursions outside the park boundary (percentage of total fixes, 1.3 %). T-LoCoH calculated the Skukuza pack 50% home range as three separate isopleths compared to the continuous areas of the other packs (bottom right, Figure 3.4a). The Skukuza pack's 10% home range was located close to the northwestern border of the KNP (bottom right, Figure 3.4a).

The Orpen pack's 100% isopleth extended slightly over the borders of the Timbavati nature reserve, with an area of only 8.38 km2 falling outside of both Timbavati and the Klaserie nature reserve (top right, Figure 3.4a). GPS fixes indicated that the Orpen pack made few excursions outside the Timbavati boundary (percentage of total fixes, 0.4 %). In total, Timbavati makes up 221 km^2 (or 26%) of the Orpen pack's total 95% home range isopleth, completely within the nature reserve's borders (top right, Figure 3.4a). The Orpen pack's 10% home range occurred within Timbavati (top right, Figure 3.4a). The Bluebank pack's home range lay within the Kruger to Canyons Biosphere Reserve (bottom left, Figure 3.4a) and stretched across Kapama Game Reserve and several private nature reserves, including the P.W. Willis, Eden, Bluebank, Welverdiend, Amsterdam, Vienna, Brussel and York. The Bluebank pack's 10% home range (bottom left, Figure 3.4a) did not overlap any nature reserves.

Table 3.2. Total local convex hull (LoCoH) area sizes (km^2) for the 10%, 50%, 95% and 100% home range isopleths of the Waterberg, Skukuza, Orpen and Bluebank wild dog packs occurring in Limpopo and Mpumalanga Provinces, South Africa.

LoCoH isopleth (%)	**Waterberg**	**Skukuza**	**Orpen**	**Bluebank**
10	13	9	11	5
50	147	120	446	113
95	847	490	848	220
100	2132	819	1071	589

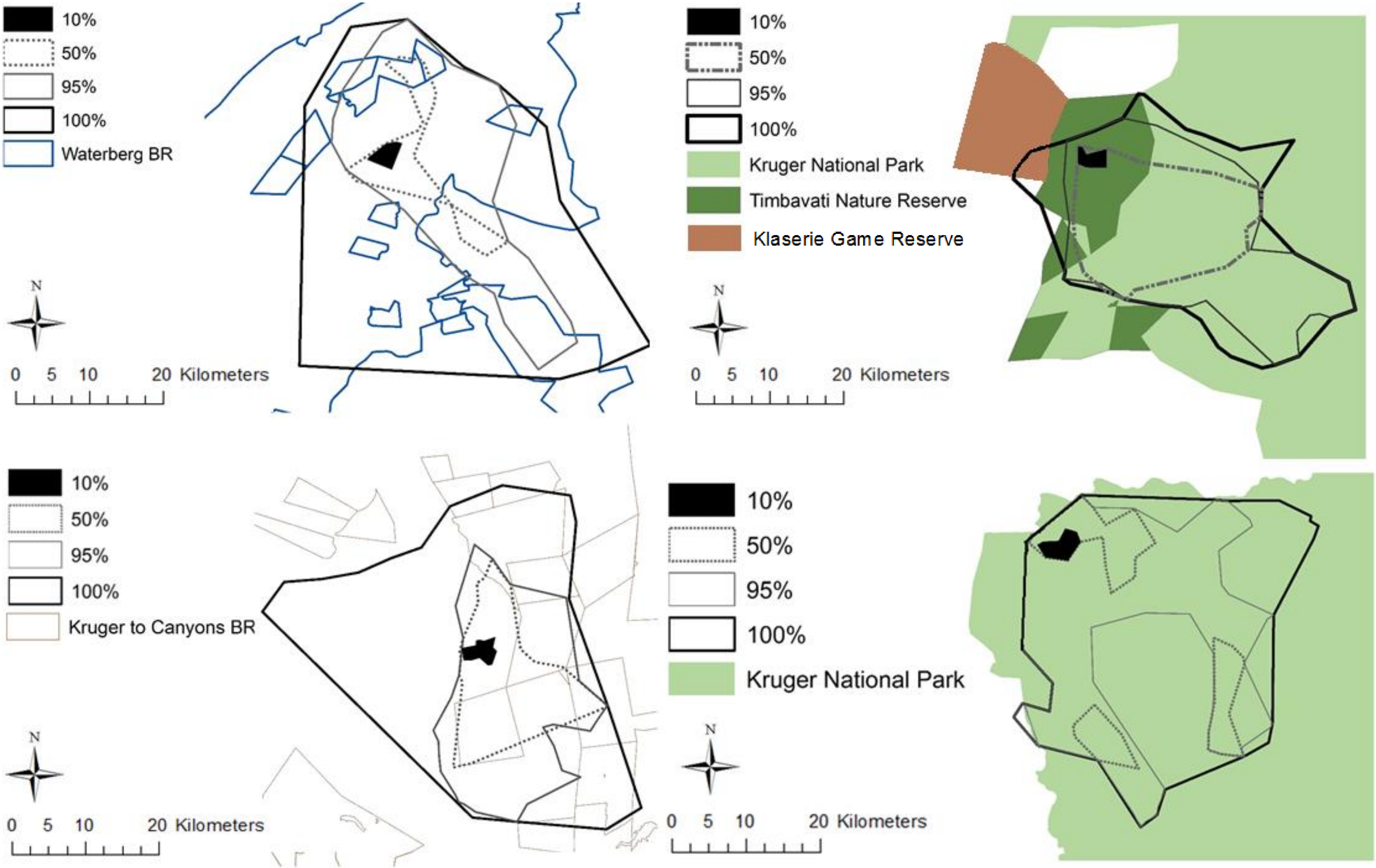

Figure 3.4a. Maps showing the 10%, 50%, 95% and 100% home ranges as local convex hull (LoCoH) polygons created from density isopleths of four wild dog packs fitted with GPS and satellite collars occurring in Limpopo and Mpumalanga Provinces, South Africa. Waterberg (top left), Orpen (top right), Bluebank (bottom left) and Skukuza (bottom right) pack home ranges are indicated with line isopleths, to show that home ranges extend outside of protected areas or overlap multiple areas. Due to space constraints, only a section of the Klaserie Game Reserve is shown (top right).

The Waterberg pack occurred in an area with the highest number of general farms, game farms and hunting lodges in the surrounding area, whilst the Skukuza pack occurred close to only one general farm that bordered the Kruger National Park (Figure 3.4b). The Bluebank pack occurred in an area that contained only fruit farms, and the Orpen pack did not occur in an area that contained any agricultural

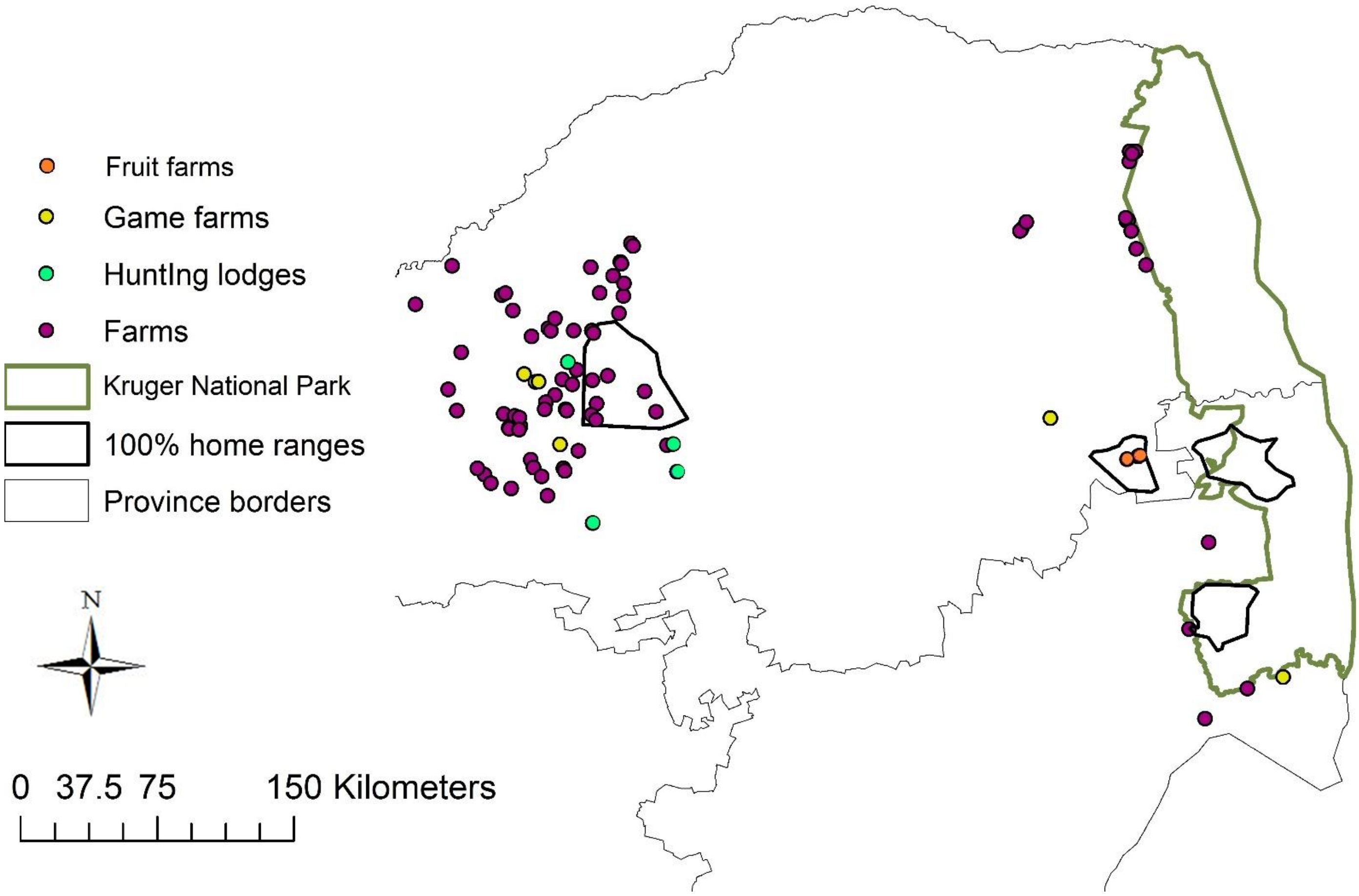

Figure 3.4b. Map depicting 100% home range isopleths (black) of four wild dog packs as local convex hull (LoCoH) polygons created from density isopleths within Mpumalanga and Limpopo Provinces, South Africa. All four wild dog packs and their locations are shown relative to different agricultural landscape features, namely fruit farms (orange), game farms (yellow), hunting lodges (light green) and general farms keeping different combinations of game and livestock (purple).

The Waterberg 100% home range isopleth overlapped several farms, although the 95% home range only overlapped two farms, and overlapped areas of low to moderate cattle densities (Figure 3.4c). The pack's 10% home range overlapped areas of low densities of cattle per km^2 (Figure 3.4c). The Waterberg pack's 95% home range overlapped areas of low goat density per km^2 (Figure 3.4d).

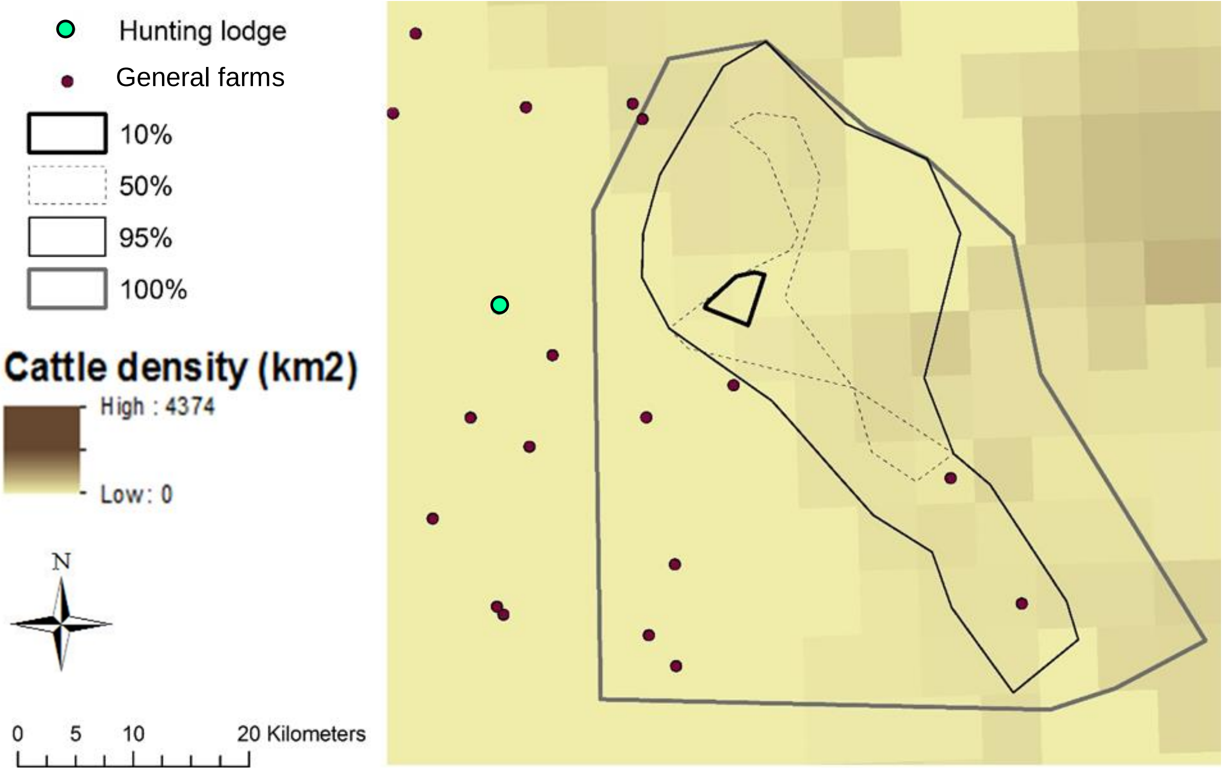

Figure 3.4c. The Waterberg pack's 10%, 50%, 95% and 100% home range isopleths as local convex hull (LoCoH) polygons created from density isopleths in relation to farms, hunting lodges and cattle density per km^2. Cattle density was downloaded and modified as a raster file from Food and Agriculture Organisation (FAO) of the United Nations.

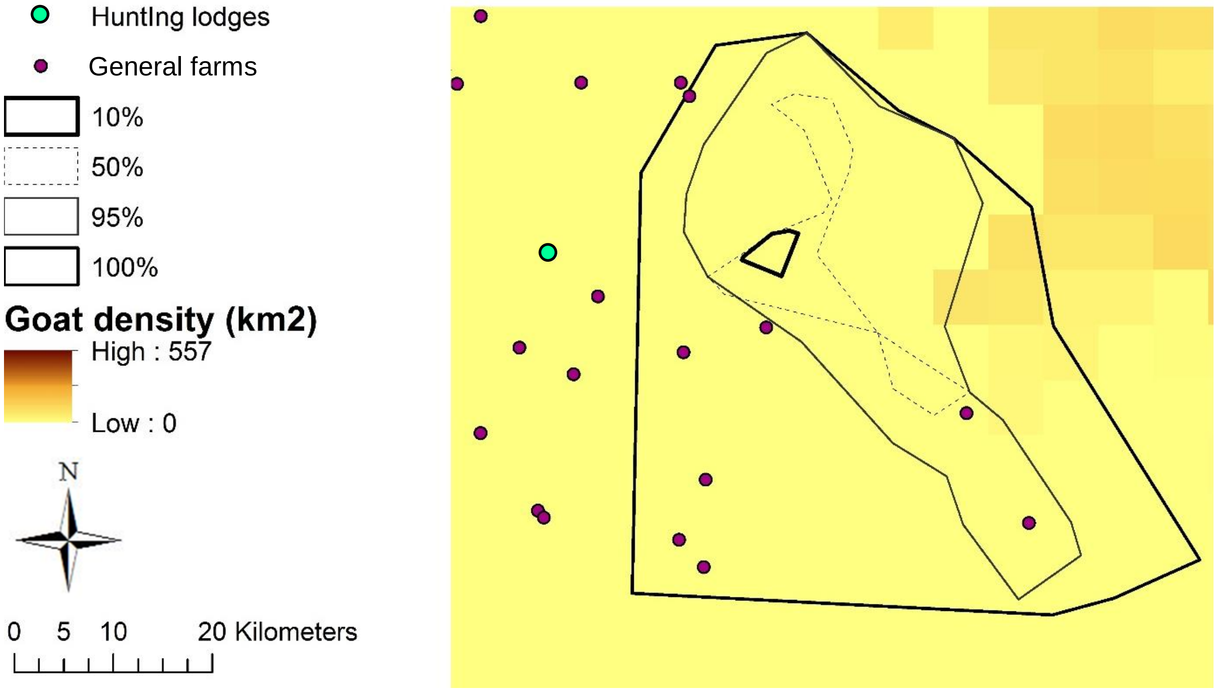

Figure 3.4d. The Waterberg pack's 10%, 50%, 95% and 100% home range isopleths as local convex hull (LoCoH) polygons created from density isopleths in relation to farms, hunting lodges and goat density per km^2. Goat density was downloaded and modified as a raster file from Food and Agriculture Organisation (FAO) of the United Nations.

The Skukuza 100% home range did not overlap a farm outside the border of Kruger, although the 100% isopleth did overlap with areas of moderate cattle density (Figure 3.4e).

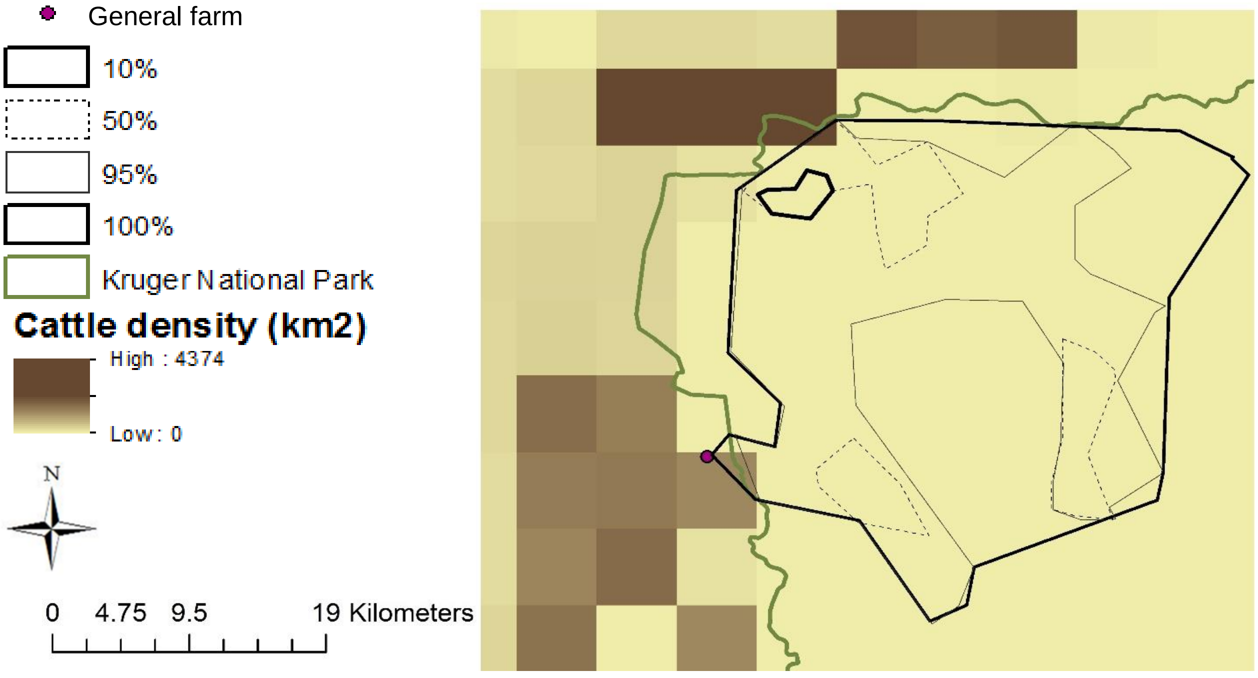

Figure 3.4e. The Skukuza pack's 10%, 50%, 95% and 100% home range isopleths as local convex hull (LoCoH) polygons created from density isopleths in relation to a general farm and cattle density per km^2. The zoomed in area shows that the 100% home range does not overlap with the farm. Cattle density was downloaded and modified as a raster file from Food and Agriculture Organisation (FAO) of the United Nations. Due to the nature of a raster file (square pixels), some cattle densities may appear to occur within the borders of Kruger, which is not the case (see inset).

The Skukuza pack's 100% home range did not overlap any areas containing high densities of goats, with higher goat densities occurring only to the North of the pack's location (Figure 3.4f).

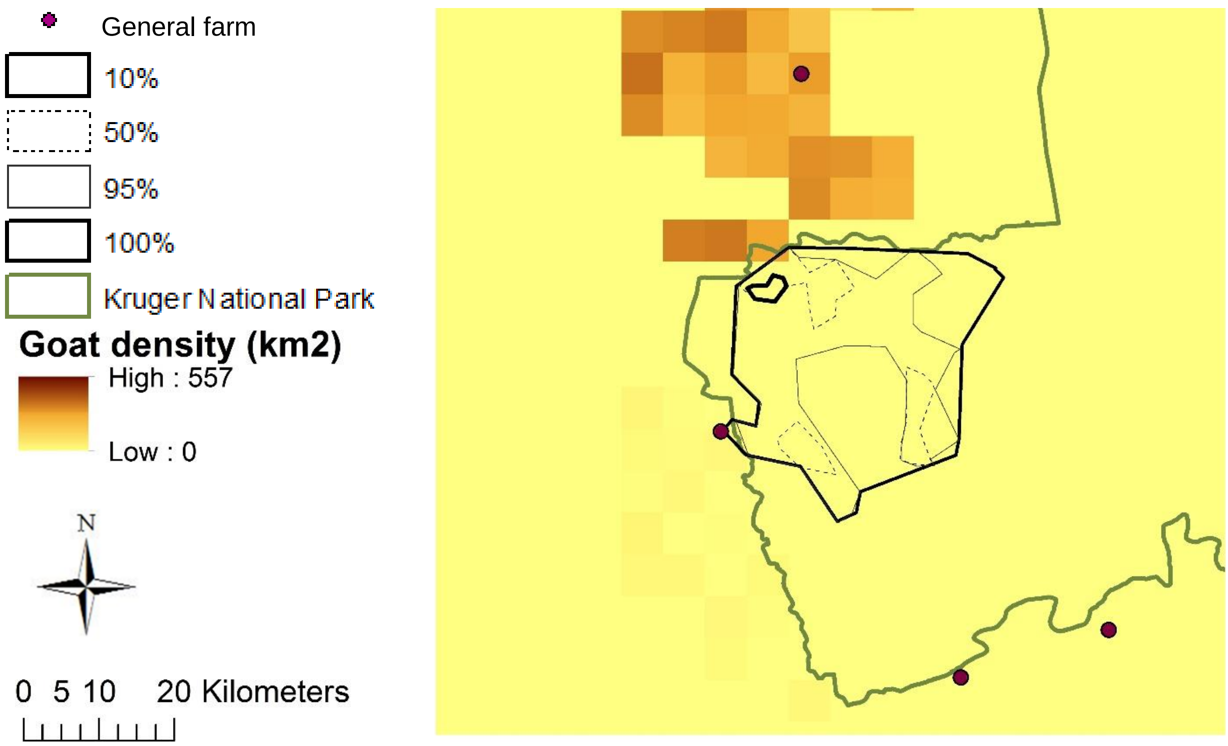

Figure 3.4f. The Skukuza pack's 10%, 50%, 95% and 100% home range isopleths as local convex hull (LoCoH) polygons created from density isopleths in relation to farms, hunting lodges and goat density per km^2. Goat density was downloaded and modified as a raster file from Food and Agriculture Organisation (FAO) of the United Nations. Due to the nature of a raster file (square pixels), some goat densities may appear to occur within the borders of Kruger, although these areas of overlap are false data for that section, and will be ignored.

The Bluebank pack's 100% home range overlapped areas that contained moderate to high densities of cattle, although the 95% home range only overlapped a small area of low to moderate cattle densities (Figure 3.4g). Three fruit farms fell within the 95% home range, with one also occurring within the boundaries of the 50% home range (Figure 3.4g). The pack's 10% home range overlapped an area of zero densities of cattle per km^2 (Figure 3.4g).

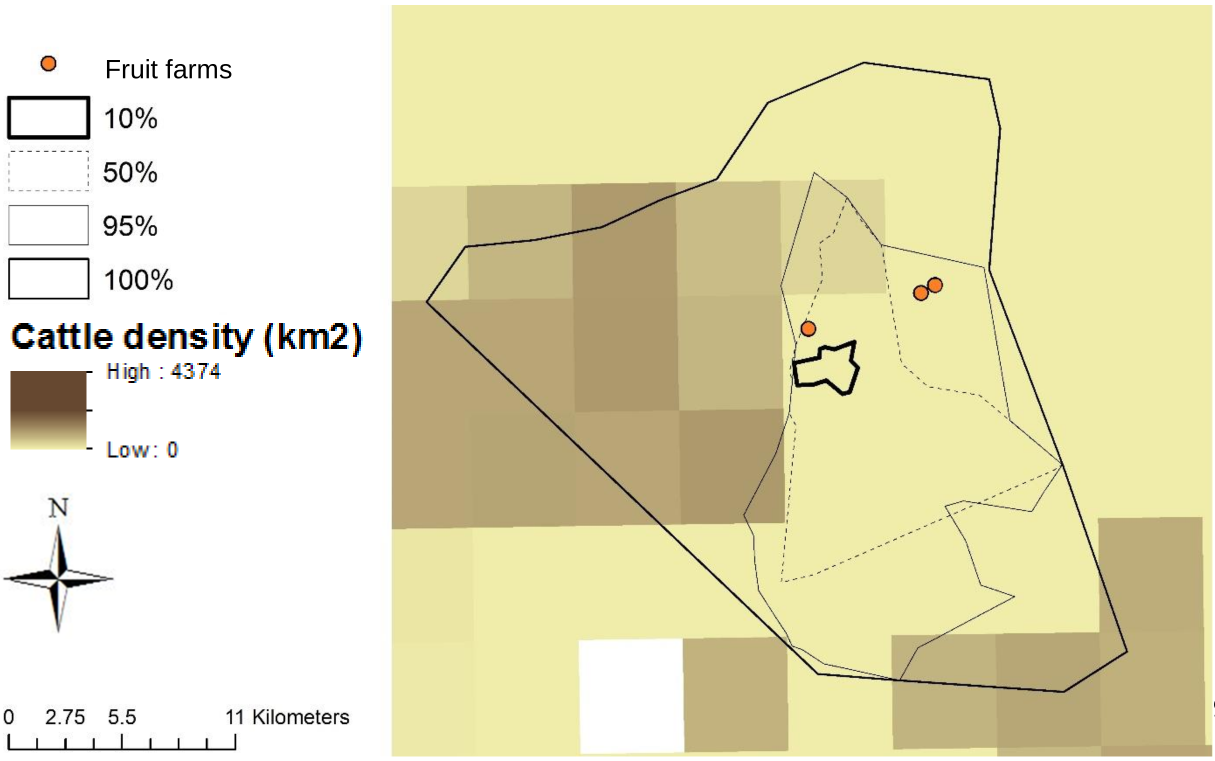

Figure 3.4g. The Bluebank pack's 10%, 50%, 95% and 100% home range isopleths as local convex hull (LoCoH) polygons created from density isopleths in relation to farms, hunting lodges and cattle density per km2. Cattle density was downloaded and modified as a raster

The Bluebank pack's 100% home range overlapped areas that contained moderate goat densities, but the 95% home range overlapped only areas of low goat densities (Figure3.4h). Again, the pack's 10% home range encompassed an area of zero densities of goats per km^2 (Figure 3.4h).

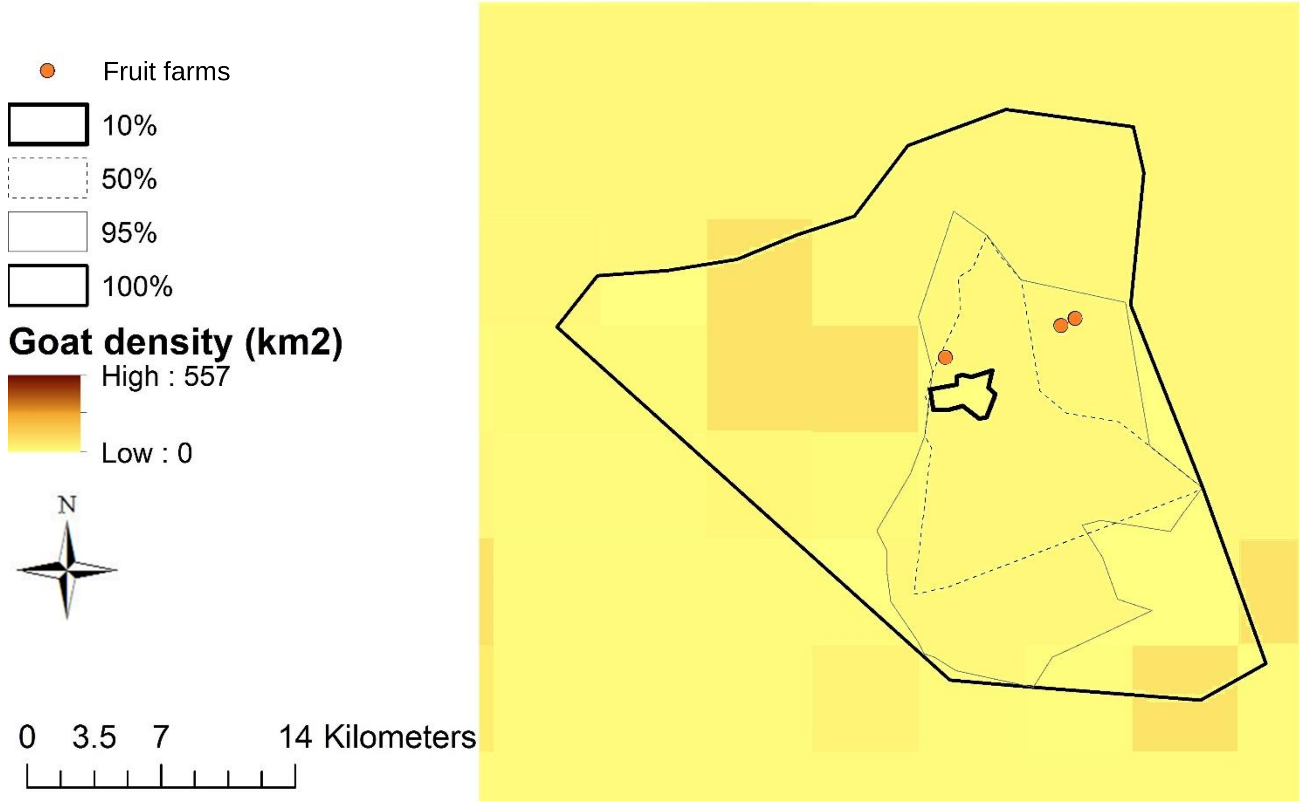

Figure 3.4h. Bluebank 10%, 50%, 95% and 100% home range isopleths as local convex hull (LoCoH) polygons created from density isopleths in relation to farms, hunting lodges and goat density per km2. Goat density was downloaded and modified as a raster file from Food and Agriculture Organisation (FAO) of the United Nations.

Resource selection

Out of the seven features tested, randomization test results identified five that were significant predictors of occurrence for all four wild dog packs, namely livestock density, roads, human land use, nature reserves and vegetation (Table 3.3). Agricultural landscape features were significant predictors of occurrence of the Waterberg, Orpen and Bluebank packs but not the Skukuza pack (Table 3.3). Rivers were a significant predictor of occurrence for the Orpen and Bluebank packs, but not the Waterberg or Skukuza packs (Table 3.3).

Table 3.3. Results of randomization tests and mean differences in distance to environmental features tested for the Waterberg, Skukuza, Orpen and Bluebank wild dog packs. Significant values are shown in bold and values that show a trend toward significance are indicated with an asterisk. Features marked with † indicate possible sources of mortality for wild dogs.

	Waterberg		Skukuza		Orpen		Bluebank	
Feature	Mean difference	Randomization test p-value	Mean difference	Randomization test p-value	Mean difference	Randomization test p-value	Mean difference	Randomization test p-value
Agricultural landscape features †	4.520	**<0.0001**	0.132	0.841	34.283	**<0.0001**	8.053	**<0.0001**
Livestock density †	8.227	**<0.0001**	22.294	**<0.0001**	0.828	**<0.0001**	4.866	**<0.0001**
Roads †	1.814	**<0.0001**	7.876	**<0.0001**	0.413	**0.011**	0.515	**<0.0001**
Human land use	5.205	**<0.0001**	1.207	**0.011**	0.809	**0.009**	5.360	**<0.0001**
Nature reserves	2.425	**<0.0001**	5.613	**<0.0001**	1.331	**0.006**	3.169	**<0.0001**
Rivers	0.277	0.088 *	0.221	0.054 *	7.876	**<0.0001**	7.880	**<0.0001**
Vegetation	0.436	**0.001**	0.217	**0.001**	0.744	**0.001**	0.035	**0.001**

Anthropogenic landscape features

Agricultural features

The Waterberg pack occurred significantly closer to agricultural landscape features than were available in the environment (χ^2 (1) = 7.9.21, p < 0.001). The Waterberg pack occurred in closer proximity to general farms than hunting lodges (χ^2 (2) = 335.14, p < 0.001) (Figure 3.5a). Occurrences at the goat farms were low. Distances to agricultural landscape features for presence data were closer during summer than spring or autumn data (χ^2 (2) = 95.98, p = 0.009) (Figure 3.5b).

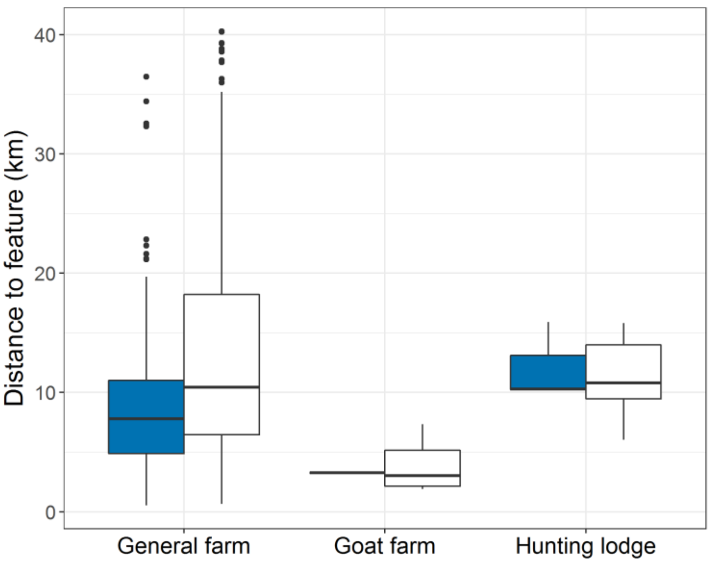

Figure 3.5a. The Waterberg wild dog pack's distance of occurrence (km) and available distances from different agricultural features in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes. Lines without boxes indicate low occurrence at features.

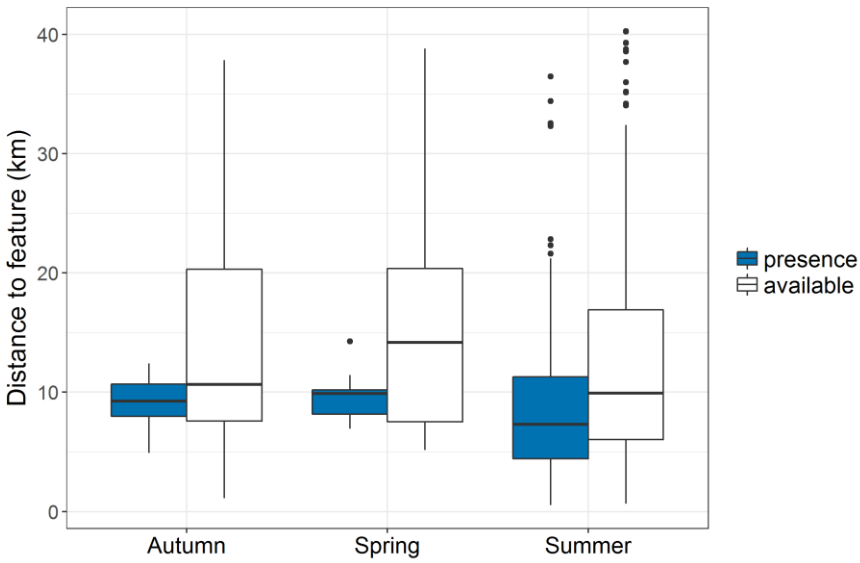

Figure 3.5b. Seasonal differences in the Waterberg wild dog pack's distance of occurrence (km) and available distances from different farm types in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Waterberg pack's odds of occurrence at agricultural landscape features were greatest for farms, with equal odds of occurrence or non-occurrence at hunting lodges (Figure 3.5c). The odds of wild dog pack occurrence at the goat farm was low (Figure 3.5c).

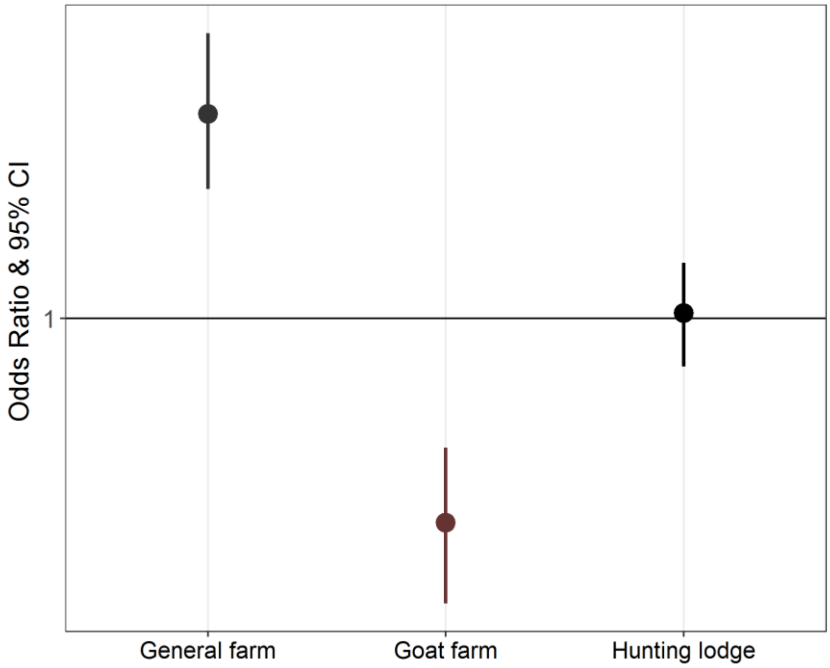

Figure 3.5c. Odds (± 95% CI) of the Waterberg wild dog pack's occurrence based on distances, at different agricultural landscape features in Limpopo Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

The Skukuza pack occurred in different proximities to agricultural landscape features than were available (χ^2 (1) = 7.03, p = 0.008). The Skukuza pack occurred further away from the poultry farm than the general farms (χ^2 (11) = 158.71, p < 0.001), with the pack occurring >10 km from general farms and > 20 km from poultry farms (Figure 3.6a). Skukuza pack presence at agricultural landscape features differed during the spring and summer (χ^2 (1) = 134, p < 0.001), occurring further away from features during summer than spring (Figure 3.6b)

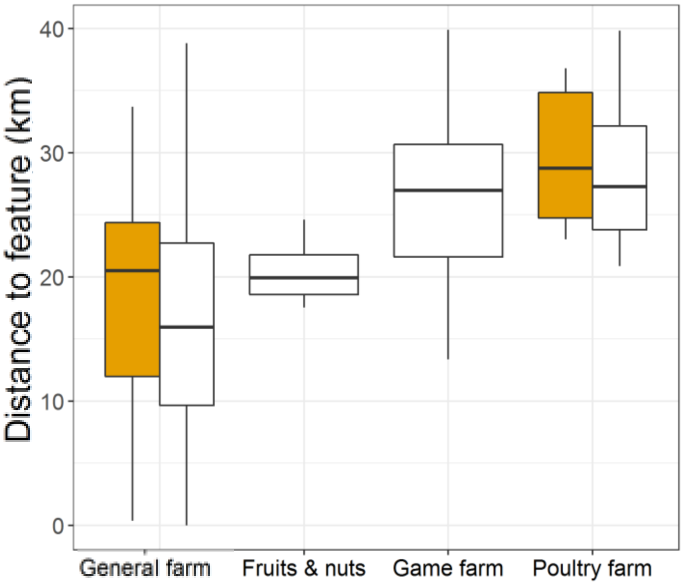

Figure 3.6a. The Skukuza wild dog pack's distance of occurrence (km) and available distances from different agricultural features in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

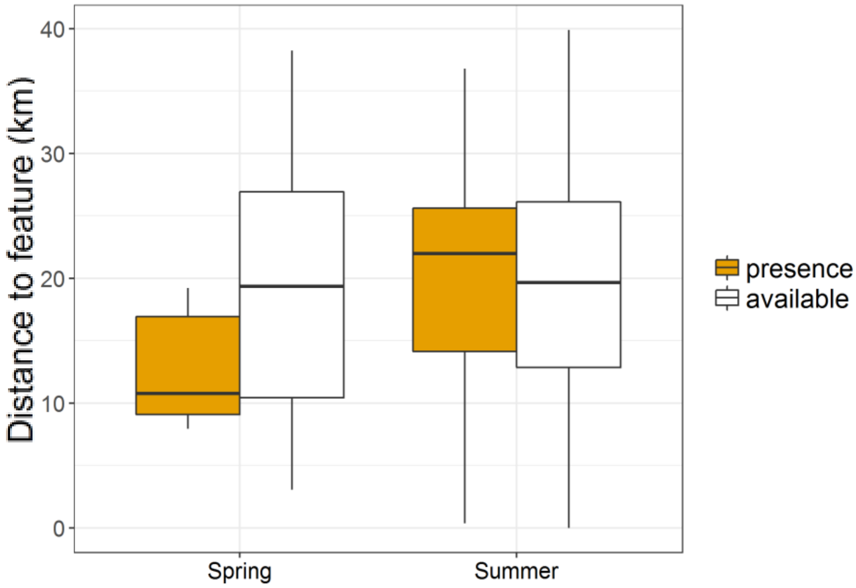

Figure 3.6b. Seasonal differences in the Skukuza wild dog pack's distance of occurrence (km) and available distances from different agricultural features in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Skukuza pack's odds of occurrence were greatest at agricultural landscape features for poultry and game farms and lower for fruit and nut farms and general farms (Figure 3.6c).

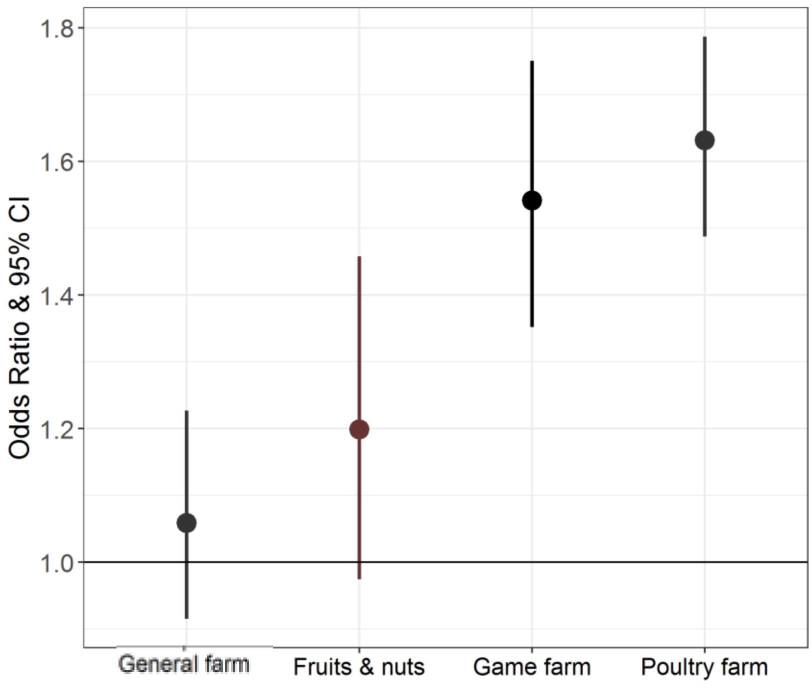

Figure 3.6c. Odds (± 95% CI) of the Skukuza wild dog pack's occurrence based on distances, at different agricultural landscape features in Mpumalanga Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

The Orpen wild dog pack occurred significantly further away from agricultural landscape features than were available in the environment (χ^2 (1) = 1720.06, p < 0.001), with available data indicating possible occurrence at distances > 5 km, and presence data indicating occurrence at distances > 40 km (Figure

3.7a). Similarly, the pack occurred significantly further away from poultry farms than fruit farms (χ^2 (3) = 56.36, p < 0.001). Orpen pack presence differed at agricultural landscape features during seasons (χ^2 (2) = 49.97, p < 0.001), occurring further away during winter (> 40 km) and closer during summer (> 20 km) (Figure 3.7b).

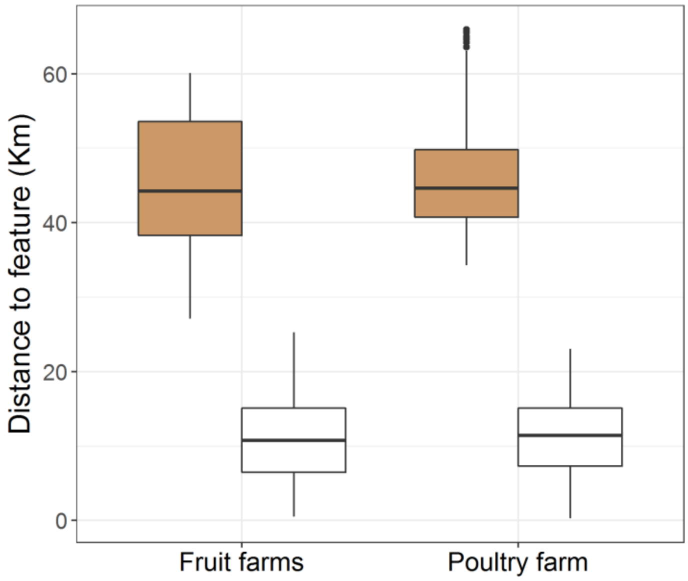

Figure 3.7a. The Orpen wild dog pack's distance of occurrence (km) and available distances from different agricultural features in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

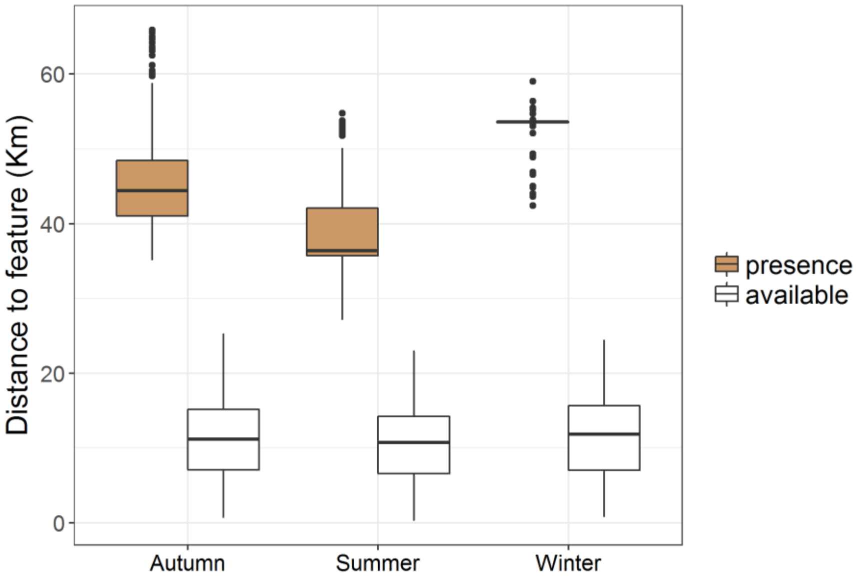

Figure 3.7b. Seasonal differences in the Orpen wild dog pack's distance of occurrence (km) and available distances from different agricultural features in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

Orpen pack odds of occurrence at agricultural landscape features were greatest at poultry farms, but were low at fruit farms (Figure 3.7c.).

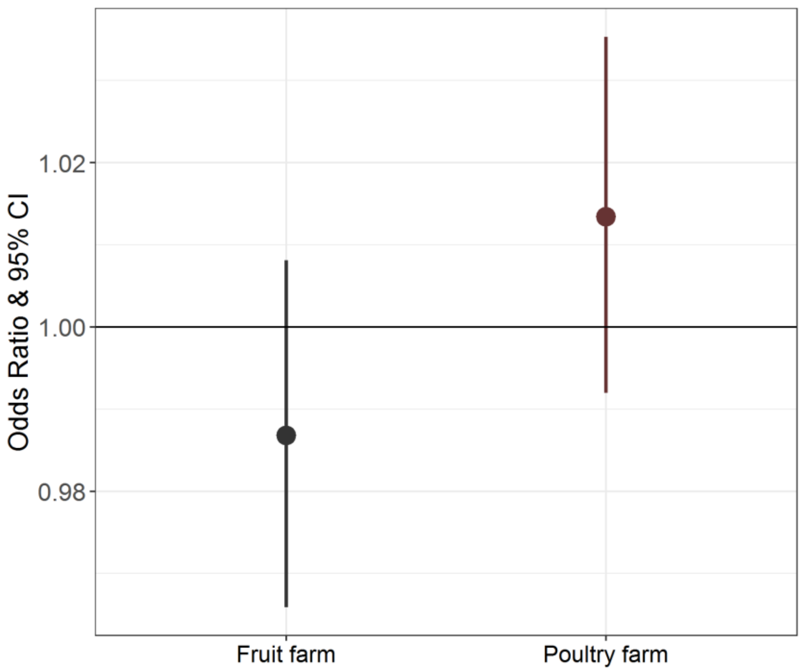

Figure 3.7c. Odds (± 95% CI) of the Orpen wild dog pack's occurrence based on distances, at different agricultural landscape feature, namely fruit farms and poultry farms s in Mpumalanga Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

The Bluebank wild dog pack occurred in closer proximity to fruit farms compared to available data (χ^2 (1) = 1485.29, p < 0.001). Presence at features differed (χ^2 (3) = 100.73, p < 0.001) with no pack occurrence close to game farms (Figure 3.8a). Bluebank pack occurrence was closer to fruit farms for all seasons compared to available data (χ^2 (3) = 100.73, p < 0.001), especially in autumn (Figure 3.8b).

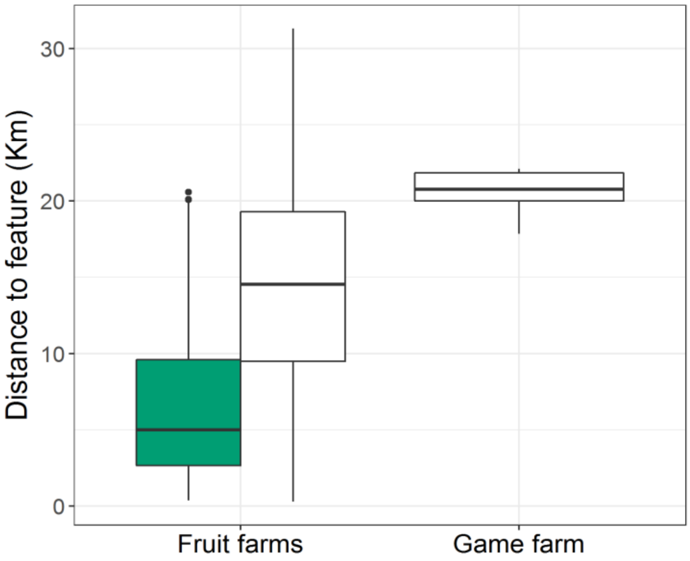

Figure 3.8a. The Bluebank wild dog pack's distance of occurrence (km) and available distances from different agricultural features in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

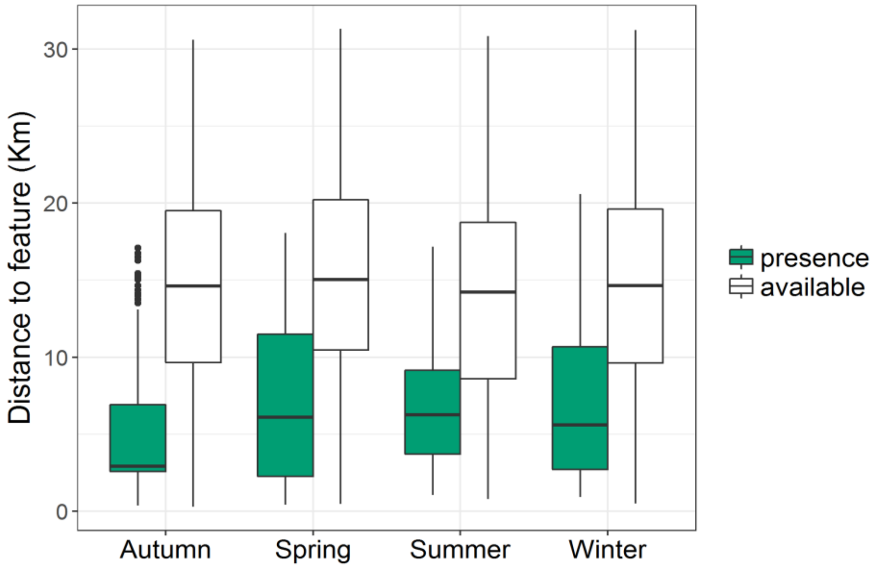

Figure 3.8b. Seasonal differences in the Bluebank wild dog pack's distance of occurrence (km) and available distances from different agricultural features in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Bluebank pack's odds of occurrence at different agricultural landscape features were high for game farms and low for fruit farms (Figure 3.8c)

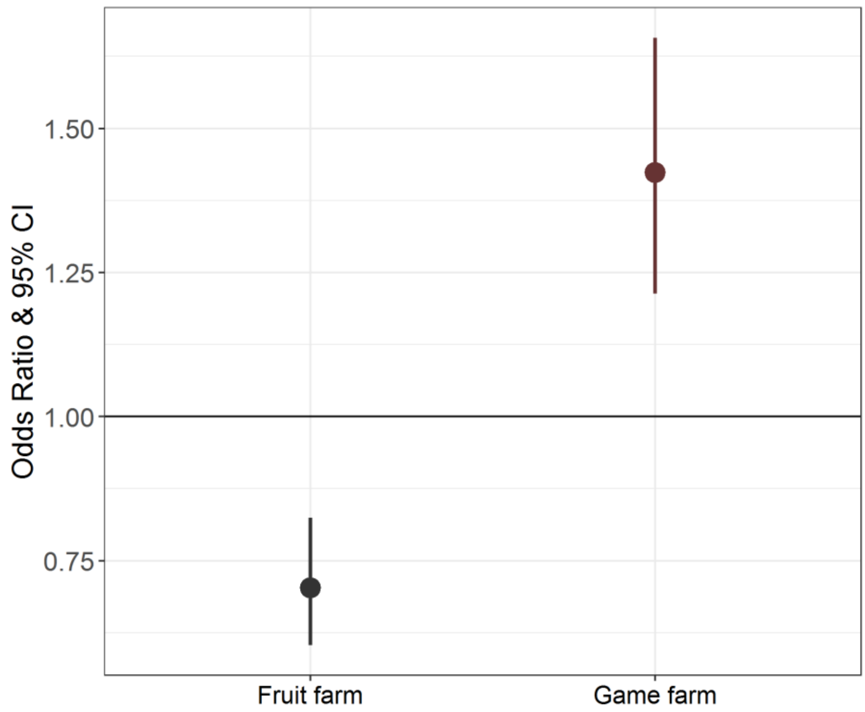

Figure 3.8c. Odds (± 95% CI) of the Bluebank wild dog pack's occurrence based on distances, at different agricultural landscape features, namely fruit farms and game farms in Limpopo Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

Livestock density

Livestock density was a significant predictor of wild dog pack occurrence. The Waterberg pack occurred in areas of lower livestock density (km^2) than were available in the environment (χ^2 (1) = 132.25, p < 0.001). Wild dog presence was higher near areas of higher poultry densities than goat or cattle densities (χ^2 (2) = 702.92, p < 0.001) (Figure 3.9a). There was no difference between presence and available data for livestock densities during different seasons (χ^2 (2) = 2.58, p = 0.275) (Figure 3.9b).

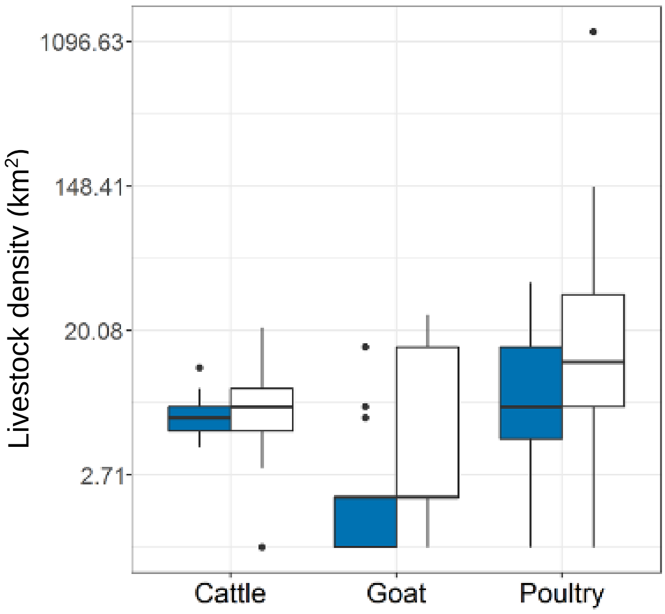

Figure 3.9a. The Waterberg wild dog pack's presence and available data in areas of differing livestock type (cattle, goats and poultry) densities (per km^2) in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

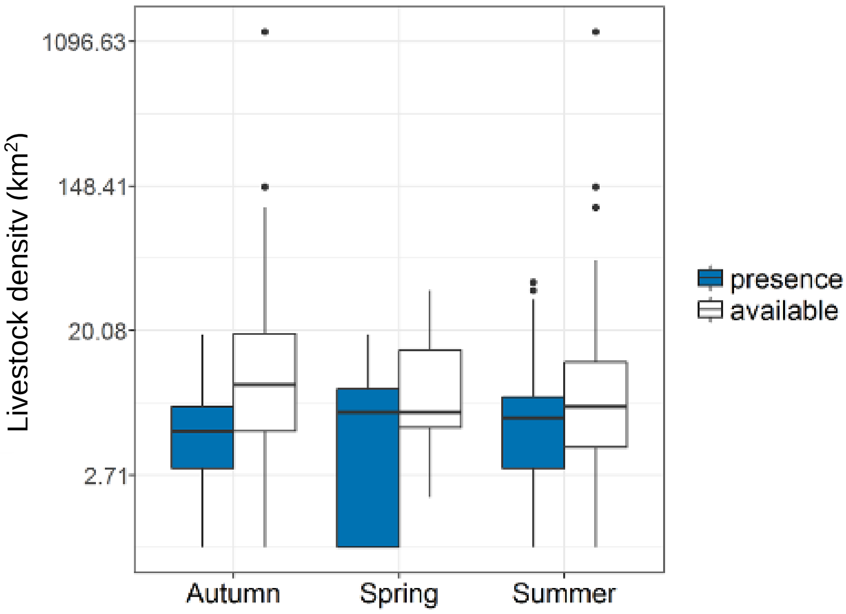

Figure 3.9b. Seasonal differences in the Waterberg wild dog pack's occurrence and available data in areas of differing livestock type (cattle, goats and poultry) densities (per km^2) in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Waterberg wild dog pack's odds of occurrence in areas of different livestock densities were high for areas that housed cattle, and lower for areas that housed poultry (Figure 3.9c). The odds of occurrence were low in areas that contained goats (Figure 3.9c).

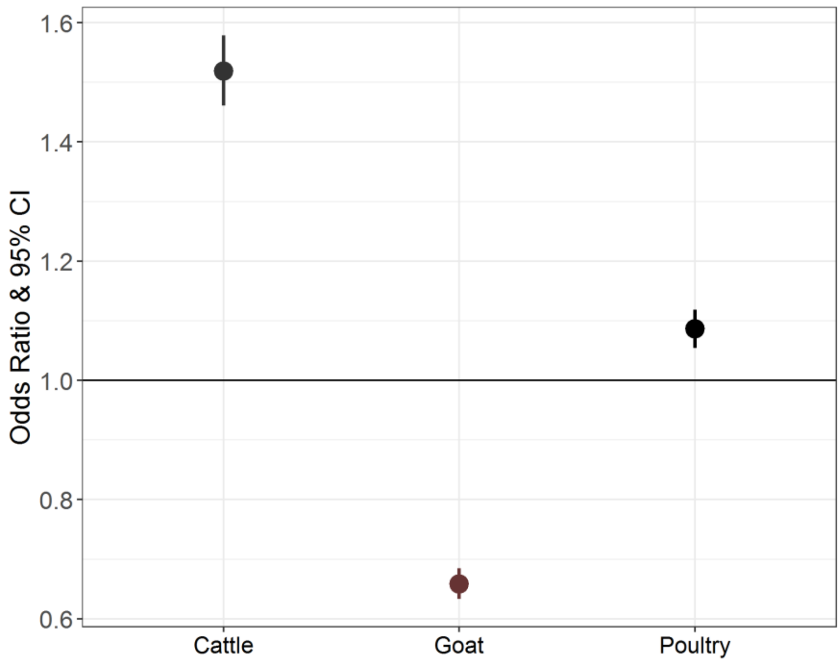

Figure 3.9c. Odds (± 95% CI) of the Waterberg wild dog pack's occurrence in areas of different livestock type (cattle, goats and poultry) densities (per km^2), Limpopo Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

Presence and available data for livestock densities for the Skukuza wild dog pack showed a trend toward significance (χ^2 (1) = 3.71, p = 0.054). Similarly, there was no difference of occurrence for the Skukuza pack near areas housing cattle, goats or poultry (χ^2 (2) = 1.69, p = 0.428) (Figure 3.10a). Pack presence in livestock areas also did not differ significantly between different seasons (χ^2 (1) = 0.41, p = 0.519) (Figure 3.10b).

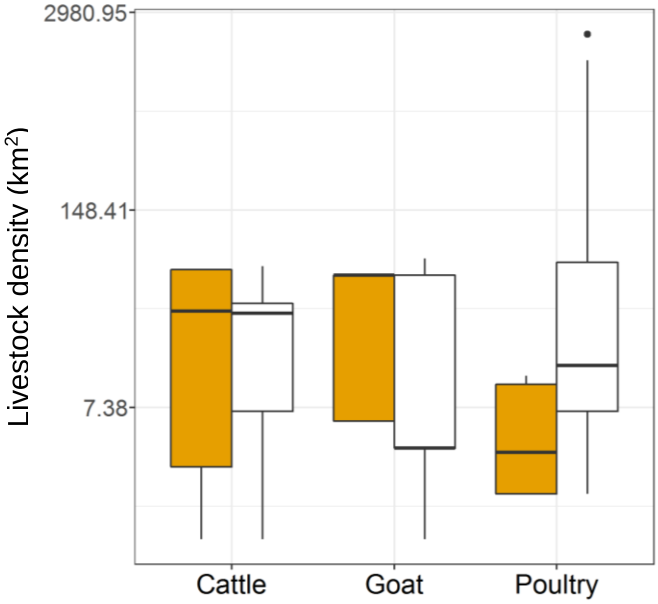

Figure 3.10a. The Skukuza wild dog pack's presence and available data in areas of differing livestock type (cattle, goats and poultry) densities (per km^2) in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

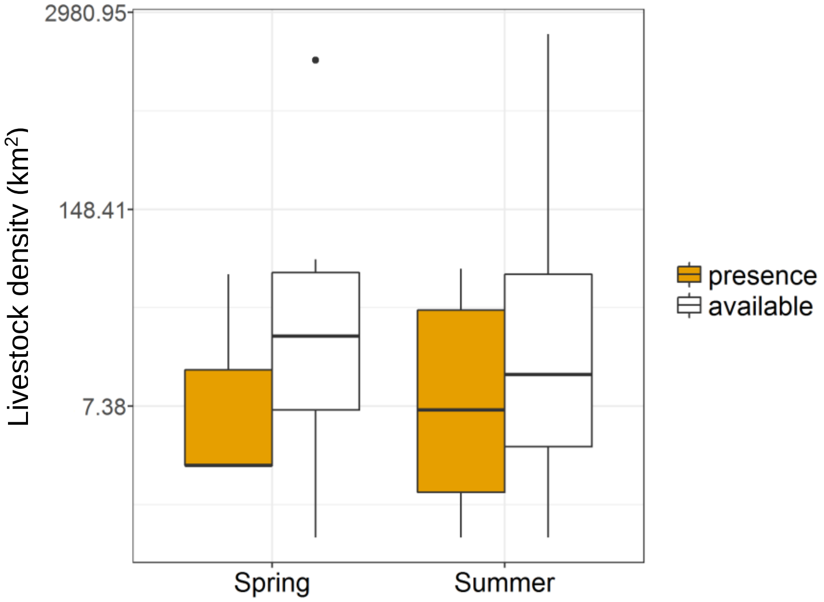

Figure 3.10b. Seasonal differences in the Skukuza wild dog pack's occurrence and available data in areas of differing livestock type (cattle, goats and poultry) densities (per km^2) in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Skukuza pack's odds of occurrence in areas of different livestock type densities were highest in areas that contained cattle (Figure 3.10c). Odds of occurrence were low in areas containing poultry, and even lower in areas that contained goats (Figure 3.10c).

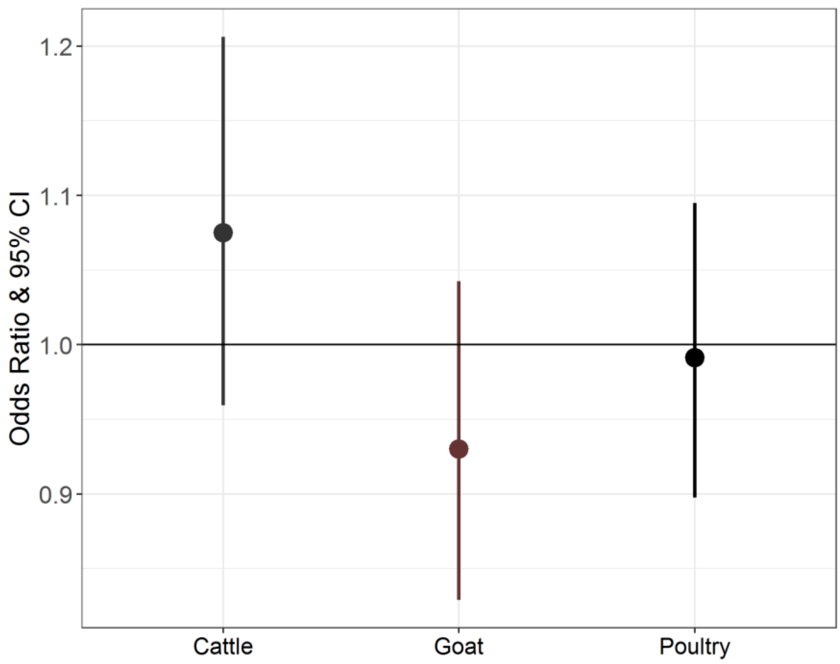

Figure 3.10c. Odds (± 95% CI) of the Skukuza wild dog pack's occurrence in areas of different livestock type (cattle, goats and poultry) densities (per km^2), Mpumalanga Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

No livestock density plots or ORs were available for the Orpen pack, as these wild dogs remained within the boundaries of the Timbavati reserve, and the occurrences outside of the borders were in areas of supposed zero livestock density.

The Bluebank wild dog pack occurred in areas of lower livestock density (km^2) than were available in the environment (χ^2 (1) = 13.64, p < 0.001). The pack occurred in areas of higher cattle densities than goat densities, but did not occur in areas of containing poultry (χ^2 (2) = 356.49, p < 0.001) (Figure 3.11a). There was significant influence of season (χ^2 (3) = 8.17, p = 0.042), with packs occurring in areas of higher livestock densities in autumn and winter than were available in the environment (Figure 3.11b).

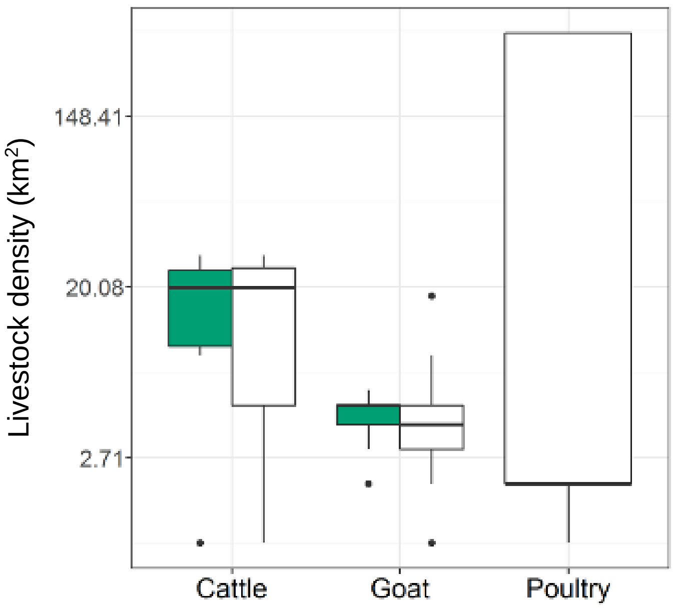

Figure 3.11a. The Bluebank wild dog pack's presence and available data in areas of differing livestock type (cattle, goats and poultry) densities (per km^2) in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

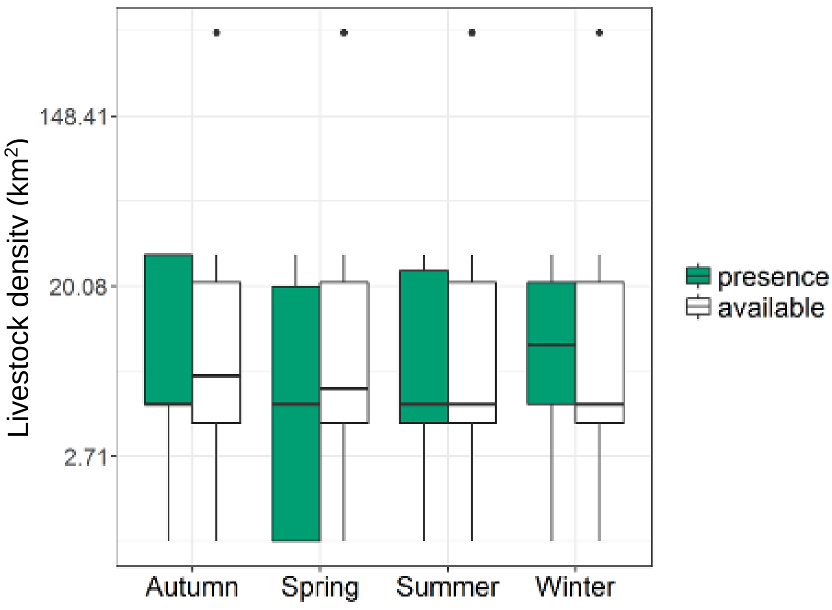

Figure 3.11b. Seasonal differences in the Bluebank wild dog pack's occurrence and available data in areas of differing livestock type (cattle, goats and poultry) densities (per km^2) in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

Odds of occurrence of the Bluebank pack in areas of different livestock type densities were highest in areas that contained cattle (Figure 3.11c). Odds of occurrence were lower in areas that contained poultry, and lowest in areas that contained goats (Figure 3.11c).

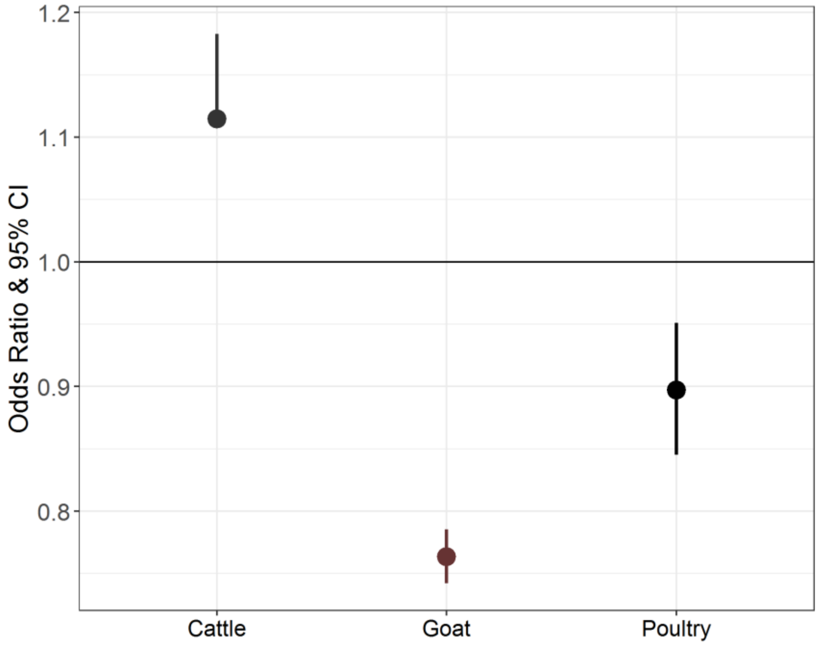

Figure 3.11c. Odds (± 95% CI) of the Bluebank wild dog pack's occurrence in areas of different livestock type (cattle, goats and poultry) densities (per km^2), Limpopo Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

Roads

The Waterberg pack occurred further from roads than were available in the environment (χ^2 (1) = 55.58, p < 0.001). There were no differences between the Waterberg pack's presence at different road types or availability of these road types in the environment (χ^2 (9) = 9.84, p = 0.363), with occurrences at > 9 km (Figure 3.12a). The pack occurred at road types differently during different seasons (χ^2 (2) = 30.07, p <0.0001), occurring further away from roads during autumn (> 9 km) and was closest to roads during summer (> 2 km) (Figure 3.12b).

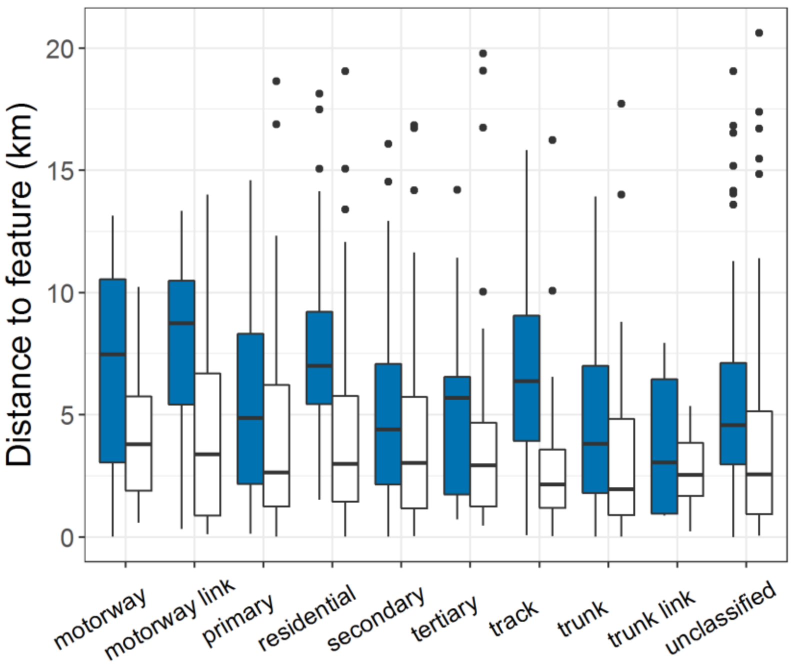

Figure 3.12a. The Waterberg wild dog pack's distance of occurrence (km) and available distances from different road types in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

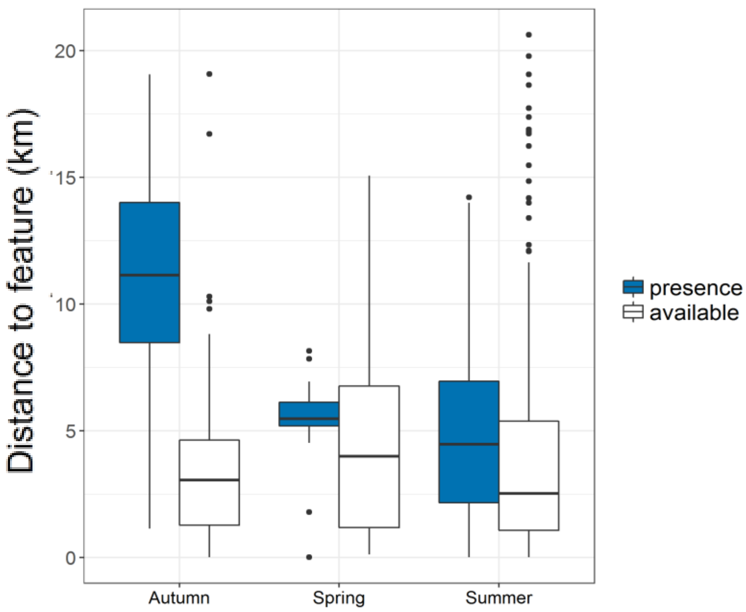

Figure 3.12b. Seasonal differences in the Waterberg wild dog pack's distance of occurrence (km) and available distances from different road types in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Waterberg pack's odds of occurrence on motorways and motorway links (both high-speed roads) were high, but were low on primary, trunk and trunk-link roads (Figure 3.12c). The odds of occurrence on residential roads (moderate-speed roads) were high, but odds of occurrence on secondary roads were low. The odds of occurrence on roads carrying slow-moving traffic (tertiary, track and unclassified) were low (Figure 3.12c).

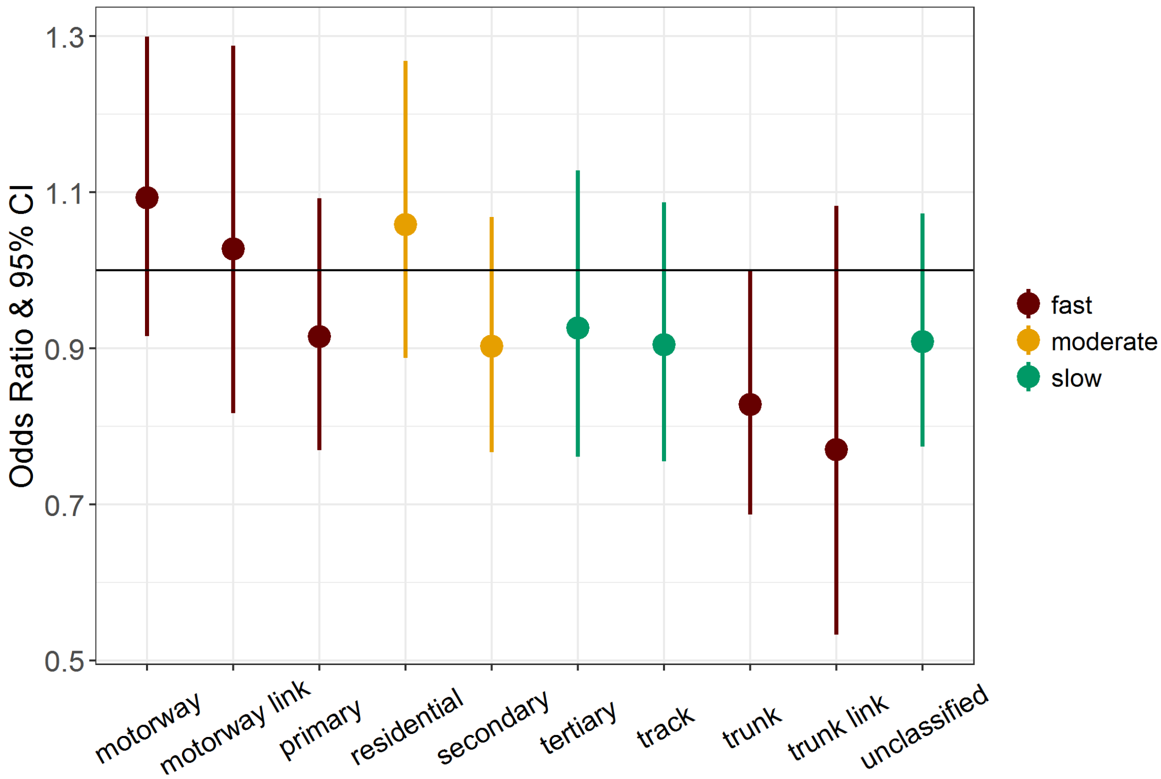

Figure 3.12c. Odds (± 95% CI) of the Waterberg wild dog pack's occurrence based on distances, at different road types in Limpopo Province, South Africa. Roads that carry fast-moving traffic (80- 120 km/h) are indicated in dark red, roads that carry moderate speed traffic (50-60 km/h) are indicated in orange and roads that carry slow-moving traffic (≤ 40 km/h) are indicated in green. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance

The Skukuza pack occurred significantly closer to roads within Kruger National Park than available in the environment (χ^2 (1) = 47.03, p <0.0001), occurring at distances < 5km (Figure 3.13a). The pack occurred different distances to different road types (χ^2 (4) = 36.51 p < 0.001), occurring jointly closer to secondary and unclassified roads (> 1 km) than tertiary or track roads (Figure 3.13a). The pack also occurred different distances to roads during different seasons (χ^2 (1) = 8.60 p =0.003), occurring closer to roads during summer than spring (Figure 3.13b)

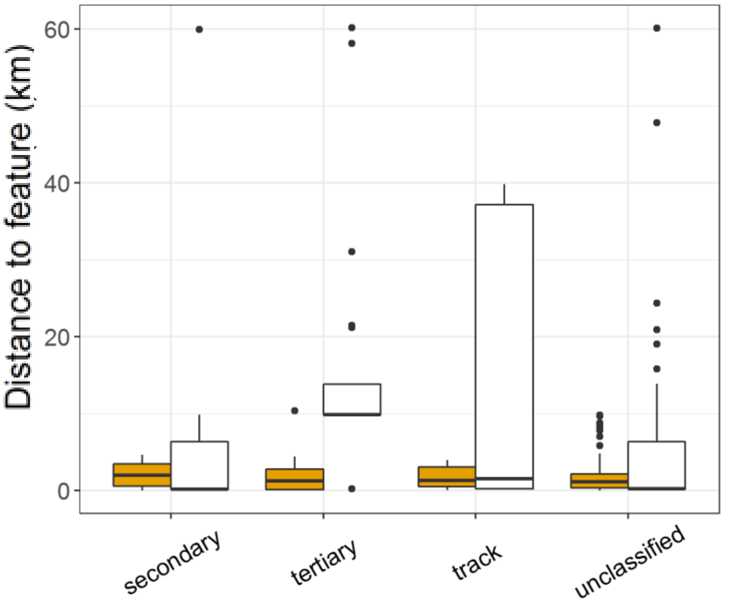

Figure 3.13a. The Skukuza wild dog pack's distance of occurrence (km) and available distances from different road types in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

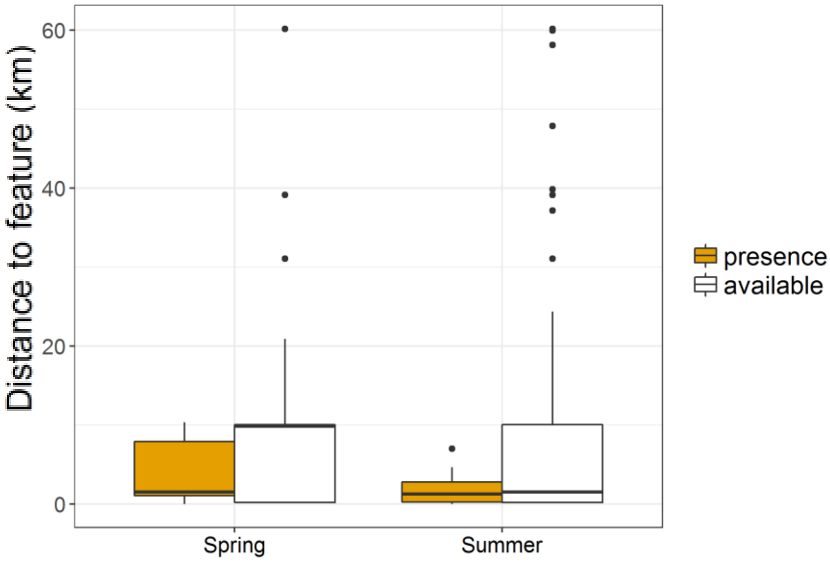

Figure 3.13b. Seasonal differences in the Skukuza wild dog pack's distance of occurrence (km) and available distances from different road types in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Skukuza pack's odds of occurrence on roads that carry slow-moving traffic (tertiary and track) were high, but odds of occurrence or non-occurrence on unclassified roads were equal (Figure 3.13c). The odds of occurrence on moderate speed roads (secondary) were low (Figure 3.13c).

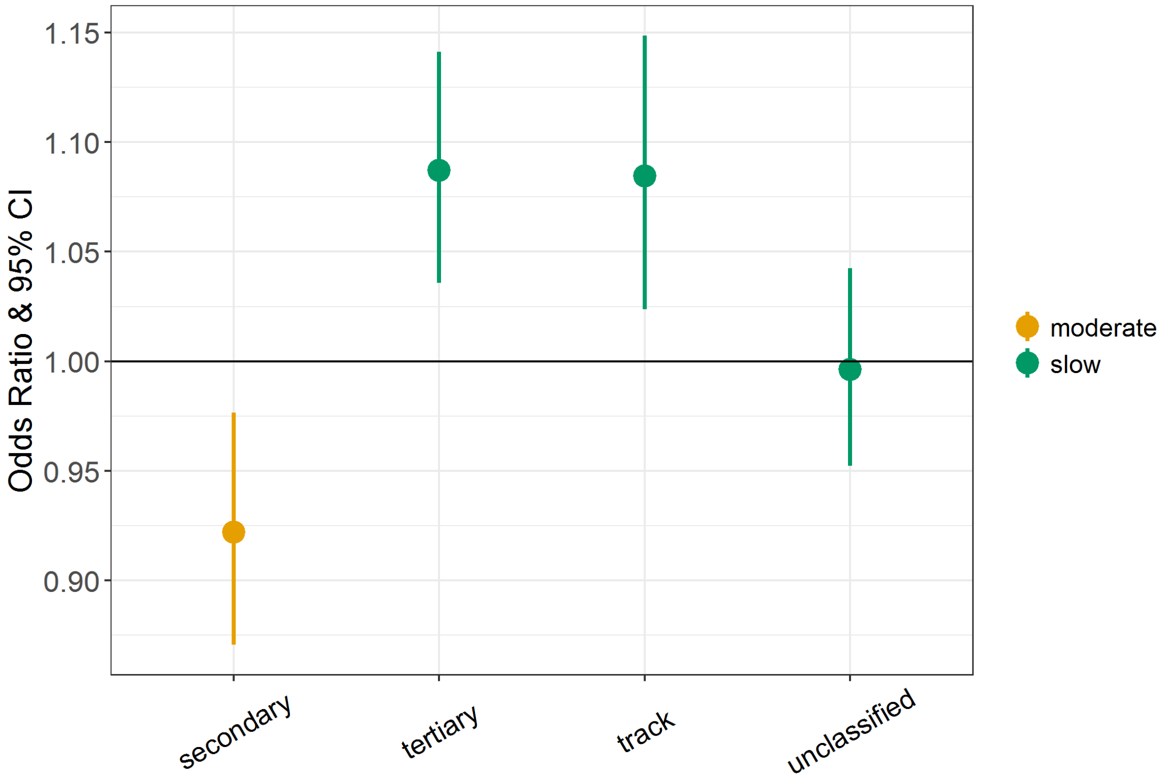

Figure 3.13c. Odds (± 95% CI) of the Skukuza wild dog pack's occurrence based on distances, at different road types in Mpumalanga Province, South Africa. Roads that carry moderate speed traffic (50-60 km/h) are indicated in orange and roads that carry slow-moving traffic (≤ 40 km/h) are indicated in green. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

There was no difference between available and presence data on roads for the Orpen pack (χ^2 (1) = 0.33 p =0.566), but this pack showed a trend for the types of roads utilised (χ^2 (9) = 16.04, p =0.066). The wild dogs showed equal presence at secondary, track and unclassified roads, although they may have shown greater presence at unclassified roads (Figure 3.14a). The pack occurred at roads at different distances during different seasons (χ^2 (2) = 183.42, p <0.001), being closer to roads in summer than autumn or winter (Figure 3.14b).

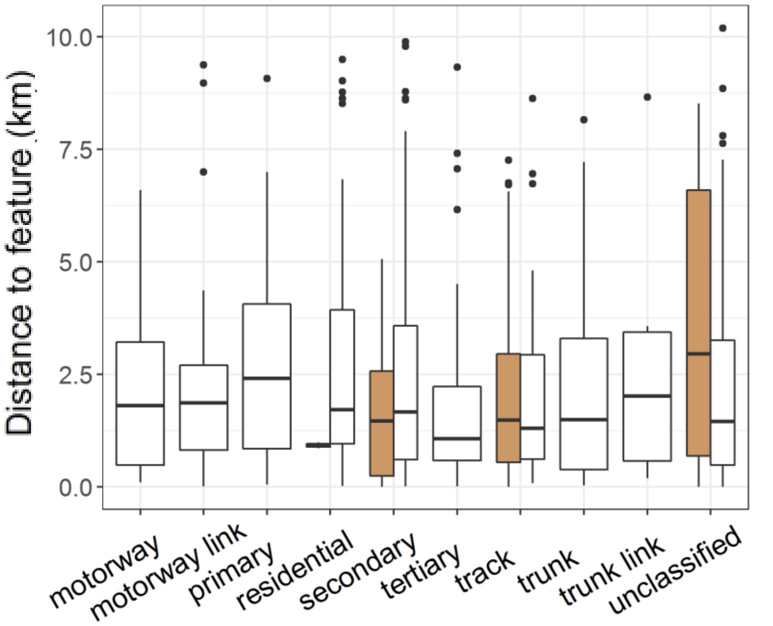

Figure 3.14a. The Orpen wild dog pack's distance of occurrence (km) and available distances from different road types in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

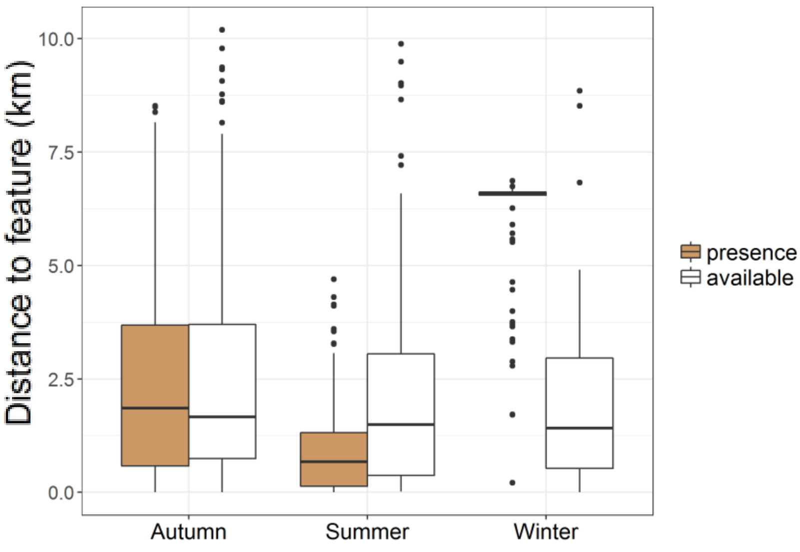

Figure 3.13b. Seasonal differences in the Orpen wild dog pack's distance of occurrence (km) and available distances from different road types in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Orpen wild dog pack's odds of occurrence were high on all roads carrying fast-moving traffic (motorway, motorway link, primary and trunk link), except for trunk roads (Figure 3.14c). Odds of occurrence for moderate-speed roads were high on residential road types, but were low secondary road types (Figure 3.14c). Pack occurrence on slow moving road types were low for tertiary and track roads, but high for unclassified roads (Figure 3.14c).

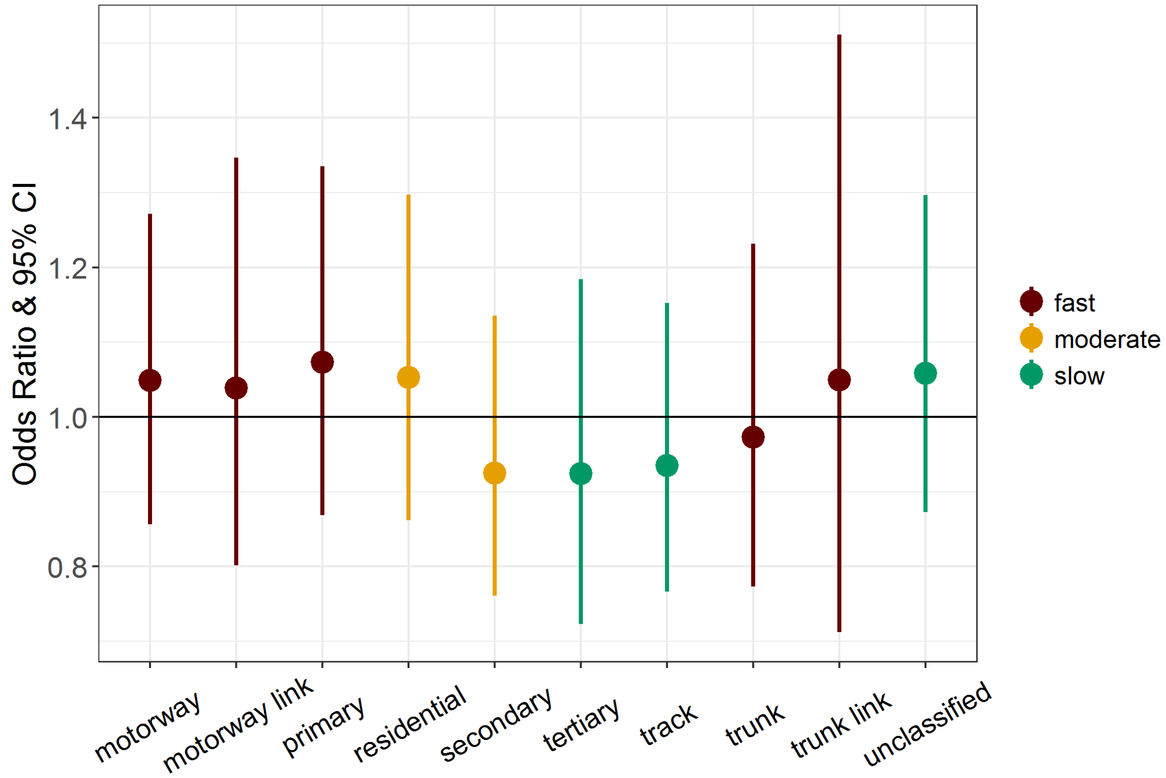

Figure 3.14c. Odds (± 95% CI) of the Orpen wild dog pack's occurrence based on distances, at different road types in Mpumalanga Province, South Africa. Roads that carry fast-moving traffic (80- 120 km/h) are indicated in dark red, roads that carry moderate speed traffic (50-60 km/h) are indicated in orange and roads that carry slow-moving traffic (≤ 40 km/h) are indicated in green. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

The Bluebank pack occurred significantly closer to roads than available in the environment (χ^2 (1) = 40.31, p < 0.001), although the pack did not occur closer to certain road types than others (χ^2 (10) = 16.61, p = 0.083), with presence to roads occurring at distances > 1 km (Figure 3.15a). The pack occurred significantly different distances to roads during different seasons (χ^2 (3) = 14.89, p = 0.001), occurring closer to roads during winter and autumn than spring or summer (Figure 3.15b).

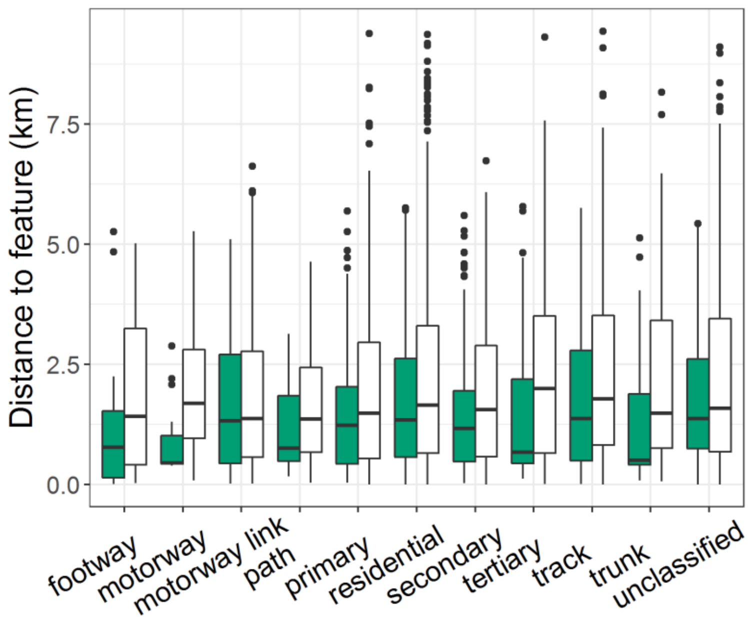

Figure 3.15a. The Bluebank wild dog pack's distance of occurrence (km) and available distances from different road types in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

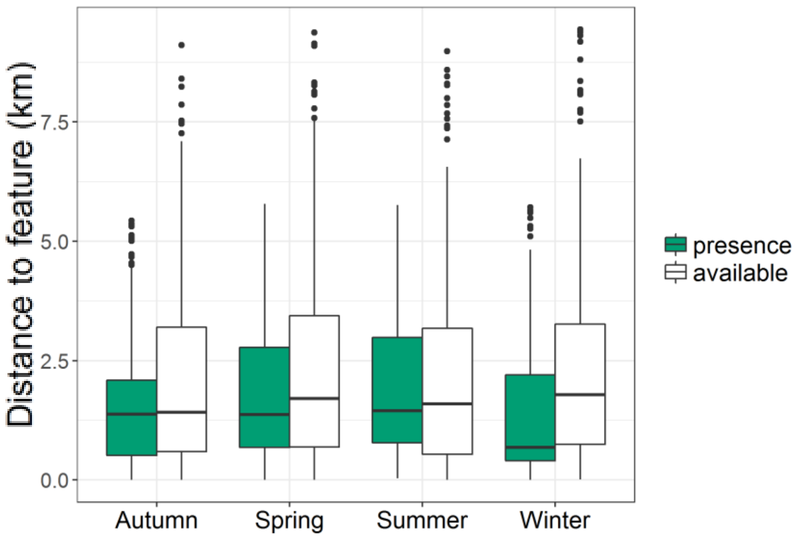

Figure 3.15b. Seasonal differences in the Bluebank wild dog pack's distance of occurrence (km) and available distances from different road types in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The odds of occurrence or non-occurrence for the Bluebank pack were equally likely for the motorway road type, but were high for all other high-speed road types (motorway link, primary and trunk) (Figure 3.15c). Odds of occurrence were high on moderate-speed road types (residential and secondary) and high for all slow-speed road types (path, tertiary, track and unclassified), except for footway road types (Figure 3.15c).

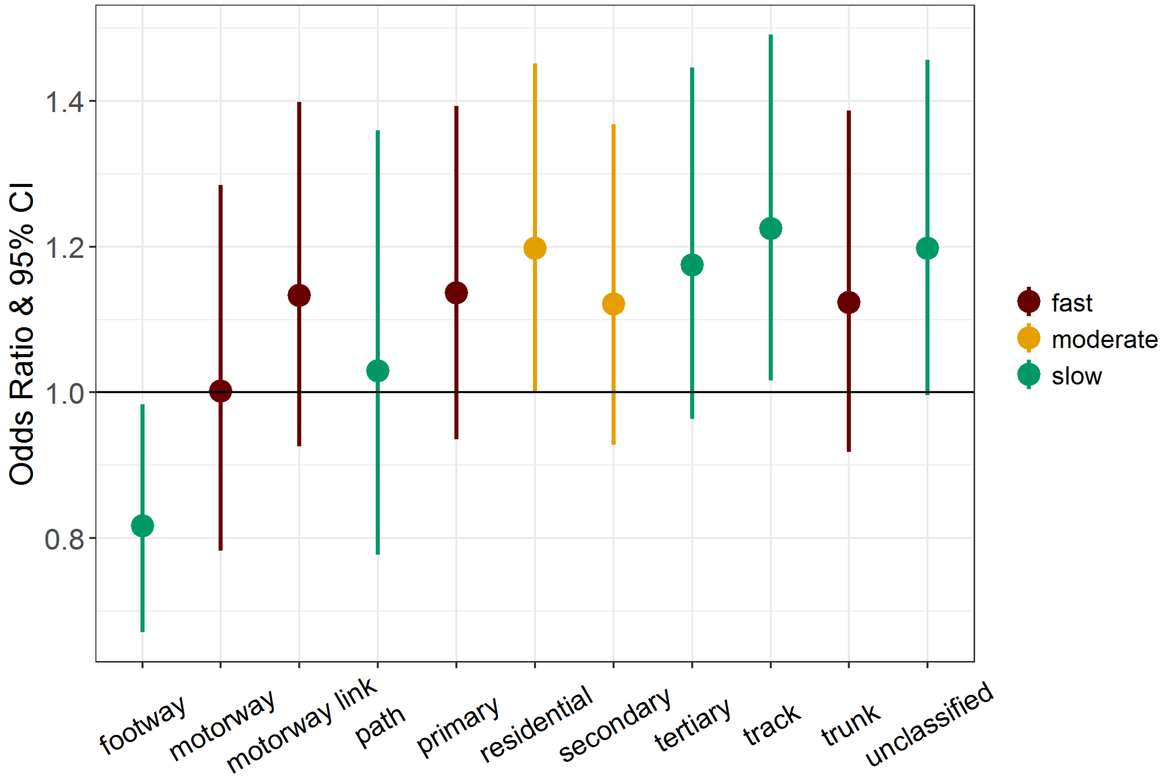

Figure 3.15c. Odds (± 95% CI) of the Bluebank wild dog pack'ss occurrence based on distances, at different road types in Limpopo Province, South Africa. Roads that carry fast-moving traffic (80- 120 km/h) are indicated in dark red, roads that carry moderate speed traffic (50-60 km/h) are indicated in orange and roads that carry slow-moving traffic (≤ 40 km/h) are indicated in green. OR= 1.0 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

Human land use

The Waterberg pack occurred significantly further away from human land use landscape features than were available in the environment (χ^2 (1) = 43.93, p < 0.001), although there was no difference between occurrence at different types of human land use features (χ^2 (14) = 21.87, p =0.081). Pack presence near features were further away during autumn than either spring or summer (χ^2 (2) = 20.40, p < 0.001).

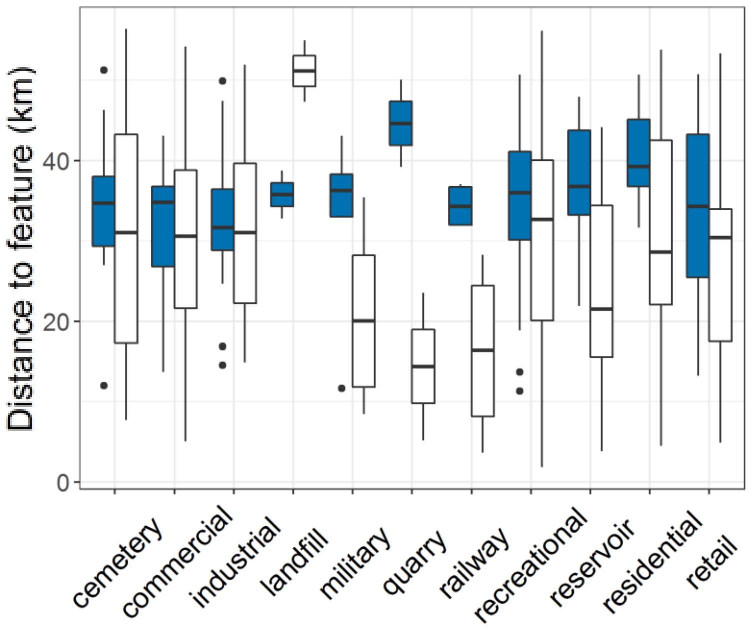

Figure 3.16a. The Waterberg wild dog pack's distance of occurrence (km) and available distances from different human land use types in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

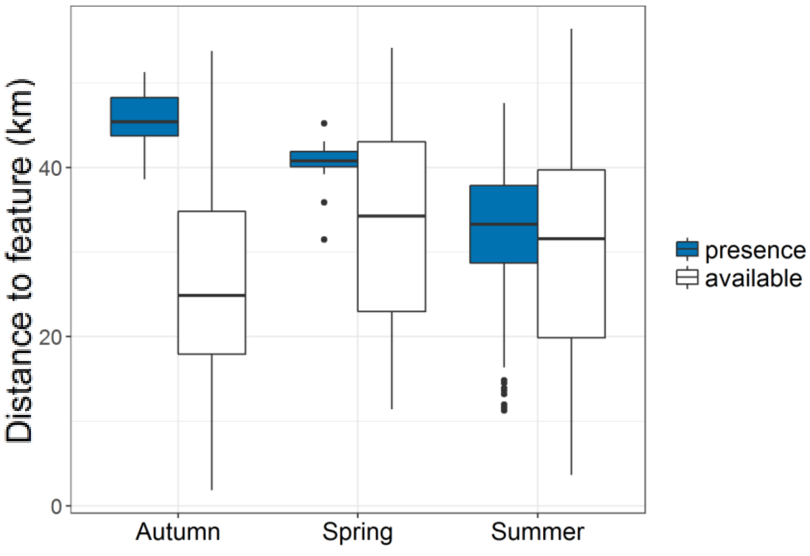

Figure 3.16b. Seasonal differences in the Waterberg wild dog pack's distance of occurrence (km) and available distances from different human land use types in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Waterberg pack's odds of occurrence or non-occurrence at human land use types were equal for industrial sites, and almost equal for cemetery, commercial, recreational and reservoir sites (Figure 3.16c). Odds of occurrence were high for landfill and residential sites, and low for military, quarry, railway and retail sites (Figure 3.16c).

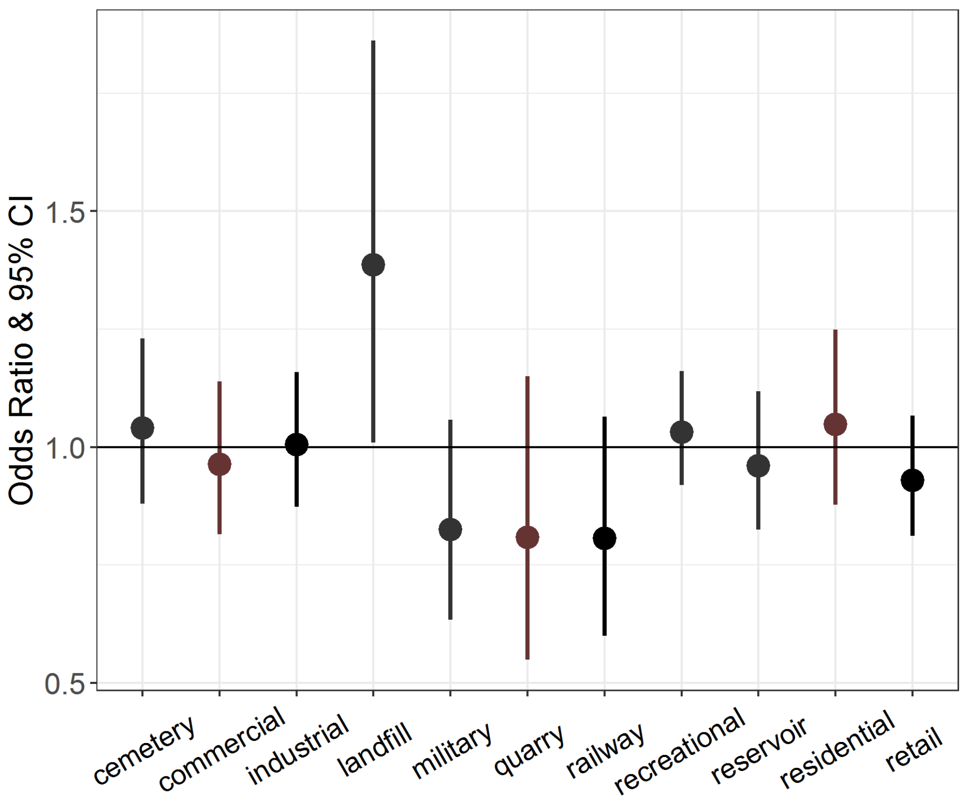

Figure 3.16c. Odds (± 95% CI) of the Waterberg wild dog pack's occurrence by distance, in areas of different human land use types, Limpopo Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

The Skukuza pack occurred significantly different distances away from human land use features that were available in the environment (χ^2 (1) = 14.79, p = 0.0001), although no differences existed between pack proximity to the different types of human land use features (χ^2 (14) = 18.57, p = 0.182) (Figure 3.17a). The pack remained further away from human land use features in both spring and summer (χ^2 (1) = 1.17, p = 0.278) (Figure 3.17b).

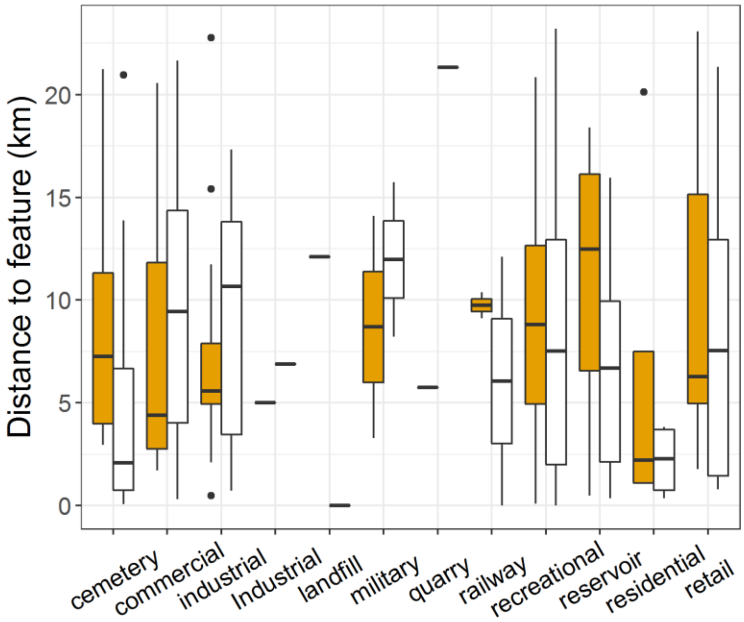

Figure 3.17a. The Skukuza wild dog pack's distance of occurrence (km) and available distances from different human land use types in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes. Lines without boxes indicate low occurrence at features.

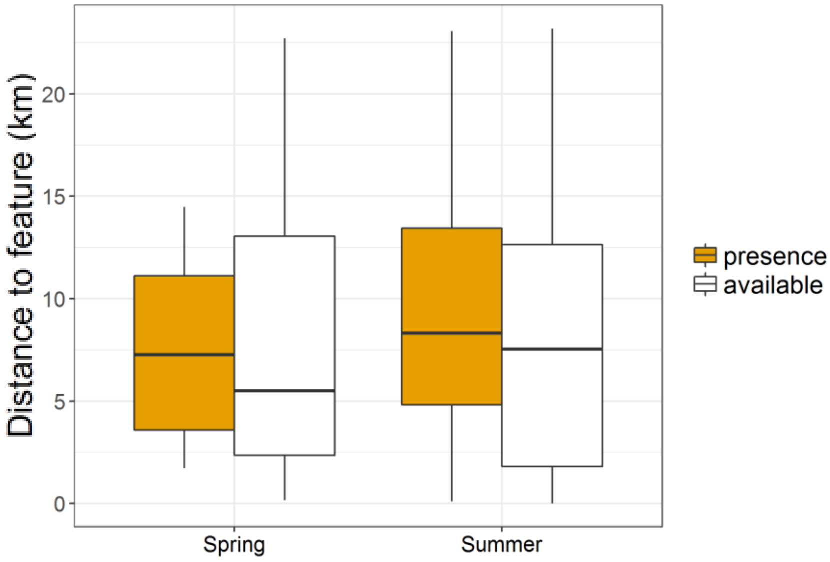

Figure 3.17b. Seasonal differences in the Skukuza wild dog pack's distance of occurrence (km) and available distances from different human land use types in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Skukuza pack's odds of occurrence at human land use types were almost equal for railway sites (Figure 3.17c). Odds of occurrence were high for commercial, industrial, military, quarry, recreational, reservoir and retail sites (Figure 3.17c). Odds of occurrence were low for cemetery, landfill and residential sites (Figure 3.17c).

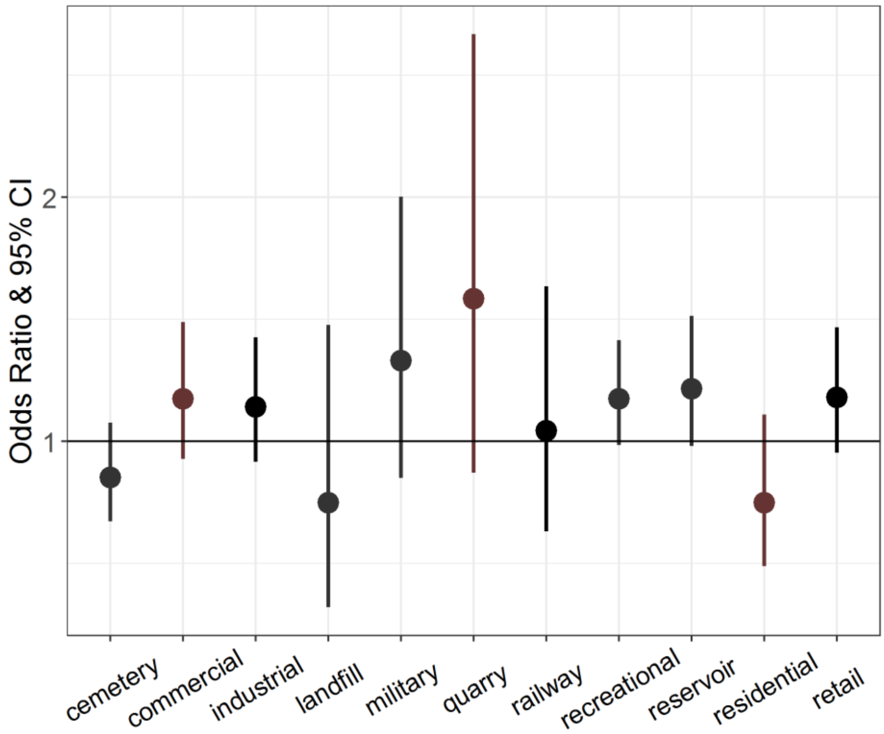

Figure 3.17c. Odds (± 95% CI) of the Skukuza wild dog pack's occurrence by distance, in areas of different human land use types, Mpumalanga Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

There was a significant difference between the available human landscape features and the presence of the Orpen pack (χ^2 (1) = 12.80, p = 0.0003), with the pack occurring close to residential and reservoir areas (χ^2 (14) = 24.43, p = 0.040) (Figure 3.18a). The Orpen pack occurred different distances to human landscape features during different seasons (χ^2 (2) = 24.43, p < 0.001), occurring closer in winter than autumn (Figure 3.18b).

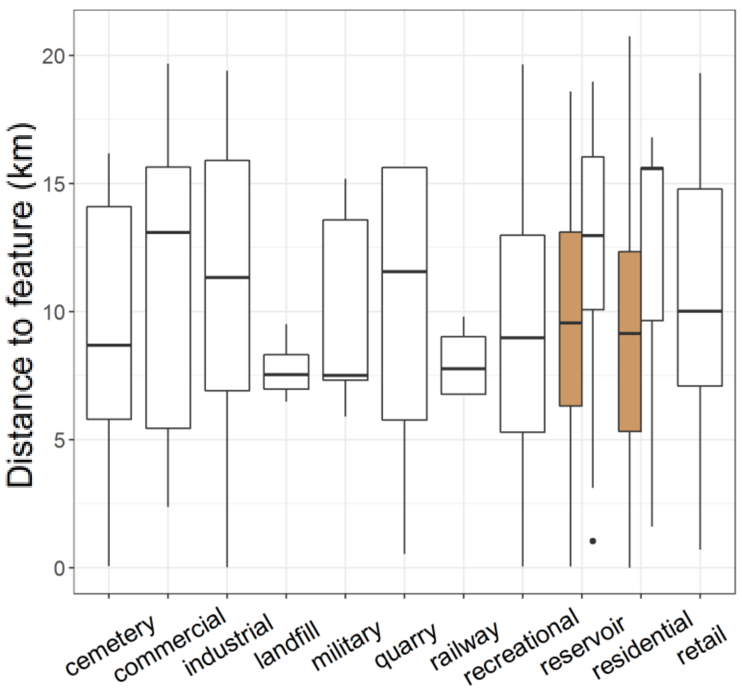

Figure 3.18a. The Orpen wild dog pack's distance of occurrence (km) and available distances from different human land use types in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

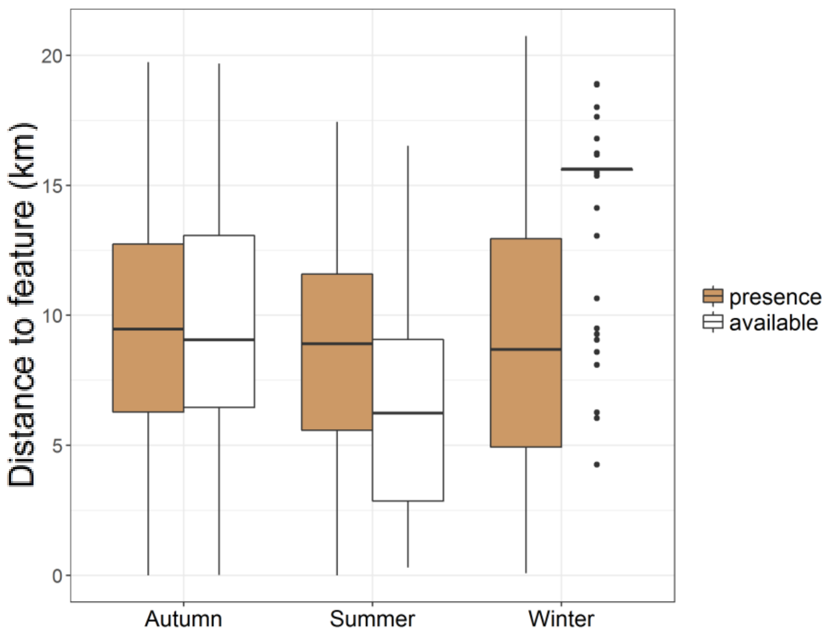

Figure 3.18b. Seasonal differences in the Orpen wild dog pack's distance of occurrence (km) and available distances from different human land use types in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Orpen pack's odds of occurrence were high for commercial, industrial, military, reservoir, residential and retail sites (Figure 3.18c). Odds of occurrence or non-occurrence were almost equal for quarry sites, and odds of occurrence were low for cemetery, landfill and railway sites (Figure 3.18c).

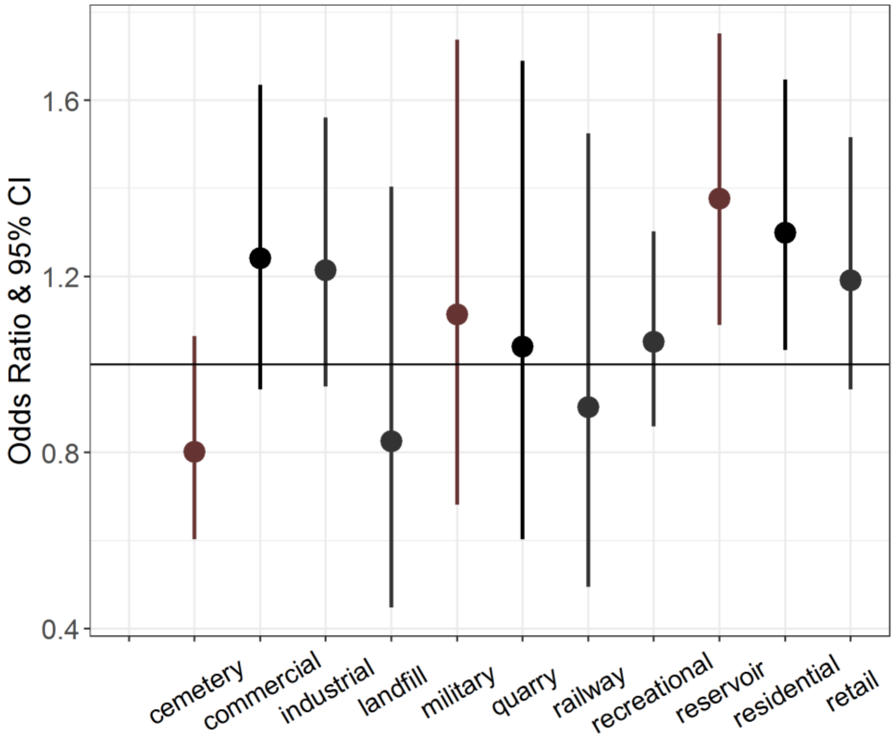

Figure 3.18c. Odds (± 95% CI) of the Orpen wild dog pack's occurrence by distance, in areas of different human land use types, Mpumalanga Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

The Bluebank pack occurred significantly closer to human landscape features than were available in the environment (χ^2 (1) = 401.42, p < 0.001), occurring close to military sites but not reservoirs (χ^2 (1) = 97.10, p < 0.001) (Figure 3.19a). Occurrence at landscape features differed during seasons (χ^2 (3) = 17.89, p = 0.0004), occurring further away in spring than autumn, summer or winter (Figure 3.19b).

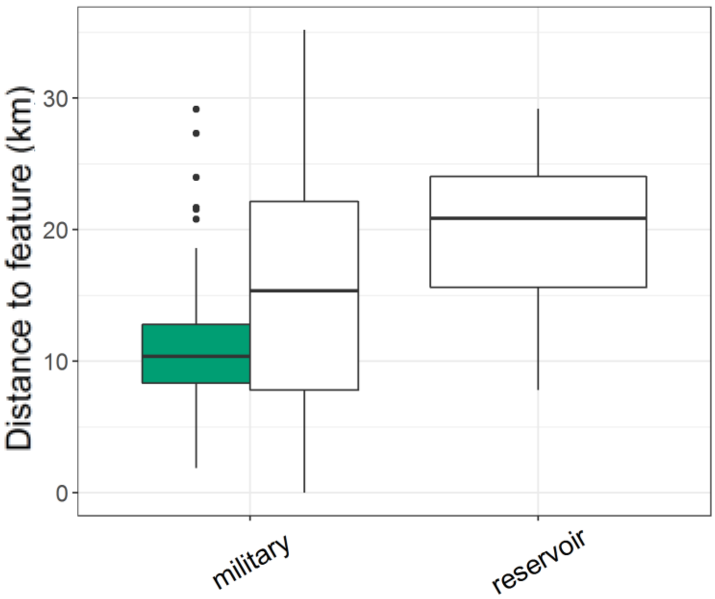

Figure 3.19a. The Bluebank wild dog pack's distance of occurrence (km) and available distances from different human land use types in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

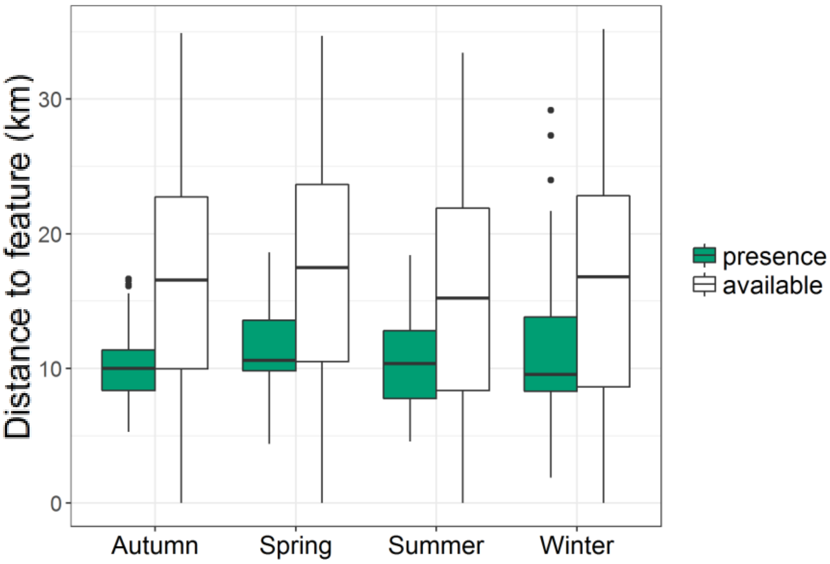

Figure 3.19b. Seasonal differences in the Bluebank wild dog pack's distance of occurrence (km) and available distances from different human land use types in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Bluebank pack's odds of occurrence at human landscape features were high at reservoirs, but low at military sites (Figure 3.19c).

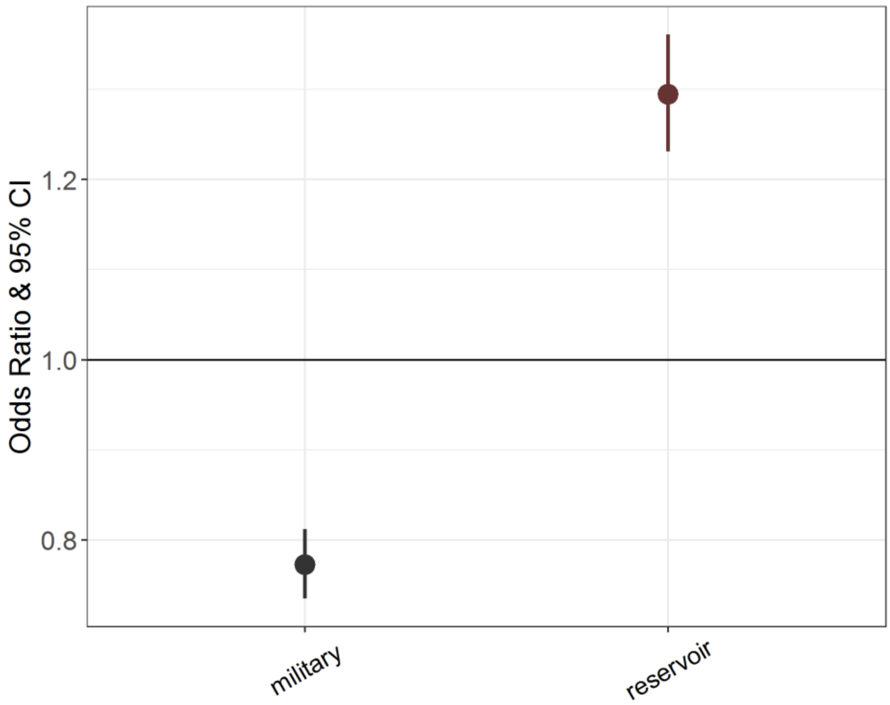

Figure 3.19c. Odds (± 95% CI) of the Bluebank wild dog pack's occurrence by distance, in areas of different human land use types, Limpopo Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

Natural landscape features

Rivers

The Waterberg pack occurred further away from rivers than was available in the environment (χ^2 (1) = 5.95, p = 0.014), although there was no difference between occurrence at perennial and non-perennial rivers (χ^2 (1) = 1.16, p = 0.280) (Figure 3.20a). The pack occurred closer to rivers during autumn than summer, but not spring (χ^2 (2) = 11.36, p = 0.003) (Figure 3.20b).

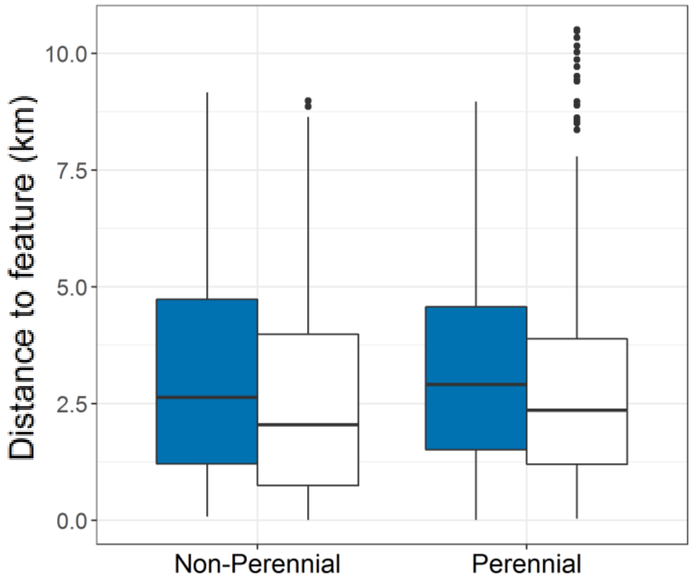

Figure 3.20a. The Waterberg wild dog pack's distance of occurrence (km) and available distances from different river types in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

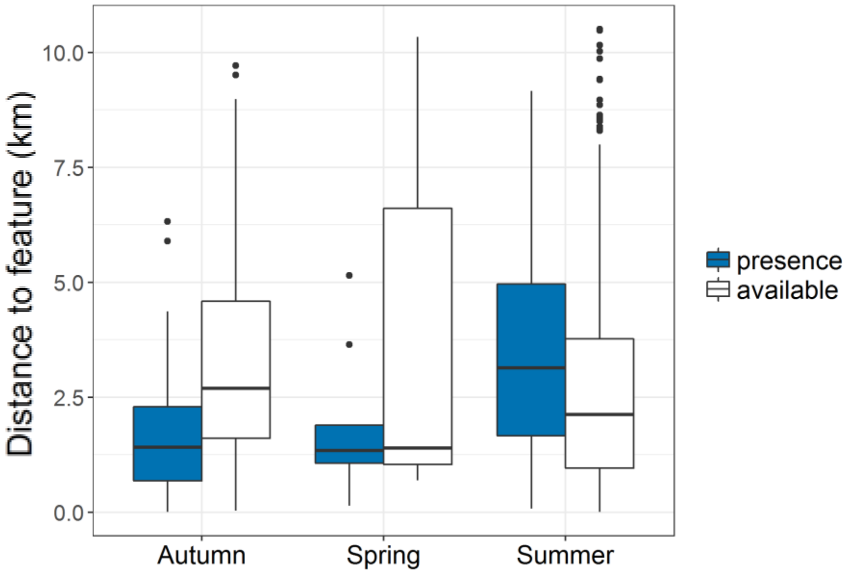

Figure 3.20b. Seasonal differences in the Waterberg wild dog pack's distance of occurrence (km) and available distances from different river types in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Waterberg pack's odds of occurrence were high at perennial rivers, but low at non-perennial rivers (Figure 3.12c).

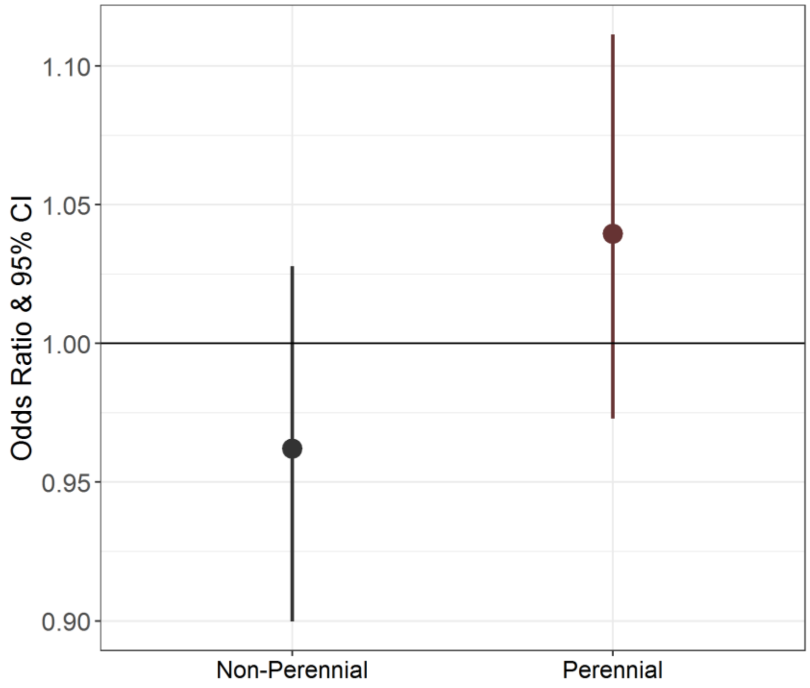

Figure 3.20c. Odds (± 95% CI) of the Waterberg wild dog pack's occurrence by distance, at different river types, Limpopo Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

The Skukuza pack did not occur further away from rivers than were available in the environment (χ^2 (1) = 3.66, p = 0.055), and did not occur different distances from perennial and non-perennial rivers (χ^2 (1) = 0.31, p = 0.573) (Figure 3.21a). Similarly, there were no differences of occurrence during spring and summer (χ^2 (1) = 0.81, p = 0.366) (Figure 3.21b).

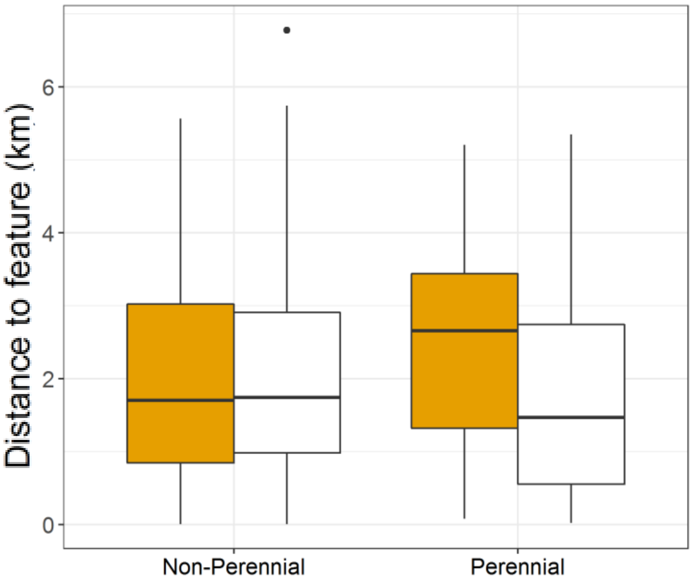

Figure 3.21a. The Skukuza wild dog pack's distance of occurrence (km) and available distances from different river types in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

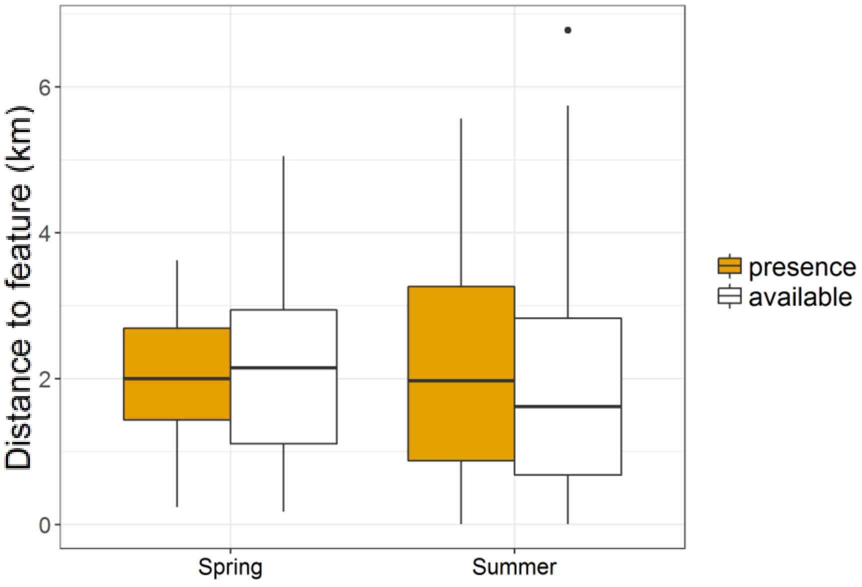

Figure 3.21b. Seasonal differences in the Skukuza wild dog pack's distance of occurrence (km) and available distances from different human land use types in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Skukuza pack's odds of occurrence were high at perennial rivers, but low at non-perennial rivers (Figure 3.21c).

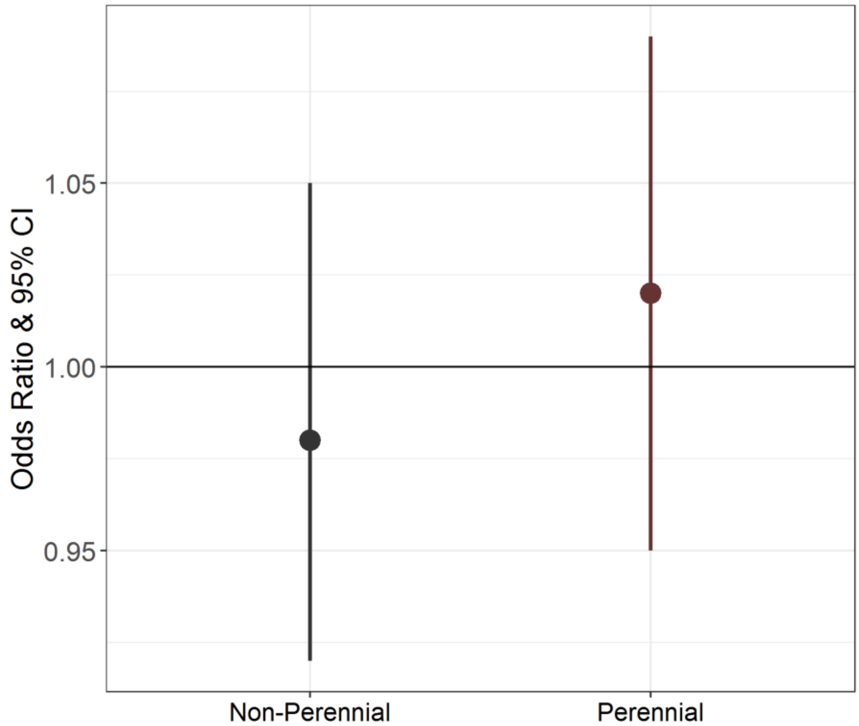

Figure 3.21c. Odds (± 95% CI) of the Skukuza wild dog pack's occurrence by distance, at different river types, Mpumalanga Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

The Orpen pack occurred closer to rivers than were available in the environment (χ^2 (1) = 187.15, p < 0.001), but occurred similar distances from non-perennial and perennial rivers (χ^2 (1) = 2.32, p = 0.128) (Figure 3.22a). Occurrence distance to rivers were > 1 km (Figure 3.22a). The pack occurred closer to rivers during winter than autumn or summer (χ^2 (1) = 8.077, p = 0.01) (Figure 3.22b).

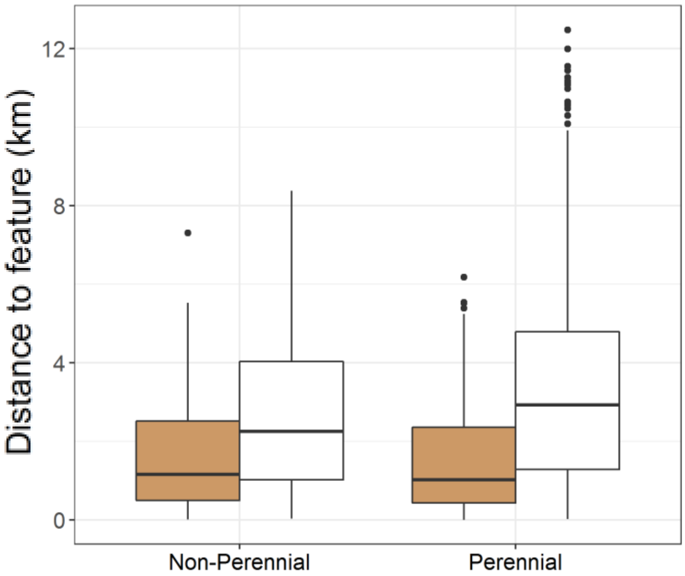

Figure 3.22a. The Orpen wild dog pack's distance of occurrence (km) and available distances from different river types in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

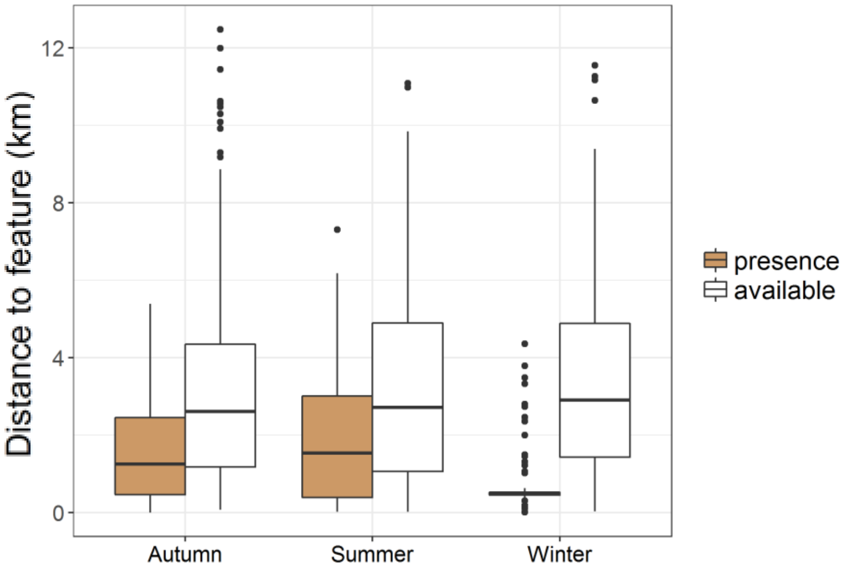

Figure 3.22b. Seasonal differences in the Orpen wild dog pack's distance of occurrence (km) and available distances from different human land use types in Mpumalanga Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). data are indicated by coloured boxes.

The Orpen packs odds of occurrence at rivers were high for perennial rivers, and low for non-perennial rivers (Figure 3.22c).

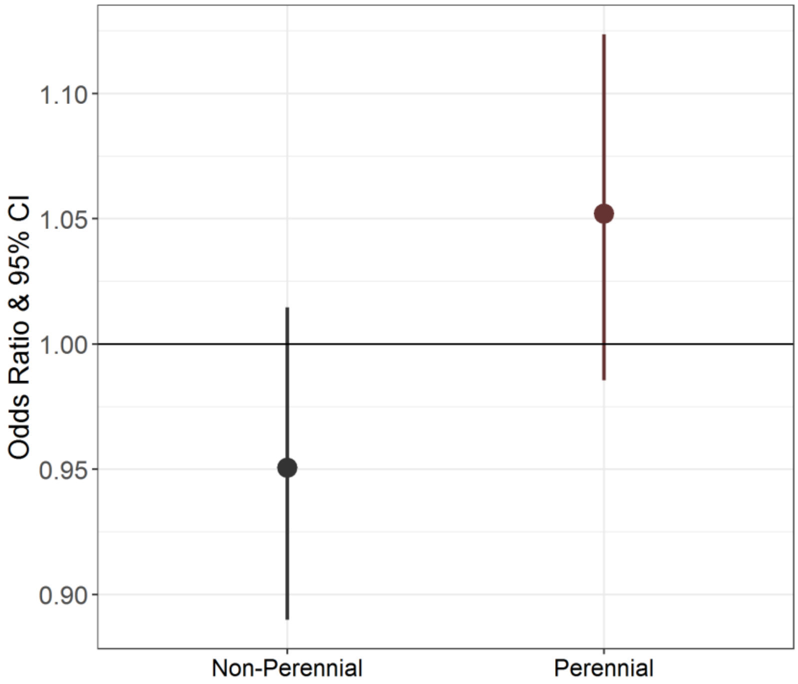

Figure 3.22c. Odds (± 95% CI) of the Orpen wild dog pack's occurrence by distance, at different river types, Mpumalanga Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

The Bluebank pack occurred closer to rivers than were available in the environment (χ^2 (1) = 376.12, p <0.0001), with the available data indicating possible occurrence at distances > 2 km (Figure 3.23a). The pack occurred closer to perennial rivers than non-perennial (χ^2 (1) = 8.65, p =0.003), occurring at perennial rivers at distances < 1 km (Figure 3.23a). The pack occurred at rivers at different distances during different seasons (χ^2 (3) = 19.92, p < 0.001), occurring closer to rivers during autumn and spring than summer or winter (Figure 3.23b).

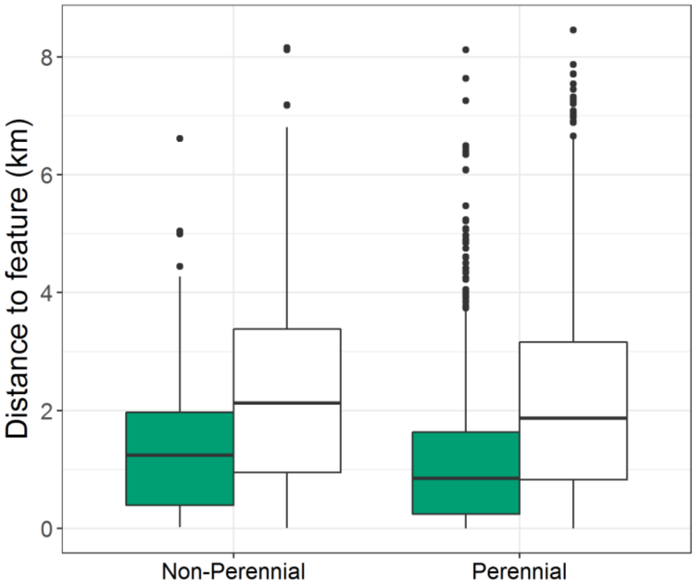

Figure 3.23a. The Bluebank wild dog pack's distance of occurrence (km) and available distances from different river types in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

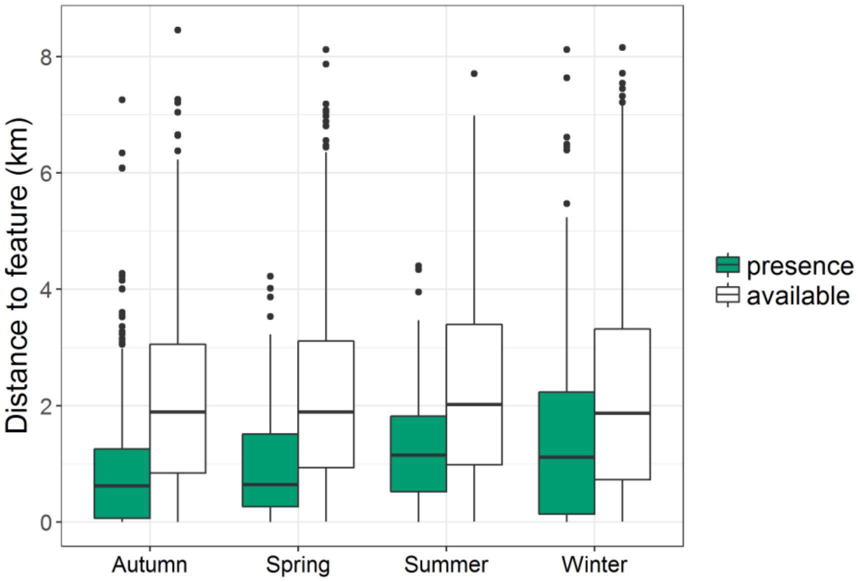

Figure 3.23b. Seasonal differences in the Bluebank wild dog pack's distance of occurrence (km) and available distances from different human land use types in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Bluebank pack's odds of occurrence were high for perennial rivers, and low for non-perennial rivers (Figure 3.23c).

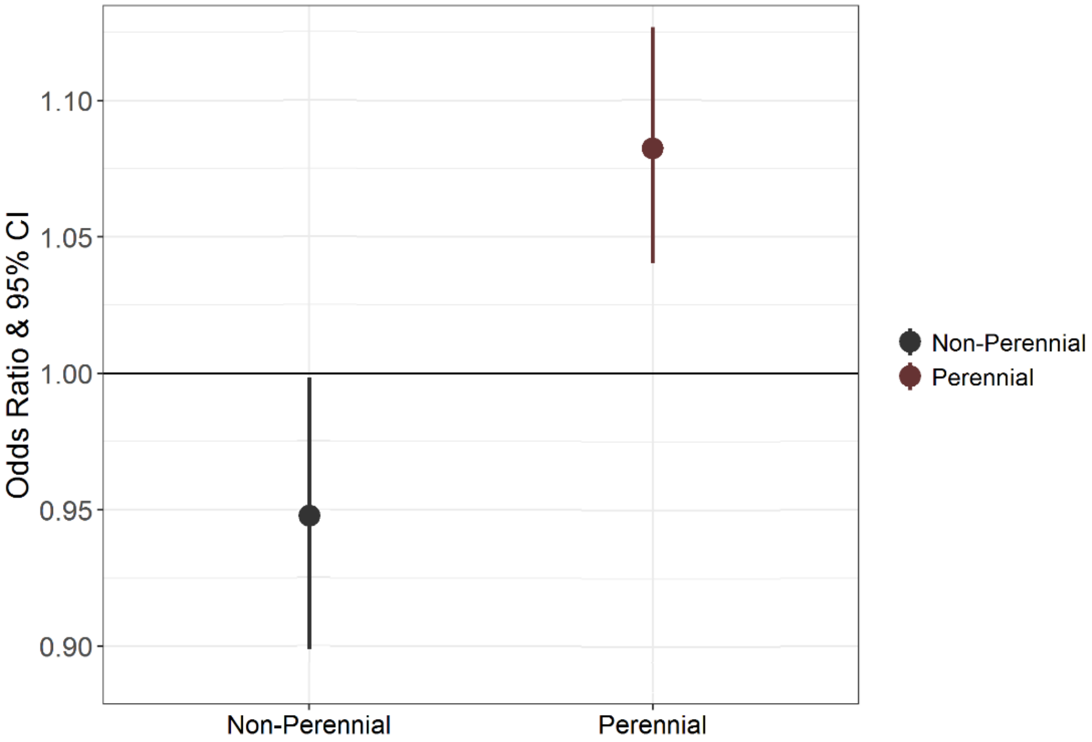

Figure 3.22c. Odds (± 95% CI) of the Bluebank wild dog pack's occurrence by distance, at different river types, Limpopo Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

Nature reserves

The Waterberg pack occurred closer to nature reserves than were available in the environment (χ^2 (1) = 10.90, p = 0.0009). The pack occurred significantly different distances to different nature reserves (χ^2 (13) = 286.73, p < 0.001), occurring within Alem, Belanie, Hen Nel and near Innes Mellet, Pearson and Pierre Fourie private nature reserves (Figure 3.24a). The pack occurred at different nature reserves differently during different seasons (χ^2 (2) = 22.13, p < 0.001), occurring closer to reserves in autumn and spring than summer (Figure 3.24b).

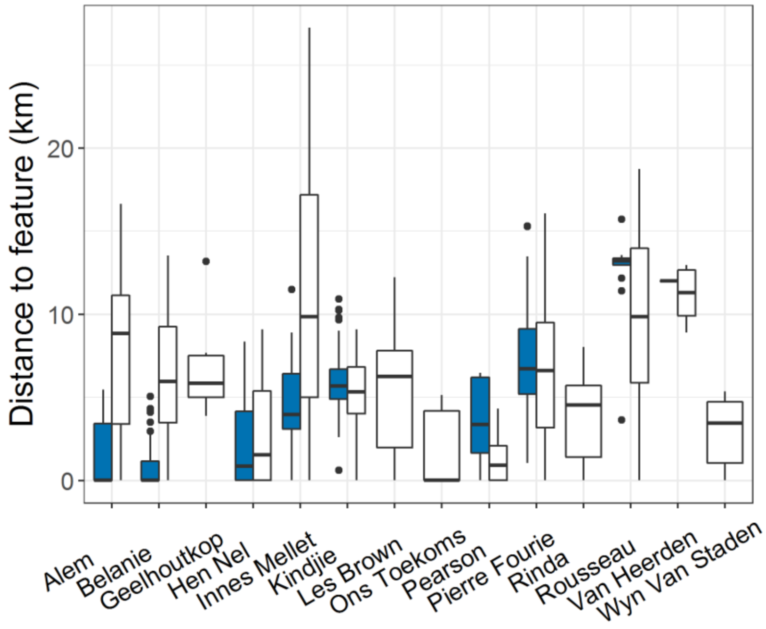

Figure 3.24a. The Waterberg wild dog pack's distance of occurrence (km) and available distances from different private-owned nature reserves in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

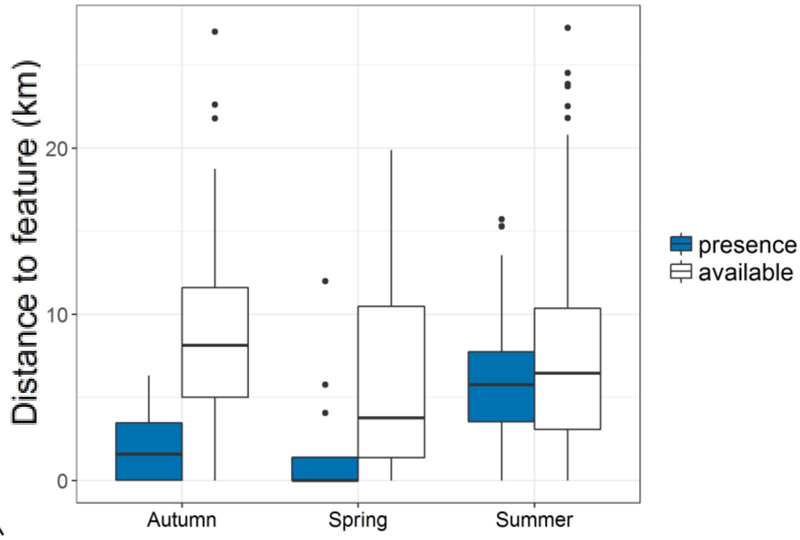

Figure 3.24b. Seasonal differences in the Waterberg wild dog pack's distance of occurrence (km) and available distances from different private-owned nature reserves in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Waterberg pack's odds of occurrence were high for Innes Mellet, Kindjie, Pierre Fourie, Rousseau and Van Heerden private nature reserves (Figure3.24c). Odds of occurrence were low for Alem, Belanie, Hen Nel, Ons Toekoms, Pearson, Rinda and Wyn van Staden private nature reserves (Figure 3.24c). Occurrence or non-occurrence was almost equal at Geelhoutkop private nature reserve (Figure 3.24c).

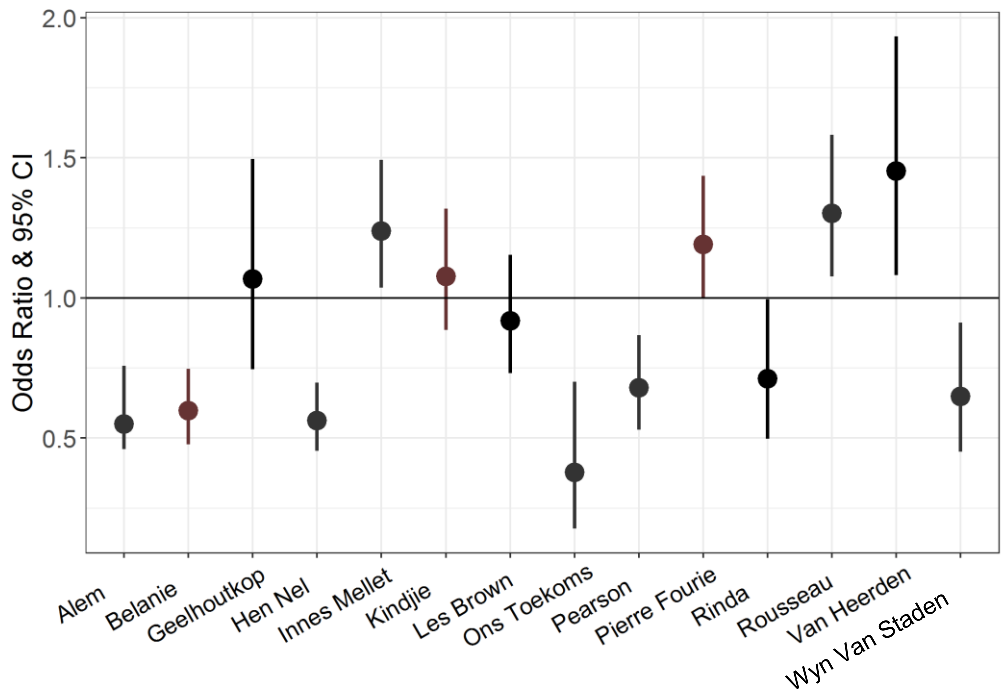

Figure 3.24c. Odds (± 95% CI) of the Waterberg wild dog pack's occurrence by distance, at different river types, Limpopo Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

The Bluebank pack occurred significantly closer to nature reserves than available in the environment (χ^2 (1) = 672.58, p< 0.0001). The pack occurred at different distances to different reserves (χ^2 (12) = 1236.39, p< 0.0001), occurring within Amsterdam, Brussel, Maroelanie and Thornybush private nature reserves and close to the Bluebank, Klaserie and Vienna private nature reserves (Figure 3.25a). Occurrence at reserves differed during seasons (χ^2 (3) = 20.98, p = 0.0001), occurring closer to reserves during summer than autumn, spring or winter (Figure 3.25b)

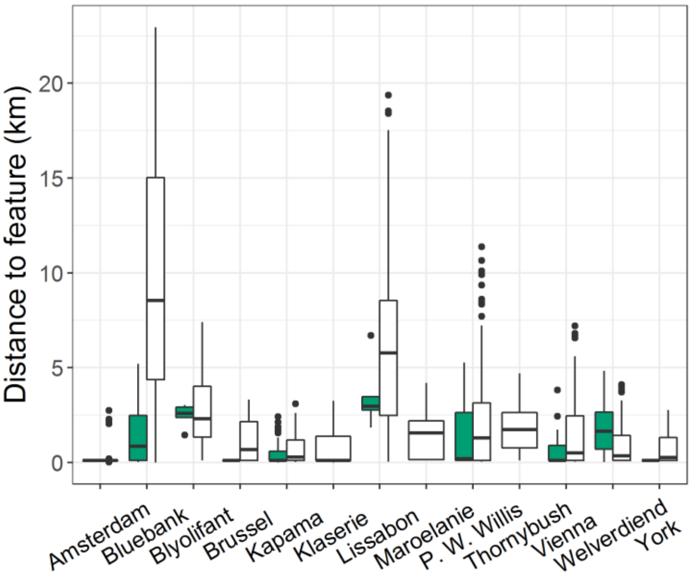

Figure 3.25a. The Bluebank wild dog pack's distance of occurrence (km) and available distances from different private-owned nature reserves in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

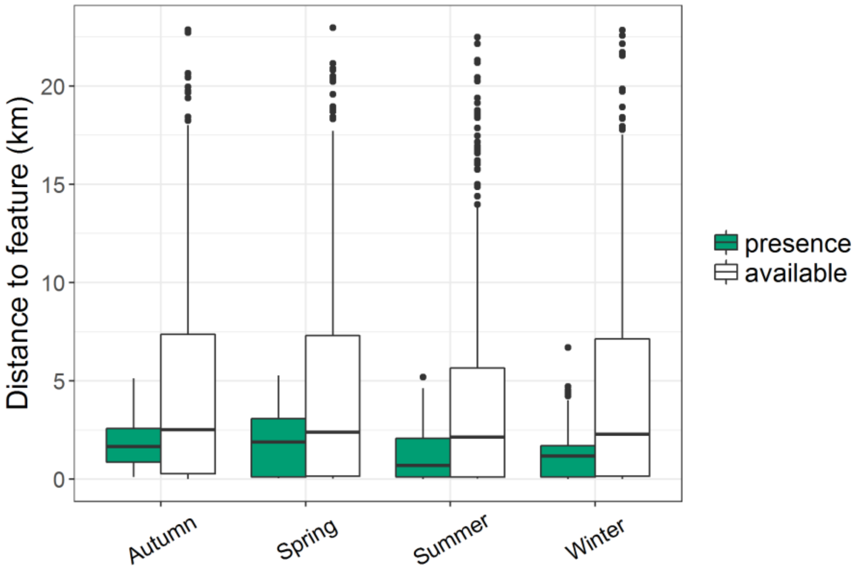

Figure 3.25b. Seasonal differences in the Bluebank wild dog pack's distance of occurrence (km) and available distances from different private-owned nature reserves in Limpopo Province, South Africa. Boxplots show medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots). Presence data are indicated by coloured boxes.

The Bluebank pack's odds of occurrence were high for all nature reserves, but were highest for Bluebank, Lissabon and Welverdiend private nature reserves (Figure 3.25c)

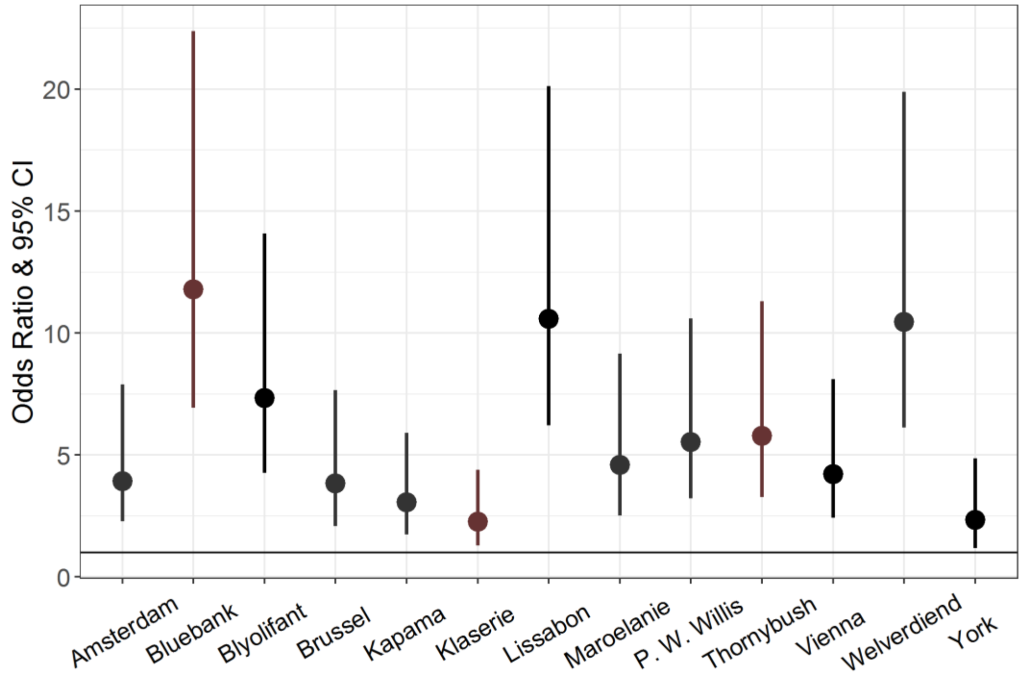

Figure 3.25c. Odds (± 95% CI) of the Bluebank wild dog pack's occurrence by distance, at different river types, Limpopo Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

Vegetation types

The Waterberg pack occurred in areas consisting of different vegetation types than were available in the environment (χ^2 (1) = 4.02, p = 0.045) (Figure 3.26a). The pack utilised different vegetation types differently (χ^2 (3) = 41.35, p < 0.001), especially utilising the Waterberg Moist Mountain Bushveld vegetation type more than other vegetation types including Clay Thorn Bushveld, Mixed Bushveld and Sweet Bushveld vegetation types (Figure 3.26a). The pack utilised different vegetation types during different seasons (χ^2 (2) = 17.27, p < 0.001), with the Waterberg Moist Mountain Bushveld utilised more during summer than either autumn or spring (Figure 3.26b).

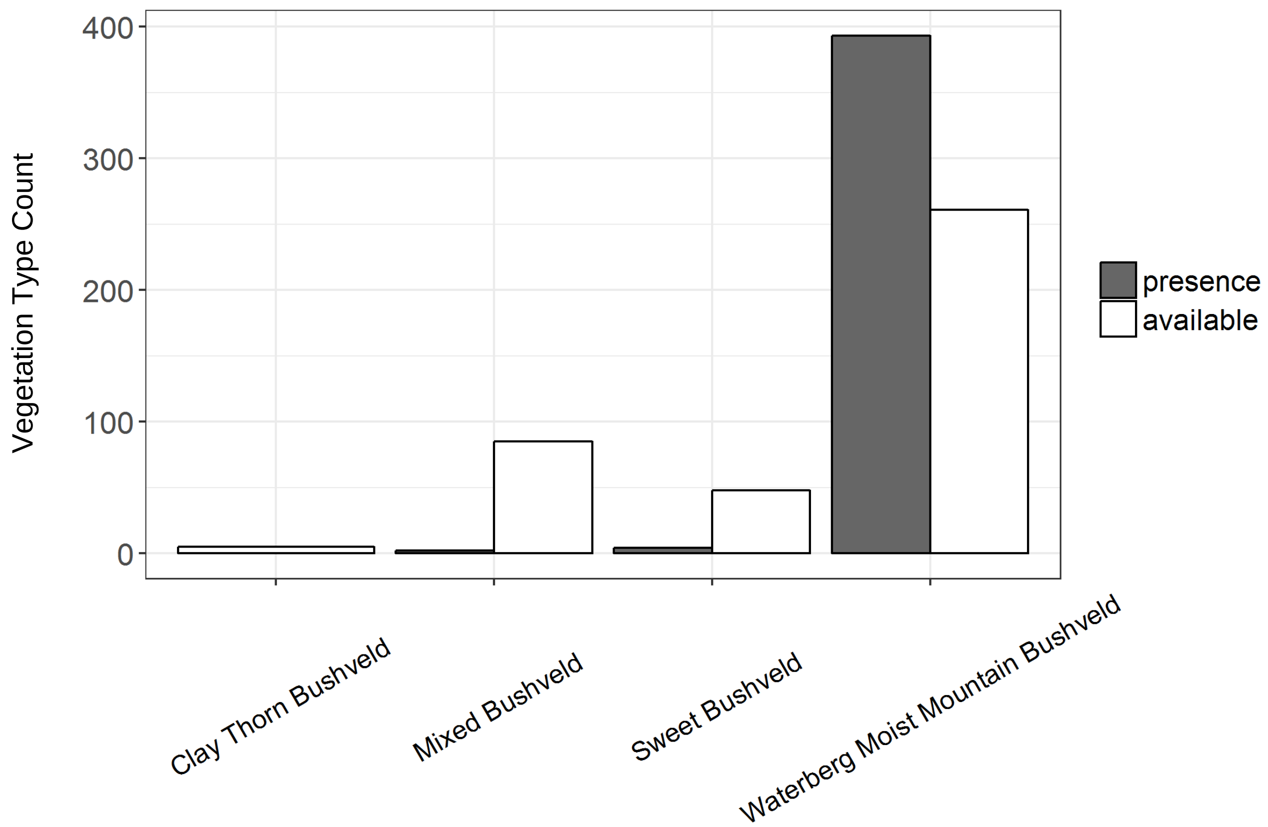

Figure 3.26a. Counts of vegetation types for the Waterberg wild dog pack for presence an available vegetation types available in the Limpopo province, South Africa. Vegetation types are as defined by in the SAFARI 2000 project undertaken by the National Botanical Institute, imported from ArcGIS online.

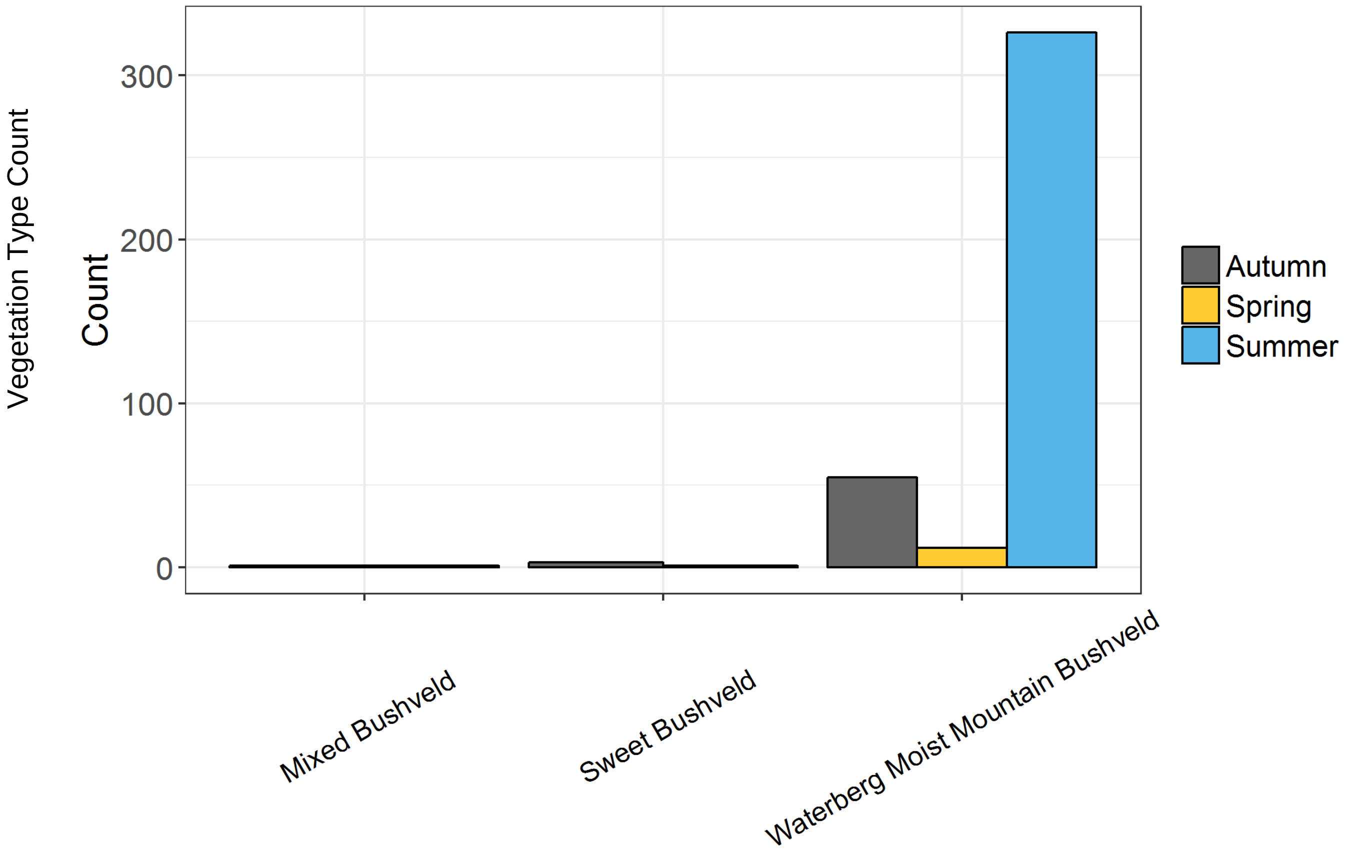

Figure 3.26b. Counts of vegetation types for the Waterberg wild dog pack for presence only data across different seasons in the Limpopo province, South Africa. Vegetation types are as defined by in the SAFARI 2000 project undertaken by the National Botanical Institute, imported from ArcGIS online.

The Waterberg pack's odds of occurrence were high for Mixed Bushveld and Sweet Bushveld and was greater for Waterberg Moist Mountain Bushveld (Figure 3.26c). Odds of occurrence or non-occurrence were equal for the Clay Thorn Bushveld vegetation type (Figure 3.26c).

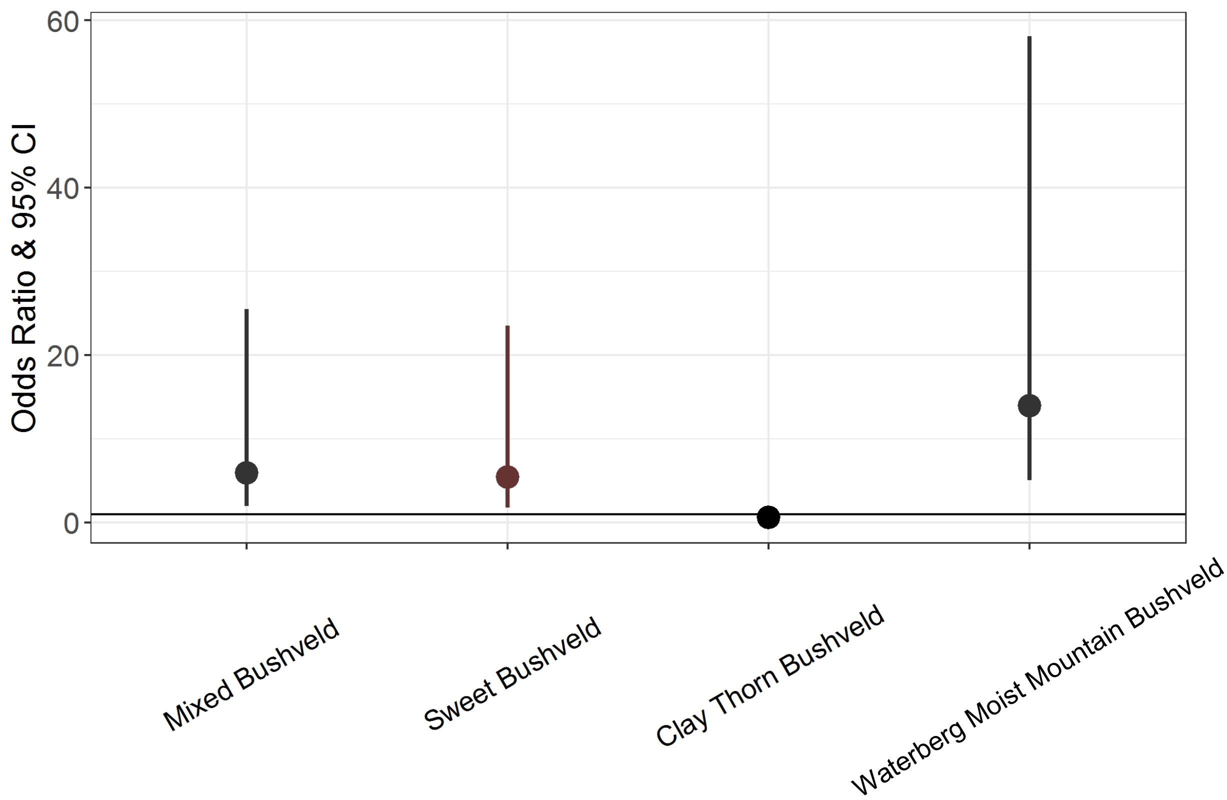

Figure 3.26c. Odds (± 95% CI) of the Waterberg wild dog pack's occurrence by count, on different vegetation types, Limpopo Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

The Skukuza pack occurred in areas consisting of different vegetation types than were available in the environment (χ^2 (1) = 0.80, p = 0.369) (Figure 3.27a). The pack was present on different vegetation types (χ^2 (1) = 15.29, p < 0.001), utilising Mixed Lowveld Bushveld more than Sour Lowveld Bushveld (Figure 3.27a). Occurrence at different vegetation types differed during seasons χ^2 (1) = 2.329, p < 0.001), utilising Mixed Lowveld Bushveld more in summer than spring and Sour Lowveld Bushveld more in summer than spring (Figure 3.27a).

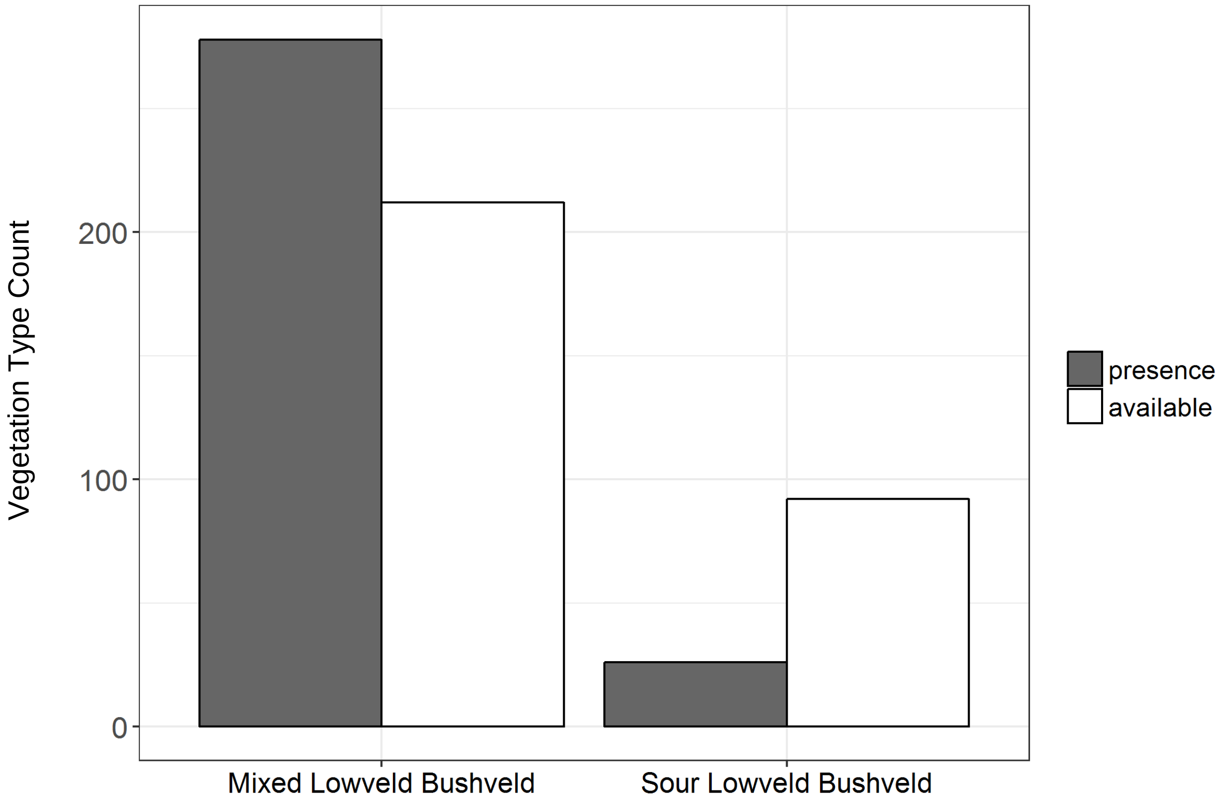

Figure 3.27a. Counts of vegetation types for the Skukuza wild dog pack for presence an available vegetation types in the Mpumalanga Province, South Africa. Vegetation types are as defined by in the SAFARI 2000 project undertaken by the National Botanical Institute, imported from ArcGIS online.

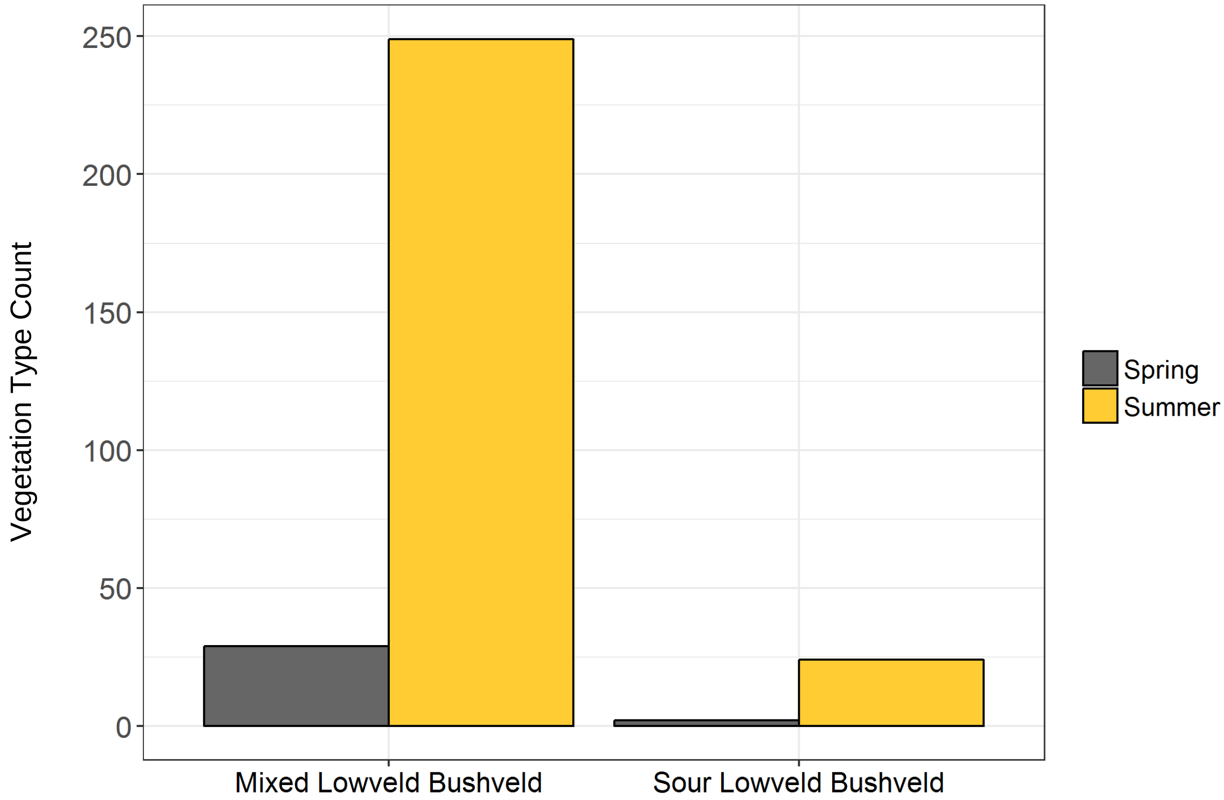

Figure 3.27b. Counts of vegetation types for the Skukuza wild dog pack for presence only data across different seasons in the Mpumalanga Province, South Africa. Vegetation types are as defined by in the SAFARI 2000 project undertaken by the National Botanical Institute, imported from ArcGIS online.

The Skukuza pack's odds of occurrence were high for Mixed Lowveld Bushveld, and low for Sour Lowveld Bushveld (Figure 3.27c).

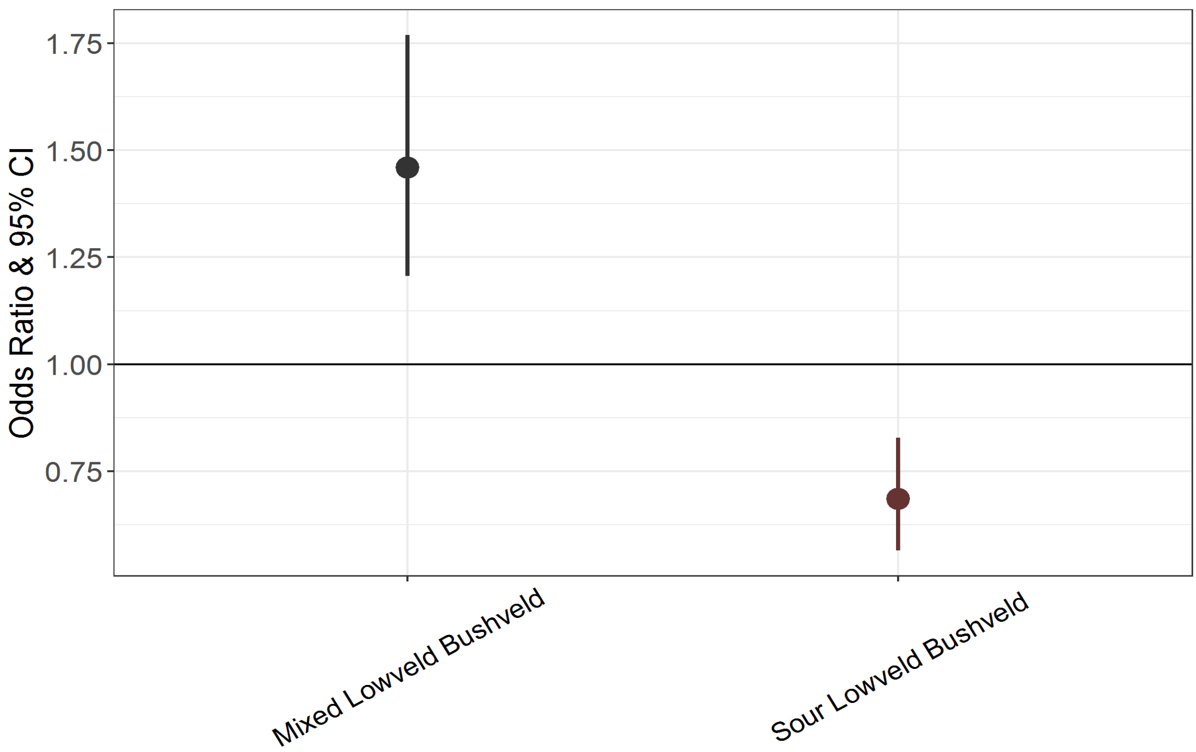

Figure 3.27c. Odds (± 95% CI) of the Skukuza wild dog pack's occurrence by count, on different vegetation types, Mpumalanga Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

The Orpen pack occurred in areas consisting of different vegetation types than were available in the environment (χ^2 (1) = 0.16, p = 0.685). The pack was present on different vegetation types (χ^2 (2) = 7.68, p = 0.021), utilising Sweet Lowveld Bushveld more than Mopane Bushveld or Mixed Lowveld Bushveld (Figure 3.28a). Occurrence at different vegetation types differed significantly during seasons χ^2 (2) = 6.73, p = 0.034), with higher occurrence on Sweet Lowveld Bushveld vegetation during autumn than summer or winter for presence data (Figure 3.28b)

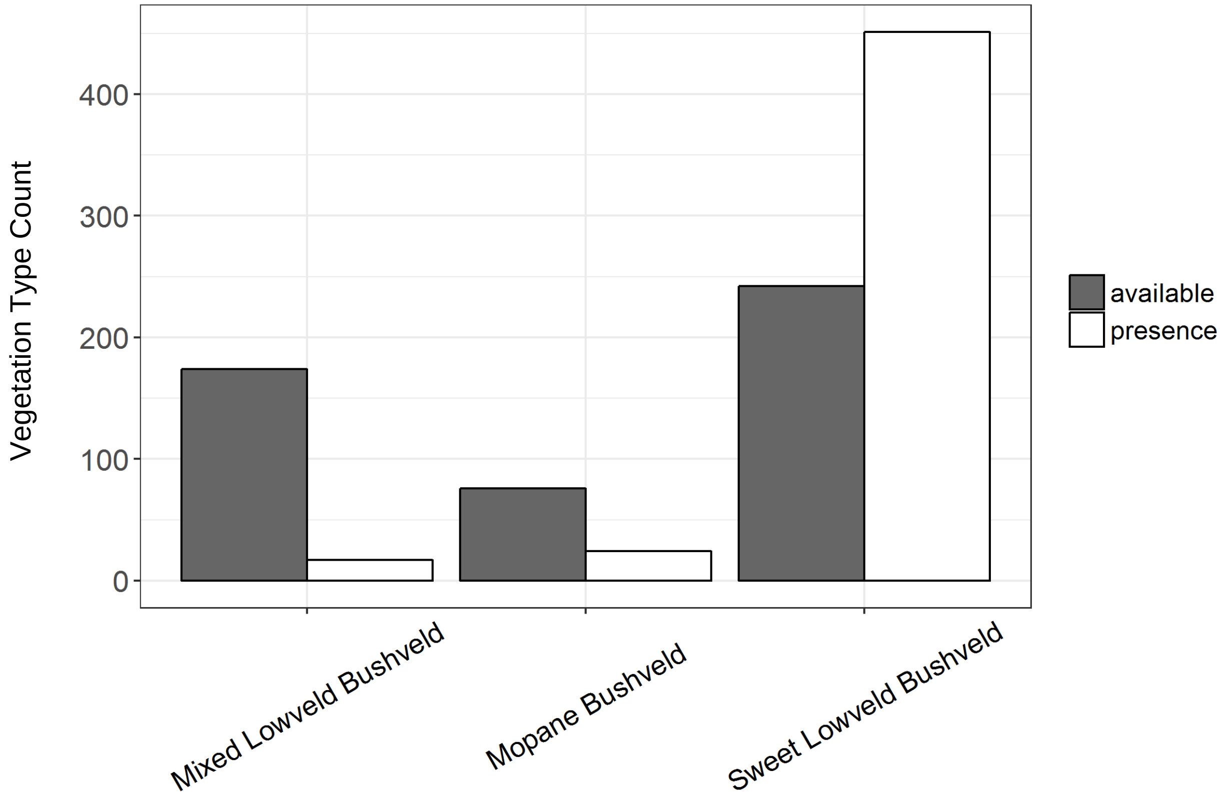

Figure 3.28a. Counts of vegetation types for the Orpen wild dog pack for presence an available vegetation types in the Mpumalanga Province, South Africa. Vegetation types are as defined by in the SAFARI 2000 project undertaken by the National Botanical Institute, imported from ArcGIS online.

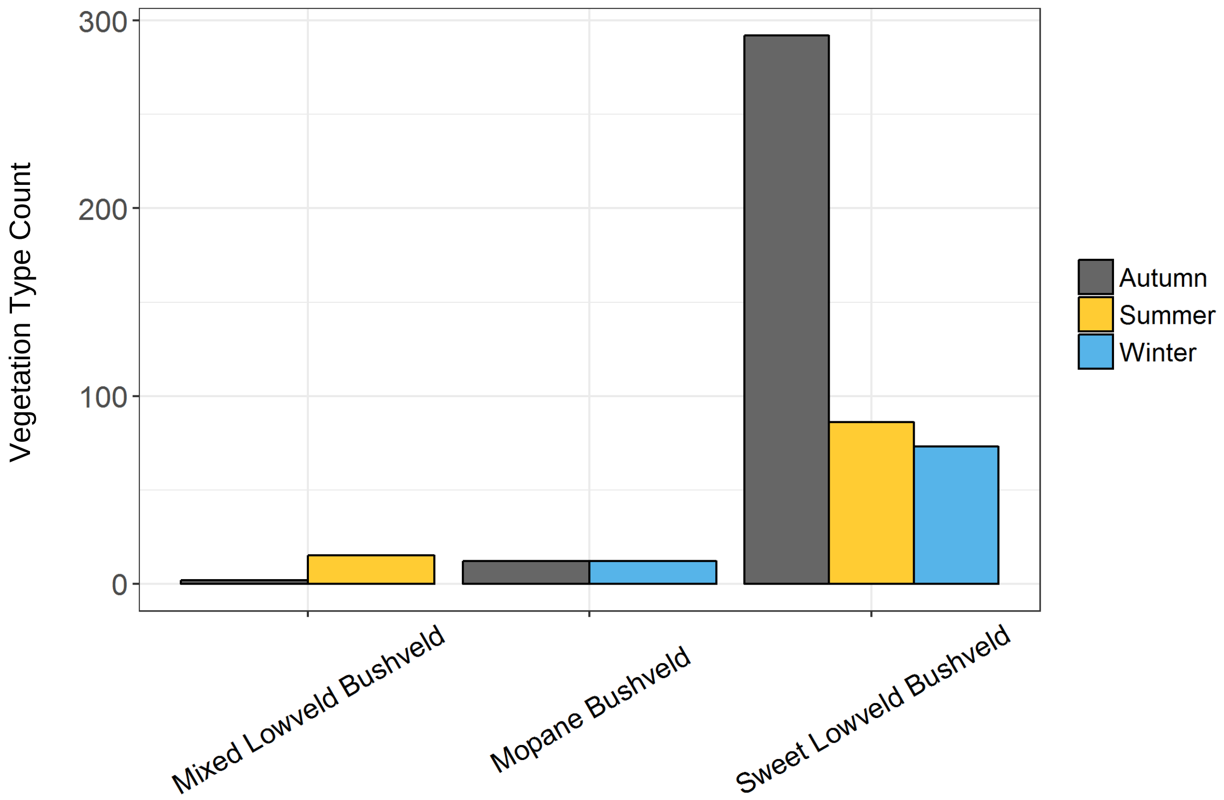

Figure 3.28b. Counts of vegetation types for the Orpen wild dog pack for presence only data across different seasons in the Mpumalanga Province, South Africa. Vegetation types are as defined by in the SAFARI 2000 project undertaken by the National Botanical Institute, imported from ArcGIS online.

The Orpen pack's odds of occurrence for vegetation types were high for the Sweet Lowveld Bushveld vegetation type (Figure 3.28c). Odds of occurrence or non-occurrence were almost equal for the Mopane Bushveld vegetation type, and odds of occurrence were low for the Mixed Lowveld Bushveld vegetation type (Figure 3.28c).

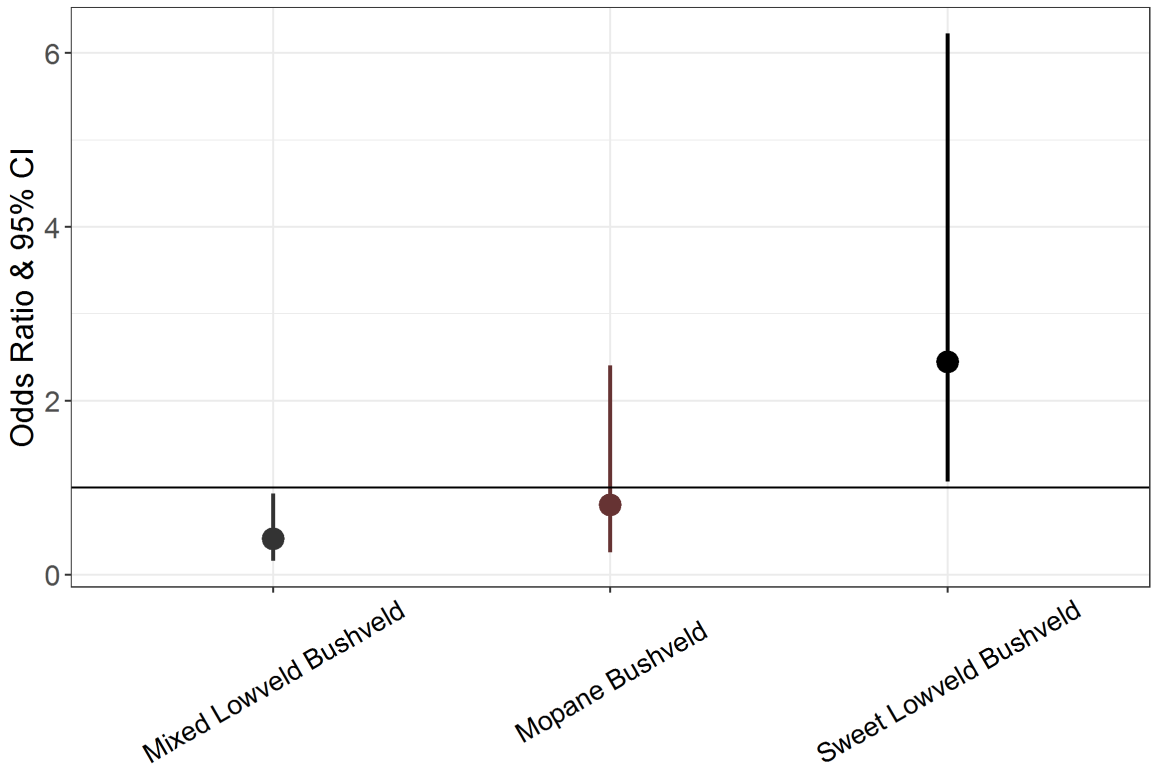

Figure 3.28c. Odds (± 95% CI) of the Orpen wild dog pack's occurrence by count, on different vegetation types, Mpumalanga Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

The Bluebank pack did not occur in areas consisting of different vegetation types than were available in the environment (χ^2 (1) = 0.69, p = 0.987). The pack was present on different vegetation types (χ^2 (4) = 71.86, p < 0.001), occurring more on the Mixed Lowveld Bushveld vegetation type than Sour Lowveld Bushveld, and showing the no occurrence in the Forest, Grassland or Mopane Bushveld vegetation types (Figure 3.29a). Occurrence at different vegetation types did not differ significantly during seasons (χ^2 (3) = 4.725 p = 0.236), with packs utilising the Mixed Lowveld Bushveld more throughout all seasons than any other vegetation type (Figure 3.29b).

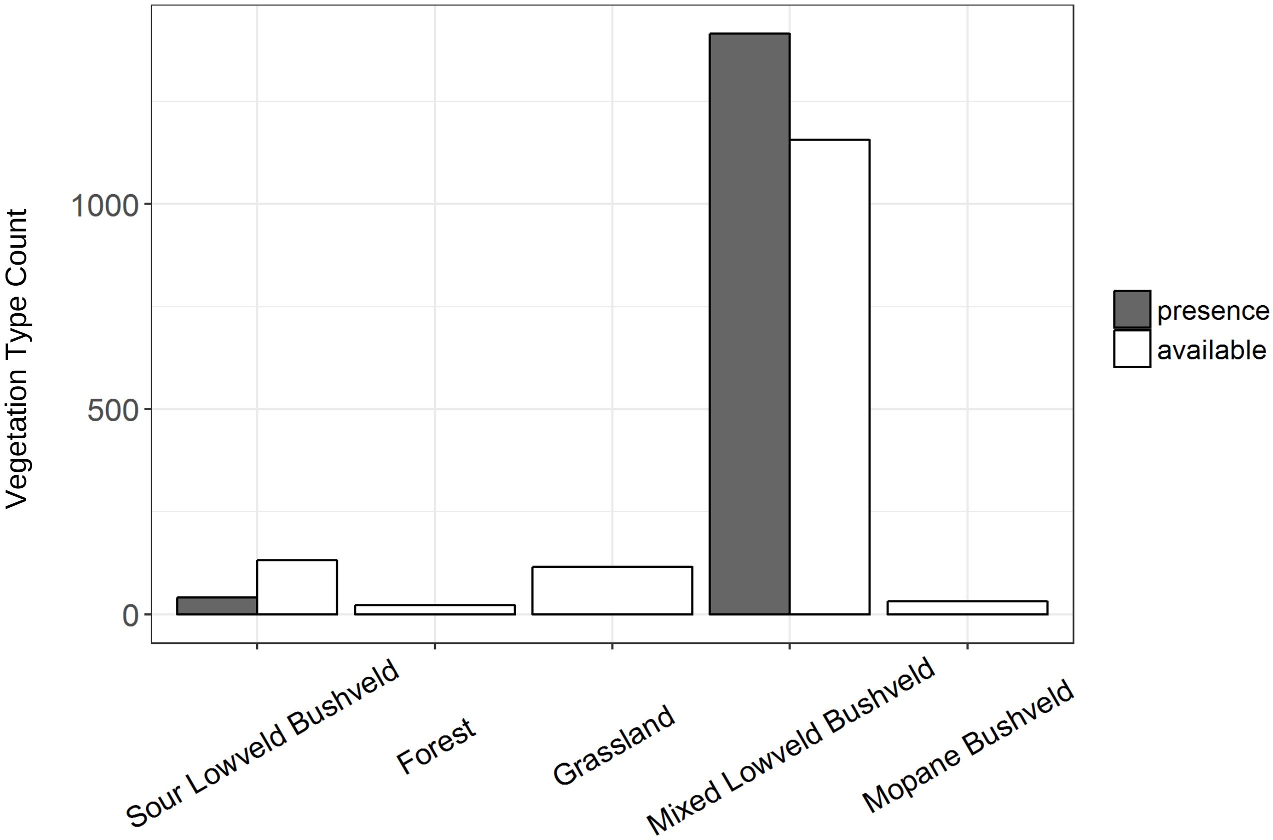

Figure 3.29a. Counts of vegetation types for the Bluebank wild dog pack for presence an available vegetation in the Limpopo Province, South Africa. Vegetation types are as defined by in the SAFARI 2000 project undertaken by the National Botanical Institute, imported from ArcGIS online. Bar width varies due to variable sample sizes

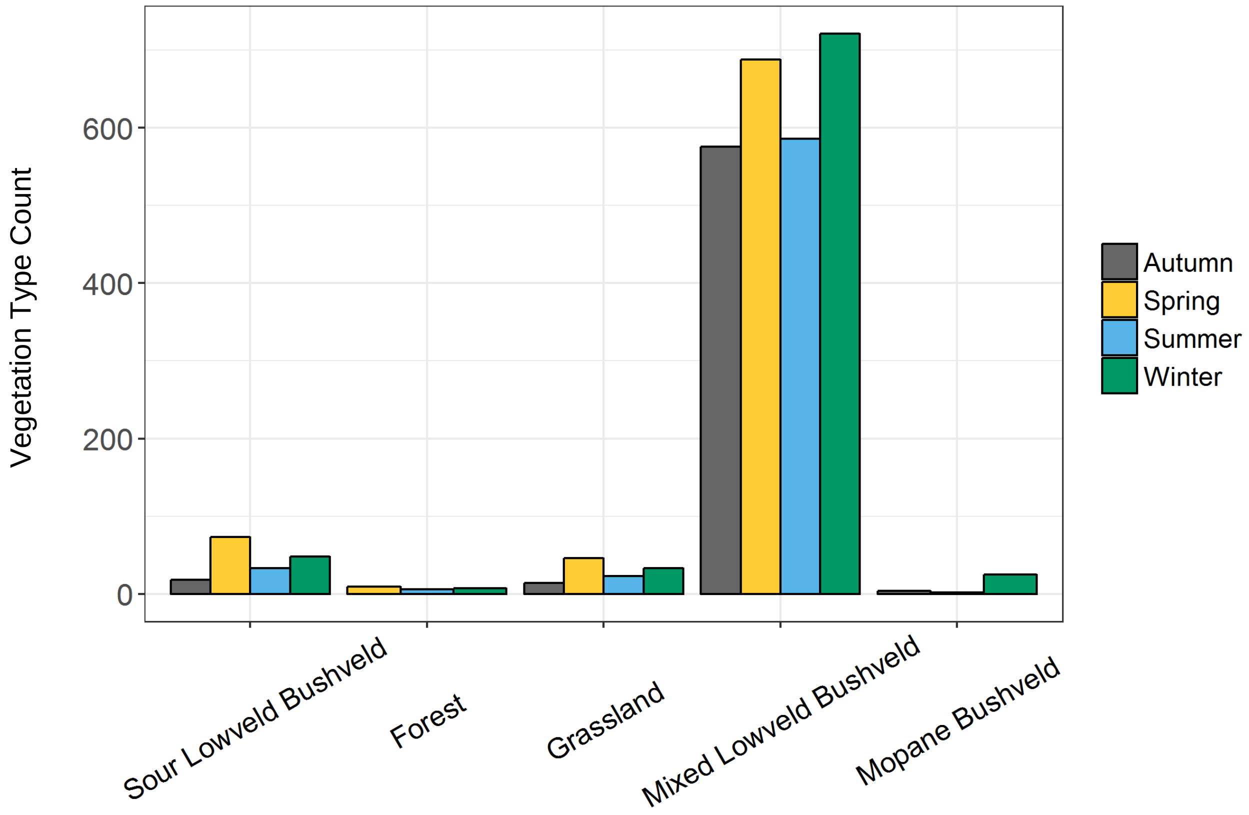

Figure 3.29b. Counts of vegetation types for the Bluebank wild dog pack for presence only data across different seasons in the Limpopo Province, South Africa. Vegetation types are as defined by in the SAFARI 2000 project undertaken by the National Botanical Institute, imported from ArcGIS online. Bar width varies due to variable sample sizes

The Bluebank pack's odds of occurrence were high for the Mixed Lowveld Bushveld vegetation type and Sour Lowveld Bushveld (Figure 3.29c). Occurrence or non-occurrence were almost equal for the Mopane Bushveld vegetation type, and odds of occurrence were low for Grassland, Mopane Bushveld, Sour Lowveld Bushveld, and Forest vegetation types (Figure 3.29c).

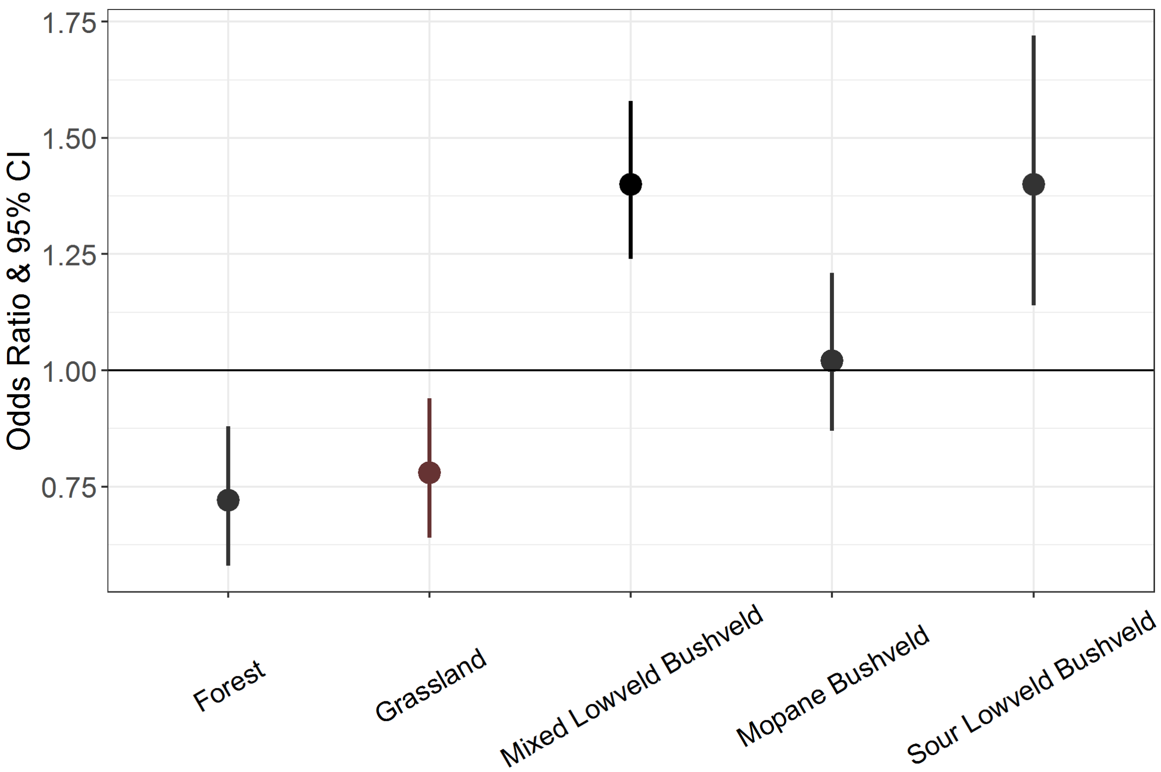

Figure 3.29c. Odds (± 95% CI) of the Bluebank wild dog pack's occurrence by count, on different vegetation types, Limpopo Province, South Africa. OR=1 indicates equal chance of occurrence, OR< 1 indicates low chance of occurrence and OR> 1 indicates high chance of occurrence.

Discussion

The aim of this study was to investigate human-carnivore conflict relating to African wild dogs at a regional scale in South Africa. I compared the spatial and temporal occurrence along with the resource selection of four packs of wild dogs occurring within and outside of protected areas in Limpopo and Mpumalanga Provinces, South Africa. I specifically focussed on examining wild dog occurrence in close proximity to agricultural landscape features and areas of high livestock density, as this would most likely lead to contact with livestock, and subsequently human-carnivore conflicts with this highly endangered carnivore.

My findings show that agricultural landscape features and livestock densities were significant predictors of wild dog occurrence, although the Skukuza and Orpen packs, with 95% home ranges remaining within protected areas, occurred further away from farms than were available in the environment, occurring on average > 20 km away from these features. In contrast, the Waterberg and Bluebank packs' 95% home ranges extended outside private reserves, and the two packs occurred closer to farms, occurring on average > 5 km away from features. The Waterberg pack had the largest 100% home range, followed by the Orpen pack. The Skukuza pack had the third largest home range, whilst the Bluebank pack had the smallest home range of all four packs. Home range size may be either a factor of pack size, with larger wild dog packs maintaining larger home ranges (Powell 2000), or a factor of spatial resource distribution (Mitchell & Powell 2004). As the Waterberg pack consisted of only seven adult individuals and the Orpen pack of 17 adult individuals when the study was conducted, pack home range size is not related to pack size. Resources such as wild herbivores or shelter may be clumped in scattered patches throughout the Waterberg region (Mitchell & Powell 2004), necessitating the Waterberg pack to utilise a larger home range. The movement of large terrestrial animals, including mammalian carnivores and herbivores, occurring within the Kruger National Park are however constrained by fences (Van Dyk & Slotow 2003), creating pockets of greater resource density that are not widely distributed (DeAngelis & Mooij 2005) and thus restricting home range size.

The Waterberg and Bluebank packs occurred in close proximity to areas that house approximately 2-20 cattle, goats and poultry per km^2, whilst the areas outside of Kruger near the Skukuza pack housed approximately 7-150 cattle, goats and poultry per km^2. The Orpen pack apparently did not encounter areas of high livestock density. Home range analyses indicate that, although 100% home ranges of wild dogs often overlapped agricultural landscape features and areas of moderate cattle and goat densities, 95% home ranges overlapped only areas of low to zero livestock densities, and only some agricultural landscape features. Therefore, even though the odds of occurrence on farms and areas housing moderate to high densities of livestock were high due to the wild dog packs' close proximity to these features, it is likely that the packs employ predictive risk avoidance of these areas, as farms and areas containing livestock likely pose a mortality risk (Valeix *et al.* 2012). Thorn *et al.* (2013) found that, whilst wild dog were resident in the Waterberg Biosphere reserve, only 6% of annual livestock losses could be ascribed to wild dog depredation, in contrast to the 75% of stock losses caused by black-backed jackal (*Canis mesomelas*).

It must be noted that encounter rate may not be indicative of hunting rate. A study on different wild dog packs in the Selous Game Reserve, Tanzania showed that while prey encounter rates for different prey species (such as impala and wildebeest) were variable for three different wild dog packs, the packs hunted only 37% of herds that they encountered, regardless of prey herd size or wild dog pack size (Creel & Creel 2002). A small wild dog pack is defined as < 10 adult individuals, because 10 adults are the minimum predicted pack size that can sustain a litter of five pups (Courchamp *et al.* 2002). If a pack size drops below five adult individuals, reproductive failure is highly likely (Davies-Mostert *et al.* 2009). Wild dog pack size affected the hunting success and size of prey hunted (Creel & Creel 1995), as small packs selected smaller prey types such as impala, whilst larger packs selected larger prey such as wildebeest, kudu and waterbuck (Creel & Creel 2002). When a successful hunt is made, each individual wild dog is capable of carrying (gastrically) an average 4.4 kilograms or more of meat, equivalent to three days' worth of food (Reich 1981). Rapid consumption of prey means a higher food intake rate per minute and less food left over, reducing the number of hunts needed (Gorman *et al.* 1998). Similarly, larger packs consume more food quicker, whilst smaller packs consume food slower (Gorman *et al.* 1998) potentially resulting in smaller packs ingesting more food per individual, meaning they are fuller for longer, thereby reducing the need to hunt. However, they are likely to have preyed upon smaller prey.

The Waterberg and Bluebank packs showed seasonal differences in proximity to agricultural landscape features, with the Waterberg pack occurring closer to farms in summer and the Bluebank pack occurring closer to fruit farms in autumn. As fruit farms (orchards) generally produce fruit and nut crops and do not keep livestock or game (Phillips 2012), they are not considered a mortality risk to the Bluebank pack. Only the Bluebank pack showed seasonal differences in relation to livestock density, occurring in areas of higher livestock density during autumn and winter. Wild dogs breed during the autumn and winter months (April – June) and the resource requirements of the pack increases, necessitating the pack to hunt more often (Creel *et al.* 1997). Most wild herbivores give birth during the summer and spring months when forage is abundant (McNaughton & Georgiadis 1986) whereas livestock may have variable breeding seasons. Beef cattle have distinct calving times from January to February (Reist-Marti *et al.* 2003), but Boerbok goats are able to produce young any time of the year, showing peaks in reproduction during the autumn months (Malan 2000). Birthing periods of these domestic animals are dependent on feed available and the age of the nannies (female goats), and a farmer may decide to breed his livestock any time of year according to these characteristics (Osinowo *et al.* 2008). During the breeding season, wild dogs might therefore occur closer to areas that house livestock due to the presence of vulnerable livestock young.

Roads were shown to be a particular potential risk to wild dogs. The Waterberg and Bluebank packs occurred in close proximity to major roads, but whilst the Orpen pack was shown to utilise only minor roads, all three packs had a high likelihood of encountering major roads that carry fast-moving vehicular traffic. Within reserves, strict maximum speed limits of 50 km/h apply on tar roads and 40 km/h on dirt roads (SANParks Regulations 2015), and therefore these roads might do not pose a mortality risk to wild dogs. While roads within reserves enhance landscape permeability to aid wild dog space use (Abrahms *et al.* 2015) and are often used for herbivore flushing and capture (Kruger *et al.* 1999), major roads outside of reserves or protected areas carry traffic moving at speeds of 120 km/h and pose a serious mortality risk due to vehicular collisions (Fahrig & Rytwinski 2009). As human-altered landscapes are increasingly expanding, animals encounter major roads more often (Dickson *et al.* 2005) and automobile collisions are ascribed as one of the leading sources of human-caused vertebrate mortality (Shepard *et al.* 2008). Wild dogs are often accidentally killed when attempting to cross major roads (Collinson *et al.* 2015), but they may also be in danger of being deliberately struck (Soron 2008). The wild dog packs showed seasonal differences in proximity to roads, with the Waterberg, Skukuza and Orpen packs occurring closer to roads in summer, and the Bluebank pack occurring closer to roads during autumn and winter. Life history events, such as dispersal or breeding season, have been shown to affect space use and therefore the chances of animals encountering roads (Coffin 2007). Animals may need to range far in search of food (Coffin 2007). For example in southern Portugal, red fox (*Vuples vulpes*) and stone marten (*Martes foina*) encounter roads more during the breeding season (when young left behind at a den must be continuously provisioned with food) and therefore the risk of road mortality increases during this period (Grilo *et al.* 2009). In addition, herbivores may seasonally use roads when moving to different foraging patches (Trombulak & Frissell 2000) attracting carnivores. For example, caribou (*Rangifer tarandus*) in Alaska use roads in winter when travelling to find new feeding sites, resulting in increased encounters with and mortality by grey wolves (*Canis lupus*) (Whittington *et al.* 2011).

No single human landscape feature predicted wild dog occurrence for all packs. The Waterberg pack occurred further away from human landscape features than were available in the environment (> 20km), the Orpen pack only occurred close to two of the 11 features available, and the Bluebank pack occurred close to only the military landscape feature. Reservoir (dam) sites may be an attractant to wild dog packs outside of reserves as a water resource (Dake 1983). Wild dogs within nature reserves may be attracted to rest camps (residential sites) due to cooking smells or due to hunting opportunities. Most of the major camps in Kruger are built close to natural or artificial water sources (Braack 2006), attracting many different herbivore species. For example, the Skukuza rest camp is built on the banks of the large, perennial Skukuza River, whilst there is a small water hole just outside the Orpen camp

(Braack 2006). Wild dogs have been documented to use camp and boundary fences as a tool to aid in prey capture, especially larger prey such as kudu and waterbuck (Van Dyk & Slotow 2003, Lindsey *et al.* 2004a, Rhodes & Rhodes 2004). The Waterberg pack did not occur in close proximity to any human landscape features, occurring at distances > 30 km. Areas such as commercial properties, industrial properties, quarries, retail properties and railway lines are highly urbanised areas that are hubs of noisy human activity (Carlino *et al.* 2007) and because wild dogs are naturally shy of humans and their activities (Breuer 2002), they would avoid these areas. Wild dog packs also did not occur in close proximity to landfill sites. Landfills are not expected to attract wild dogs, because unlike other predators, they almost never scavenge food (Creel & Creel 2002).

In addition to anthropogenic landscape features, I also assessed which natural landscape features were important determinants of wild dog packs occurrence. Rivers were not significant predictors of wild dog occurrence, and both non-perennial and perennial river classes were utilised similarly by all packs. The odds of occurrence at perennial rivers were high for all packs. Additionally, most grazers, such as wildebeest, warthog, roan and zebra, are highly dependent on water sources and will often occur close to rivers or other reliable water sources (Valeix *et al.* 2008), with herbivore presence decreasing as distance to permanent water sources increases (De Leeuw *et al.* 2001). Waterbuck, an often-hunted herbivore by wild dogs, are particularly constrained by surface water availability, never occurring far from water sources (Redfern *et al.* 2003). The Waterberg, Bluebank and Orpen packs showed seasonal differences in proximity to rivers, occurring closer to rivers during the dry months (autumn and winter). The need to drink becomes greater when water becomes scarce (Valeix *et al.* 2008), therefore prey will likely be found closer to water sources during the drier seasons.

Nature reserves were important predictors of wild dog occurrence for all packs. Nature reserves were of particular importance to the Waterberg and Bluebank packs, as the home ranges of these packs overlapped several reserves, although both packs' core 10% home ranges were outside of the nature reserves. The Orpen pack also utilised the adjacent Timbavati Nature reserve, and the pack's 10% home range lies within Timbavati, indicating that this reserve is an important part of the pack's home range. Although the Skukuza pack was observed to remain within Kruger, the Sabie Sands private nature reserve would be easily accessible for the pack, as it occurs adjacent to the Northwest of Skukuza, separated from KNP by the Sabie River. Protected areas are important habitats for wide-ranging or migratory animals, because they provide valuable resources such as shelter and food (Thirgood *et al.* 2004). The value of protected areas have also been made apparent for the establishment of meta-populations, as animals may move between different protected areas and mate with unrelated individuals, improving fitness of individuals and species persistence (Hanski & Ovaskainen 2000). Outbreeding is particularly critical for endangered species, such as the wild dog, because due to small population sizes, they are particularly prone to Allee effects and the resultant problems, such as disease outbreaks (Somers *et al.* 2008).

Vegetation was a significant predictor of wild dog occurrence. The Waterberg pack utilised Waterberg Moist Mountain bushveld (described as a dense vegetation type, De Klerk 2003) more than any other vegetation type, whilst the Skukuza and Bluebank packs utilised Mixed Lowveld Bushveld, and the Orpen pack utilised Sweet Lowveld Bushveld. Although these vegetation types were most abundant in the regions where the different packs occurred, and presence may be due to availability, other vegetation types were available in the environment but not used. The wild dog packs may therefore prefer these vegetation types to others. Vegetation may be used as refugia, because wild dogs move between human-modified habitats to avoid contact with humans, a tactic often employed by carnivores in human-altered landscapes (Schuette *et al.* 2013). Spotted hyena (*Crocuta crocuta*) in Kenya have been observed to utilise areas with dense vegetation to avoid areas where livestock are grazed (Boydston *et al.* 2003), and red fox in northern Illinois, USA, utilise dense woodland habitat on the edges of human settlements, even though prey abundance in these areas are lower (Randa & Yunger 2006). Most herbivores, including Burchell's zebra (*Equus quagga burchellii*) and blue wildebeest prefer certain grass types, due to palatability, digestibility and availability in the environment (Hanley 1982, Ben-Shahar & Coe 1992, Bodenstein *et al.* 2000), and therefore wild dogs may also favour vegetation types due to presence of prey. Cheetah favour habitats with 25– 50% woody cover and medium height grasses as these provide the best cover when stalking prey (Gros and Rejmánek 1999), and without adequate vegetation cover while stalking, cheetah hunts are three times less successful (FitzGibbon 1990). Whilst the height of surrounding vegetation does not affect wild dog hunting success (Fanshawe & Fitzgibbon 1993), vegetation may affect prey availability and offer cover whilst moving through farmland or other human-altered landscapes

Conclusion

Space use patterns and resource selection of four packs of African wild dog in Mpumalanga and Limpopo Provinces indicate that, whilst wild dogs may occur in close proximity to farms and areas that house livestock, these carnivores (at least the two packs outside reserves) establish home ranges in areas with few farms and low livestock densities. This indicates that wild dogs predictively avoid farms and areas of high livestock densities, as frequent or prolonged occurrence in these areas would lead to mortality. Wild dogs in the Mpumalanga and Limpopo Provinces in South Africa therefore do not seem to be avid depredators of livestock. The Waterberg pack may however be particularly vulnerable to human-carnivore conflict due to their close proximity to farms and high livestock density areas, necessitating management strategies and the cooperation of livestock farmers and game breeders specifically in this area. Of the seven anthropomorphic and natural landscape features considered here, livestock density, human land use, roads, nature reserves and vegetation were important predictors of wild dog occurrence. Wild dog occurrence on major roads are of particular concern, as this would be source of wild dog mortality, in addition to conflicts with farmers. Agricultural landscape features were predictors for three wild dog packs and rivers were predictors of two wild dog packs, indicating that these landscape features and the resources they represent may be of pack-specific importance. RSFs have therefore shown that multiple features in the landscape affect wild dog spatial and temporal occurrence.

Supplementary material

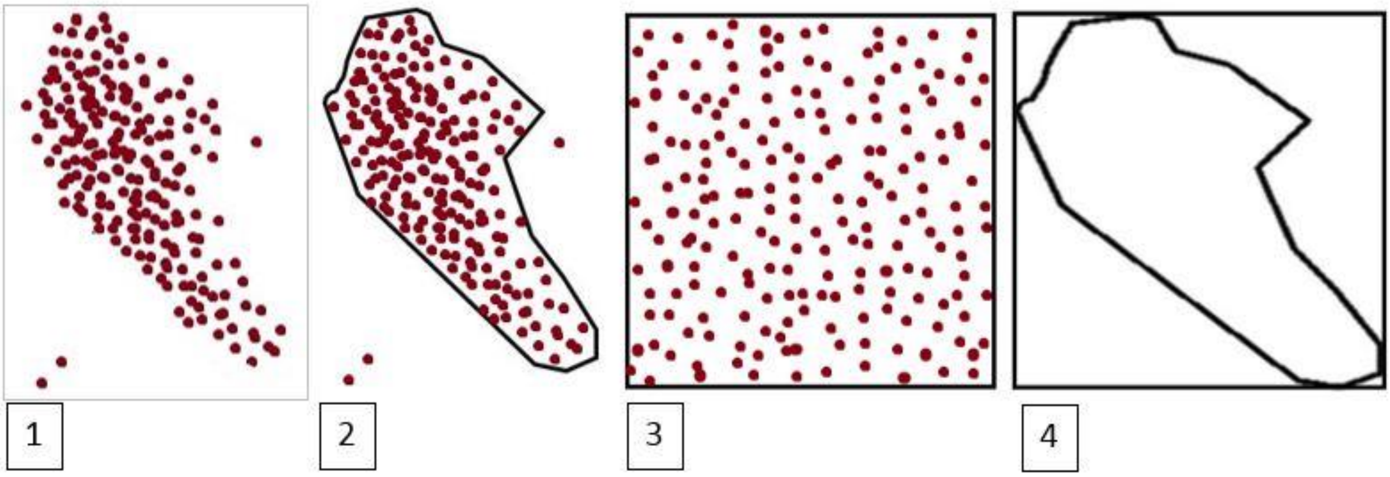

Figure S1. Visual representation of why a Home Range Square (HRS, square black outline) is a better method for the creation of random points than a Minimum Convex Polygon (MCP, black outline).

1. Original number of 200 GPS fixes for a fictitious organism.
2. When a MCP is created, it only encompasses 90% of the original number of points, excluding outlier points.
3. A HRS with 200 random points. It can be seen that the configuration of points are more "random" in a HRS than would be in a MCP.
4. A MCP overlaid on a HRS. The HRS encompasses more area without being larger in dimension than the original set of points.

Table S1. Description and characteristics of environmental features used in Resource Selection Function analyses for four African wild dog packs in Limpopo and Mpumalanga Provinces, South Africa. Feature subclasses and descriptions were taken from pre-existing shapefile attribute tables in ArcMap, except for agricultural landscape features, which I defined. Features marked with † indicate possible sources of mortality of wild dogs.

Feature group	Feature name & File type	Feature subclasses	Feature description
Anthropogenic	**Livestock density** † - raster file	Cattle Goats Poultry	Global livestock density per km^2 downloaded and modified from the FAO. Sheep were omitted of this analysis, as the raster indicated that my study sites contained zero (low) densities of sheep, with high densities occurring in the drier, south-western parts of South Africa
	Agriculture † -shapefile	General farm Hunting lodge Game farm Poultry farm Goat farm Fruit and Nut	- farms keeping multiple livestock types, game or both (mixed-purpose). - lodge where plains game are kept for the purpose of trophy/meat hunting - farms where plains game are bred for sale/conservation purposes - farms producing exclusively poultry products (meat/eggs/feathers) - farms producing exclusively goat products (meat/milk/cheese/mohair) - farms producing exclusively fruit and nut crops
	Roads † - shapefile	Motorway Motorway link Trunk Trunk link Primary Secondary Residential Tertiary Track Unknown Footway	- highway, speed limit 120 km/h - connecting road for highways, speed limit 120 km/h -major road, speed limit 120 km/h - connecting road for major roads, speed limit 80 km/h - public road outside urban area, speed limit: 100 km/h - public road within a nature reserve, speed limit 50 km/h - public road within an urban area, speed limit 60 km/h - dirt road, speed limit: 30 km/h - secondary rough dirt road, speed limit 20km/h - unclassified road, speed limit 20km/h - trails used by humans t travel on foot
	Human land use -shapefile	Residential Commercial Reservoir Quarry Cemetery Recreational Grounds Retail Industrial Military Landfill Railway	- housing predominated area - area predominated by businesses and office complexes - artificial storage area for water - excavation site for rock and other construction aggregate - burial place of human remains - grassy area designated for sports and other outdoor activities - area predominated by shopping centres - heavily urbanised area with many factories - areas occupied by the Department of Defence - site for the disposal of waste materials - permanent track for transportation by train
Natural	**Nature reserve** -shapefile	National Private	State owned or privately run areas under formal protection for the conservation of wildlife and ecosystems
	Rivers -shapefile	Perennial Non-perennial	- flowing water is available year-round in parts of the stream bed - flowing water is available only for short periods during some times of the year, usually only after rainfall events
	Vegetation -shapefile	Waterberg Moist Mountain Bushveld Mixed Bushveld Clay Thorn Bushveld Mixed Lowveld Bushveld Forest Mopane Bushveld Grassland Sweet Lowveld Bushveld	Vegetation types found in the Limpopo and Mpumalanga provinces as used in the SAFARI 2000 project undertaken by the National Botanical Institute

Chapter 4

Discussion

My study set out to investigate human-wildlife conflict relating to the African wild dog (*Lycaon pictus*) in a global and regional context and the home range characteristics and resource selection of these carnivores to ascertain predictors of their occurrence and their vulnerability to persecution by people. The mosaic of heterogeneous livestock farming practices and protected area landscapes in South Africa, the endangered status of the wild dog and the ongoing persecution of this carnivore, provides abundant opportunity to study human-carnivore conflict.

In Chapter 2, I aimed to assess patterns of human-carnivore conflicts relating to wild dog in southern Africa compared to other carnivores both locally and globally through a meta-analysis of published scientific literature. This study showed that high carnivore densities, high livestock densities and poor communities with poor husbandry practices might contribute to heightened human-carnivore conflicts in developing regions, making carnivores in these regions, like the wild dog, specifically vulnerable to retaliatory killings. Wild dog caused comparable levels of livestock depredation when viewed in a global context, but caused fewer livestock losses in an African context compared to other African carnivores, such as lion and spotted hyena. The findings of Chapter 2 also highlighted gaps in the literature about captive game depredation by wild dog, a topical issue in South Africa. In Chapter 3, I aimed to assess human-carnivore conflict relating to wild dog at a regional scale, with particular focus on comparing the spatial and temporal occurrence patterns and resource selection of four wild dog packs in the Limpopo and Mpumalanga Provinces, South Africa. The analyses indicated that whilst wild dog packs may occur in close proximity to farms, home ranges were established in areas with fewer farms and lower livestock densities, possibly indicating predictive avoidance of high conflict zones. Additionally, occurrence on roads with fast-moving traffic and road mortality was highlighted as a concern for wild dogs, whilst other anthropogenic and natural landscape features varied in importance as predictors of wild dog pack occurrence.

Worldwide biodiversity losses are an ever-growing concern during the last decades, with considerable numbers of species lost due to human activities such as agricultural intensification (Tscharntke *et al.* 2005). Conflict between farmers and carnivores is an ongoing global issue (Treves & Karanth, 2003) and is ascribed as a major reason of carnivore declines due to retaliatory killings for loss of livestock (Michalski *et al.* 2006). This makes species that are already considered as endangered, such as the wild dog, particularly vulnerable to conflicts with humans. My results have shown that globally, similar types of livestock, especially goats and cattle, are most at risk of depredation by carnivores. These two particular livestock types are often kept at high densities throughout the world due to their ease of keeping, hardiness, high fertility and flexible birthing seasons (Strydom *et al.* 2000, Snowder

& Duckett 2003). These high livestock densities can be associated with a higher vulnerability to depredation from different types of mammalian carnivores.

When compared globally, African carnivores are comparable depredators to non-African carnivores, although South Africa has unique carnivore assemblages (Dalerum 2013) and is one of the most biotically diverse countries in the world, ranking 6th out of 17 other megadiverse countries (Brooks *et al.* 2006). It is important to consider is that South Africa is one of the smallest out of these other regions, second only to Madagascar (Thuiller *et al.* 2006), making South Africa unique in the human-carnivore landscape. Another unique aspect to South Africa is that of game depredation. Whilst other regions may keep game (such as reindeer in Norway, Johannesen & Skonhoft 2011), it is not on such a large scale or with such booming profitability as the South African game ranching and hunting industry (Bothma 2005). Because many areas in South Africa are unsuitable for crop production (Shackleton *et al.* 2001), game species are relatively easy to keep on natural feed, with little supplementary feed usually needed (Trollope 1990). Additionally, game can be more productive than livestock as they may breed faster, be less disease-prone and require less intensive labour and range management (Carruthers 2008). The game ranching industry not only supplements the meat market, but also provides income from sport hunting, an activity that generates R3.1 billion in profits compared to game meat production generating R42 million (Du Toit 2007). This creates a large potential for conflict with carnivores which depredate these game species.

Another unique aspect that contributes to human-carnivore conflict in South Africa is the histories of protected areas and the bordering communities. These communities were evicted form lands set out for conservation (DeGeorges & Reilly 2008) and moved into impoverished areas adjacent to reserves (Anthony 2007). Consequently, my results have shown that goats are especially prevalent in poorer, developing regions and are therefore often popular in subsistence agriculture. These poorer communities generally cannot afford expensive livestock husbandry practices or sophisticated equipment (Morton 2007), thus magnifying their vulnerability to human-carnivore conflicts. Considering the importance of food security needs in developing countries, such as South Africa (Samberg *et al.* 2016), the depredation of livestock as important food resources (Atwood & Breck 2012), the poverty of many rural communities (Anthony 2007) and adverse climatic conditions hindering crop production (Blignaut *et al.* 2009). Human-carnivore conflict within South Africa is therefore likely to influence the food security of many people, especially those in rural areas.

Protected areas provide important resources for wildlife, such as the wild dog. Wild dog are therefore likely to occur in these protected areas, either resident (such as the Skukuza wild dog pack) or moving between several different protected areas (such as the Waterberg and Bluebank packs). This increases the likelihood of wild dog packs occurring outside of large protected areas encountering communities bordering protected areas, likewise increasing their vulnerability to conflict with humans. Due to the proximity of agricultural areas to protected areas in South Africa, resulting from the historical occurrences mentioned earlier, and greater carnivore densities, the likelihood of human-carnivore conflicts is greater in these areas than regions where carnivores are mostly free roaming and occur in lower population densities per km^2 (such as North America). Maintaining large home ranges stretching over a mosaic of protected areas and farmland (in the Waterberg and Bluebank packs) may expose wild dogs to threats along boundaries of small protected areas or reserves, including snares, major roads, domestic dog diseases and hostile farmers (Jenkins *et al.* 2015). Additionally, wild dog packs within reserves are under risk from bordering human communities that harvest game illegally (Rangarajan 2003), often by using wire snare traps (Balme *et al.* 2010). A study in Mkuze Game Reserve recorded multiple wild dog deaths and injuries from snaring (Jenkins *et al.* 2015).

Agricultural areas affect wild dog probability of presence. My results have however shown that, though they are reported to depredate cattle and goats and may occur in areas of high cattle and goat densities (Chapter 2), home ranges (95%) are established in areas housing few-zero livestock, whilst 10% home ranges were only established in areas of zero livestock densities (Chapter 3). Wild dog may pre-emptively avoid farmland due to previous negative experiences, such as observing mortality of pack members, also known as predictive avoidance (Valeix *et al.* 2012, Broekhuis *et al.* 2013). Predictive avoidance behaviour has been shown in other species, such as lion (*Panthera leo*) in Botswana avoiding cattle posts (Valeix *et al.* 2012), puma (*Puma concolor*) in California avoiding areas of high human activity such as housing neighbourhoods (Wilmers et al. 2013) and brown bear (*Ursus arctos*) in Scandinavia avoiding areas of human habitation during the daytime, when humans were most active (Martin *et al.* 2010). Additionally, wild dog may be naturally cautious of farmlands due to their innate fear of humans (Breuer 2002).

Depredation of livestock might therefore be isolated incidents and if wild dogs do avoid farmland areas, they may possibly be preying on captive bred game or wild herbivores. The lack of literature on game depredation by wild dog, as well as by other carnivores in South Africa, necessitates future studies on this specific type of human-wildlife conflict. Wild dogs are diet flexible with a broad dietary niche (Hayward *et al.* 2006b), and can easily switch from smaller-bodied prey such as Oribi (*Ourebia ourebi*) to their preferred prey impala (*Aepyceros melampus*), or large-bodied prey such as waterbuck (*Kobus ellipsiprymnus*) or kudu (*Tragelaphus strepsiceros*) (Owen-Smith & Mills 2008). Wild dog prefer natural prey, even in the presence of free-roaming livestock (Fuller & Kat 1990, Rasmussen 1999, Woodroffe *et al.* 2005b) but will switch to livestock if natural prey is severely depleted (Woodroffe *et al.* 2005a). Areas outside of protected areas are prone to contain less natural prey (Robinson & Bennett 2004), caused by unsustainable harvesting from humans, a common occurrence in poorer countries where humans rely on natural resources to supplement their calorie requirements (Madhusudan & Karanth 2002). Wild dogs may be utilising areas between high livestock densities to avoid not only farmers, but also other, larger predators such as lion. Wild dog often avoid lion through adjustments of core space use within their home ranges to evade competition, kleptoparasitism and mortality (Darnell *et al.* 2014). If areas containing low livestock densities attract fewer lion, such areas may serve as refugia for wild dog and may be important for their survival in human-altered landscapes.

Whilst biosphere reserves, such as the Waterberg Biosphere Reserve (BR) and Kruger to Canyons BR, promote sustainable use of the environment by local people (Dogsé 2004), many municipalities are rife with corruption and suffer from funding shortages (Manyaka & Nkuna 2014). Additionally, the environmental authority within the South African Department of Finance and Economic Development (DFED) is marginalised and under-staffed (Anthony 2006). These problems mean that the implementation of policies and active monitoring by local authorities are neglected (Anthony *et al.* 2010). This implies that, if wild herbivores in the Waterberg region were scarce due to over-harvesting, wild dogs, along with other carnivores in this region, would switch to livestock or captive-bred game for their food requirements. Carnivore preference for wild prey over domestic stock would thus be encouraged by efforts to keep wild prey populations mostly stable, especially in areas where livestock occur. It must however be considered that the occurrence of conflict with carnivores, though stemming mostly from depredation, is not uniformly spread in the landscape (Kushnir *et al.* 2010), and would be determined by a complex number of different factors (Winterbach *et al.* 2013). Hence, in accordance with suggestions by Muntifering *et al.* (2006), assessing human-carnivore conflict at a local scale would be important for the development of site-specific mitigation strategies.

The magnitude of wild dog conflict with farmers and communities still requires further investigation even though it is a topical issue due to livelihood concerns of people and conservation needs. I identified vulnerabilities and other landscape features of varying importance for the wild dog in about ~10% of the population. Based on the predicted number wild dogs in South Africa (<500, Dr Kelly Marnewick in litt), I effectively sampled 10% of the population. However, my findings may be location-specific for the north-eastern parts of South Africa. Packs in other parts of the country, such as those occurring in KwaZulu-Natal Province, would be subject to different climatic conditions, geography and vegetation structures as well as encountering different herbivore and livestock assemblages. These packs might therefore employ different resource selection strategies. I suggest that future studies incorporate more wild dog packs to complement the results I have presented here.

Wild dog behaviour and morphology may influence the likelihood of these carnivores coming into conflict with humans. Whilst being highly social (Estes 1991) means that wild dog packs have large home ranges (for example the Waterberg pack's 100% home range comprises 2,132 km^2) and may encounter herds of livestock and farms whilst roaming, this does not make them more likely to depredate livestock (such as cattle or goats) than an ambush or opportunistic predator. The highly social nature of the wild dog also does not make them more likely to depredate livestock than solitary or social carnivores. Due to the obligate sociality of wild dog (Van Den Berghe *et al.* 2012), however , the loss of a single individual wild dog is not only damaging to the already endangered population as a whole, but may be devastating to a pack, that relies on all individuals for hunting and raising of pups (McNutt & Silk 2008). The critical size threshold for a wild dog pack has been established as five adult individuals (Courchamp *et al.* 2002). This means that if individuals are killed during human-carnivore conflict or hit by a vehicle, it affects the wellbeing of an entire pack, especially for smaller packs.

With less than 500 individual wild dogs left in the wild (Dr Kelly Marnewick in litt), it is clear that there is a need for effective management of wild dog populations and the cooperation of communities and farmers to aid the recovery of this species on the brink of extinction. Wild dogs have been regularly killed for being suspected livestock depredators (Woodroffe *et al.* 2005a) and although the literature implicates these carnivores as culprits, my study has indicated that the view of these carnivores as avid stock-killers may not be justified. The fact that many wild dog killings result from superstitious beliefs (Page 2014) and negative perceptions (Woodroffe *et al.* 2005b) reaffirm the need for the education of rural communities and farmers to improve the public image of the wild dog and dispel myths. My study has provided novel insights into the historical depredation of livestock and the resource selection behaviour of the wild dog and will aid in the identification of wild dog vulnerabilities and areas of potential occurrence for use in conservation plans.

Conclusion

My study is unique and the first to evaluate and quantify the historical depredation reported by publications for wild dog in comparison with other carnivores both locally and globally, as well as the resource selection of these carnivores using multiple anthropogenic and natural landscape features. Though wild dog have been reported to kill stock such goats and cattle, my investigations indicate that these carnivores predictively avoid farmland and areas housing livestock, at least in two packs that would have encountered anthropogenic landscapes. Packs outside of formal protected areas would however still be vulnerable conflict with farmers that encounter these carnivores in close proximity to their livestock or captive trophy game species. The survival of the wild dog is already precarious, given small population sizes prone to deadly infectious disease outbreaks like canine distemper, competition with other carnivores, vehicular collisions on roads and retaliatory killings for depredation. The dichotomy between the different farming sectors (subsistence vs commercial) in South Africa, coupled with the history of protected areas and the livelihood needs of people and the conservation needs result in unique resource conflicts between humans and the wild dog. This situation makes clear the need for the cooperation of farmers and conservationists and the education of communities to aid the population recovery of this uniquely African carnivore.

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