

Mesopredator release and the effectiveness of camera traps for estimating mammal abundances in the Eastern Cape, South Africa

A thesis submitted in fulfilment of the requirements for the degree of

MASTER OF SCIENCE

of

RHODES UNIVERSITY

By

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November 2015

Abstract

Remotely operated cameras (camera traps) have become an indispensable tool for many ecologists, particularly those studying rare and elusive animals. A plethora of camera trap makes and models are now commercially available, yet the effects of their varying design features on the quality and quantity of data recorded remains principally unknown. Better understanding of differing camera trap designs is needed before adequate management policies can be implemented, especially when the aim is to protect vulnerable and endangered species such as many carnivores. Habitat loss and human conflict has prompted worldwide declines of apex predator populations. Following this, many smaller predators have undergone population 'explosions' due to the lack of top-down forcing, a phenomenon known as mesopredator release. Land use changes in the Eastern Cape of South Africa have caused extensive degradation and fragmentation of the Subtropical Thicket Biome. In addition, coupled with anthropogenic persecution, apex predators including lions (*Panthera leo*), leopards (*P. pardus*), and brown hyaenas (*Hyaena brunnea*) have been extirpated from large areas of their historic range. Removal of these apex predators may provide opportunity for mesopredators, such as black-backed jackals (*Canis mesomelas*) and caracals (*Caracal caracal*), to be released from top-down forcing and possibly initiate trophic cascade effects. Therefore, using randomly distributed camera traps, my study aimed to explore the quality and quantity of data collected by different camera trap designs, and to investigate the mesopredator release hypothesis in the Eastern Cape of South Africa. A total of 2,989 trap nights was used to compare camera trap designs. Camera traps with narrow detection zones and fast trigger speeds (≤ 0.25 seconds) recorded a higher diversity of carnivores, but there was no significant difference in the relative abundances of carnivore species recorded by different camera trap models. A total of 19,659 trap nights was used to assess mesopredator relative abundance, occupancy, distribution and daily activity patterns at one site with, and one site without, apex predators. Consistent

with the mesopredator release hypothesis, black-backed jackal relative abundance was significantly higher in the absence of apex predators, and this was supported by occupancy analyses. Further, black-backed jackal distribution was significantly concentrated in areas where apex predator activity was low, possibly indicating spatial avoidance. There was no significant difference in caracal relative abundance, occupancy, distribution, or daily activity between sites. These results provide the first indication of mesopredator release of black-backed jackals in the Eastern Cape. The implications of black-backed jackal release including prey population structure, local extinctions, altered seed dispersal and disease dynamics are discussed.

Key words: Camera trap, *Caracal caracal*, *Canis mesomelas*, Mesopredator release, Occupancy, Relative abundance, Trophic cascade.

This thesis is dedicated to my mother, Anne Taylor, also my brothers James and Joseph Taylor. Their unwavering love and support, in all I have ever attempted, has sustained me when I needed them most. I love you all dearly.

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Acknowledgements

- ✿ First and foremost I would like to thank my supervisor Dr. Daniel Parker. His financial support during the first year of this project helped turn my dreams into reality. Furthermore, this project would not have been possible without his research vehicle and field equipment for which I am extremely grateful. Additionally, he provided support and motivation when personal issues overshadowed my research. For that I am particularly thankful.

- ✿ Thanks also go to my good friend Armand 'Chutters' Kok for all his help with field work. Thicket vegetation and less than perfect weather conditions made field work tough, though his company throughout has left me with many memories. I hope one day we can release songs such as 'kevlar kudu and the bulletproof bontebok' that were written on the fly during long hikes between camera stations.

- ✿ I would also like to thank all other members of the Wildlife and Reserve Management Research Group (WRMRG) at Rhodes University, particularly Gareth Mann and Charlene Bissett. Critical and creative discussion during 'oggend diens' has helped tremendously.

- ✿ Arthur Bissett also deserves recognition for his exquisite craftsmanship in producing safe and secure housings for cameras. Several cameras were 'investigated' by baboons, elephants and warthogs, but no damage occurred thanks to the metal casings he provided.

- ✿ The PhotoGoFer team in Albuquerque, New Mexico, are also hereby acknowledged for allowing me to use the development version of their software. It helped immensely with processing images, and I hope my feedback helped in some way with development of the final release.

- ✿ Research such as this is only possible with co-operation of land owners. Therefore, sincere thanks go to the owners and managers of reserves that were part of this study. Furthermore, I would like to thank all the reserve staff members for their help and support during field work.

- ✿ My good friend Graham Parker also deserves thanks for taking the time to proof read this thesis. I now consider myself well schooled in consistent use of the comma, and will never again be thwarted by the sub-ordinate clause.

- ✿ Last, but by no means least, I would like to thank all my friends and family that have supported me through life's journey. Ultimately, they have shaped me into who I am, and have helped me find my way. They have listened when I needed to consolidate in them, and they have provided advice when it was needed. I am honoured to have such amazing people in my life, I thank you all.

Chapter 1

General Introduction

1.1 A brief history of camera trapping

Since the invention of the camera in the nineteenth century, many people have sought to photograph wildlife. It was soon realised that wildlife photography may shed light on aspects of animal biology that had never before been known. For instance, in 1878, Eadweard James Muybridge placed 12 cameras in a row and had a horse (*Equus ferus*) run past them (Kucera & Barrett 2010). As the horse ran, it broke strings that activated each individual camera shutter. The resulting sequence of photographs showed that at certain points, a horse has all four feet off the ground during a full gallop (Kucera & Barrett 2010). Muybridge's work was also one of the first instances of an animal triggering pictures of itself (Kucera & Barrett 2010).

George Shiras III later became known as the father of remote photography (Kucera & Barrett 2010). He constructed mechanisms whereby baited strings or tripwires simultaneously lit magnesium flash powder and activated a camera (Figure 1.1.1) (Shiras III 1935a). Using different baits, Shiras used his automated system to photograph a wide range of wildlife. For example, carrion baited strings captured photographs of black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*), and cheese baited strings resulted in photographs of racoons (Figure 1.1.1) (Shiras III 1935a). Further, using dislodged sticks of American beaver (*Castor canadensis*) lodges as 'bait', beavers photographed themselves as they repaired their lodges (Shiras III 1935a). Furthermore, trip wires placed across game paths produced images of a wide range of deer species including white-tailed deer (*Odocoileus virginianus*) (Figure 1.1.1), caribou (*Rangifer tarandus*), moose (*Alces alces*), and elk (*Cervus canadensis*) (Shiras III 1935a, b).

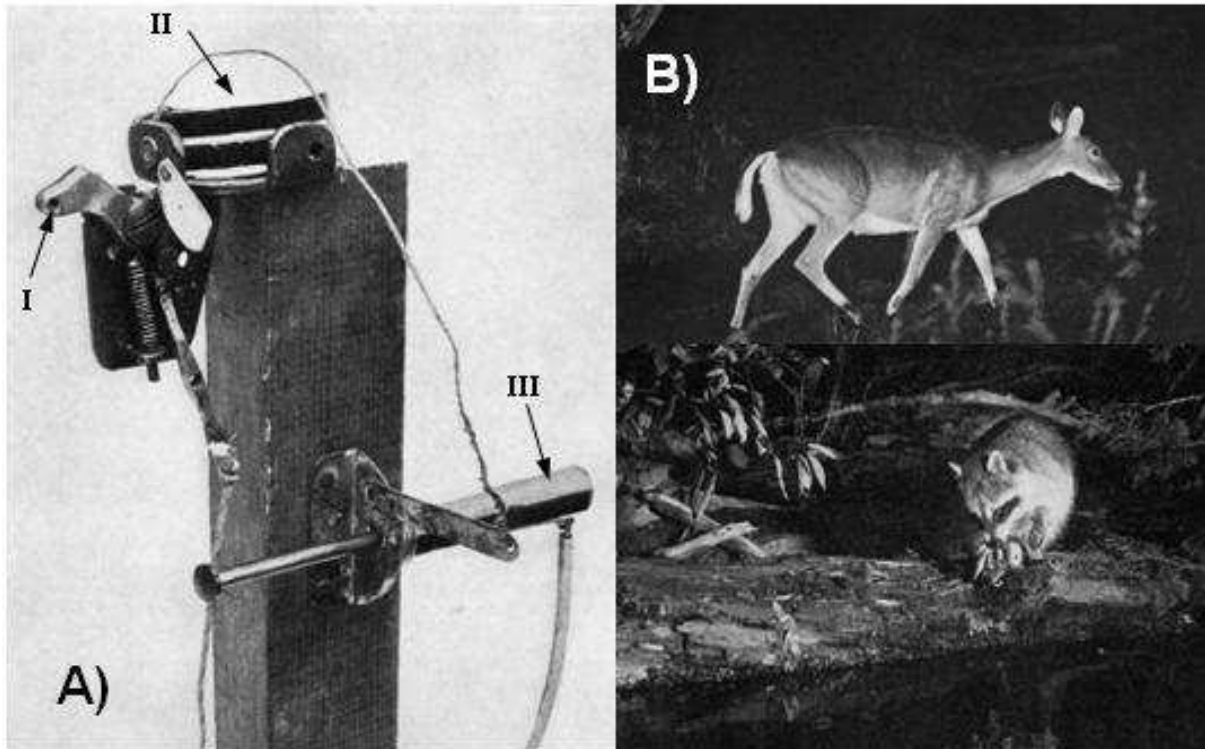


Figure 1.1.1 One of the mechanical triggers used by George Shiras III (A). A trip wire or baited string was attached to the trigger (I). When activated, magnesium flash powder ignited and forced the lid off the powder box (II). In turn, the curved wire leading from the powder box released the spring actuated air pump (III), which activated the camera shutter. This apparatus produced many successful photographs (B), including species such as white-tailed deer (*Odocoileus virginianus*) (above) and raccoons (*Procyon lotor*) (below). Images modified from Shiras III (1935a).

Camera traps became commercially available in the early 1990's (Swann, Kawanishi & Palmer 2010). Technological advances have allowed for infrared (IR) sensors to replace the mechanical devices used by George Shiras and others. Additionally, digital cameras have replaced film cameras, allowing for more images to be captured and stored. Further, miniaturisation of components such as batteries and flashes, coupled with improved camera and sensor technologies, means that modern day camera traps are compact, unobtrusive and can be left in the field for extended periods (McCallum 2013). Following this, camera traps have been adopted by many wildlife enthusiasts for recreational use; have been used as security and surveillance tools; are used to monitor game species important to the hunting industry, and have seen wide scale application in ecological research (Rovero *et al.* 2013).

1.2 Food web dynamics and their role in structuring ecological communities

Following the trophic dynamics model of Lindeman (1942), general consensus among ecologists was that all trophic levels within any food web are solely regulated by 'bottom-up' forcing effects. Bottom-up forcing argues that ecological communities are ordered and maintained by structural factors such as habitat availability, and by energetic factors including nutrient availability. For example, sunlight, water and soil nutrient content determine the rate at which primary producers, *i.e.* plants, can fixate carbon via photosynthesis. Furthermore, plant secondary metabolites such as tannins are often difficult to digest or even toxic (Marsh *et al.* 2003; Barbehenn & Constabel 2011), which may limit the flow of energy from primary producers to primary consumers, *i.e.* herbivores (Sorensen, Heward & Dearing 2005; Sorensen, McLister & Dearing 2005). In turn, energy lost during metabolic processes, and the efficiency at which these primary consumers convert energy into body mass, imposes limits on the available energy for secondary consumers, *i.e.* a predator (Hairston & Hairston 1993). In this way, bottom-up forcing suggests that the biomass comprising each trophic level is limited exclusively by the amount of energy available in the preceding trophic level (Lindeman 1942; Fryxell, Sinclair & Caughley 2006; Molles Jr 2013).

Without doubt, the bottom-up effect of energy flow through ecosystems plays a significant role in shaping ecological communities. However, Hairston, Smith & Slobodkin (1960; Hereafter 'HSS') changed the way many ecologists view ecosystems by introducing the idea of top-down forcing. HSS highlighted that vegetation levels were seldom completely depleted by native herbivores alone, *i.e.* primary production levels are often under exploited by primary consumers. They therefore concluded that herbivores must be limited by top-down forcing, *i.e.* predation, from higher trophic levels (Hairston, Smith & Slobodkin 1960). Though HSS did not use the phrase themselves, their work became known as the 'green world hypothesis'. The hypothesis states that the world is green because predators limit herbivore abundance which, in turn, allows vegetation to flourish (Power 1992; Polis & Strong 1996; Steneck 2005; Morris 2008).

One example used by HSS to demonstrate this theory was the story of mule deer (*Odocoileus hemionus*) on the Kaibab Plateau of Arizona, U.S.A (Hairston, Smith & Slobodkin 1960). Unfortunately, complete data regarding the history of the Kaibab deer herd are lacking, yet the story is common in many ecology textbooks prior to the 1970s (Binkley *et al.* 2006). In 1906, as an attempt to conserve a herd of roughly 4,000 individuals, Theodore Roosevelt declared the plateau a national reserve. He banned sport hunting of the deer, ordered the removal of livestock and together with the United States Forest Service

encouraged the removal of predators including mountain lions (*Puma concolor*), wolves (*Canis lupus*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*) (Burk 1973). Following livestock and predator removal, the deer population irrupted from 4,000 individuals in 1906, to an estimated figure of 100,000 individuals in 1924 (Burk 1973). The plateau became severely over-grazed by such high deer densities, and within two years starvation had reduced the herd by roughly 60% (Caughley 1970). HSS implied that predation had maintained the herd at a size below food limited levels, allowing vegetation to thrive, and that removal of predators had allowed the herd to increase in size and over-exploit food resources (Hairston, Smith & Slobodkin 1960).

The increase in the Kaibab deer population between 1906 and 1924, though poorly documented, is fairly indisputable. Indeed, studies of the age structure of aspen (*Populus tremuloides*) on the Kaibab Plateau are consistent with overgrazing attributable to high deer populations in the 1920s (Binkley *et al.* 2006). However, many ecologists (e.g. Caughley 1970) question whether the increase was a direct result of predator removal, or whether other factors may have been the cause of the deer irruption. An estimated 195,000 domestic sheep (*Ovis* spp.) were removed from the plateau between 1889 and 1908 (Burk 1973), and it could be argued that being released from competition for food with livestock allowed the deer population to increase via bottom-up mechanisms (Caughley 1970). Importantly, HSS did not deny the effects of bottom-up forcing. They acknowledged that with no higher trophic level, predators must ultimately be resource limited (Hairston, Smith & Slobodkin 1960). Furthermore, if predators keep herbivore abundance low enough to prevent plants from being over-exploited, the plants themselves must also be limited by resource availability.

While contemplating HSS's 'the world is green' hypothesis, Fretwell (1977) questioned why the world is not uniformly green. He also noted that primary productivity affects the number of trophic levels that can be sustained, and asked if HSS's theory would hold in systems with more or fewer than three trophic levels. Firstly, Fretwell (1977) identified four underlying assumptions of HSS's theory; (i) populations are either resource or predator limited, but not both; (ii) predator limited populations *do not* limit the populations on which they feed; (iii) resource limited populations *do* limit the populations on which they feed; and (iv) each trophic level acts as a single population. Applying these assumptions to food chains of one to four links, Fretwell (1977) noticed a clear pattern whereby plants are always resource limited in food chains with an odd number of trophic levels. Conversely, in chains with an even number of trophic levels, plants are always 'predator' (herbivore) limited (Figure 1.2.1).

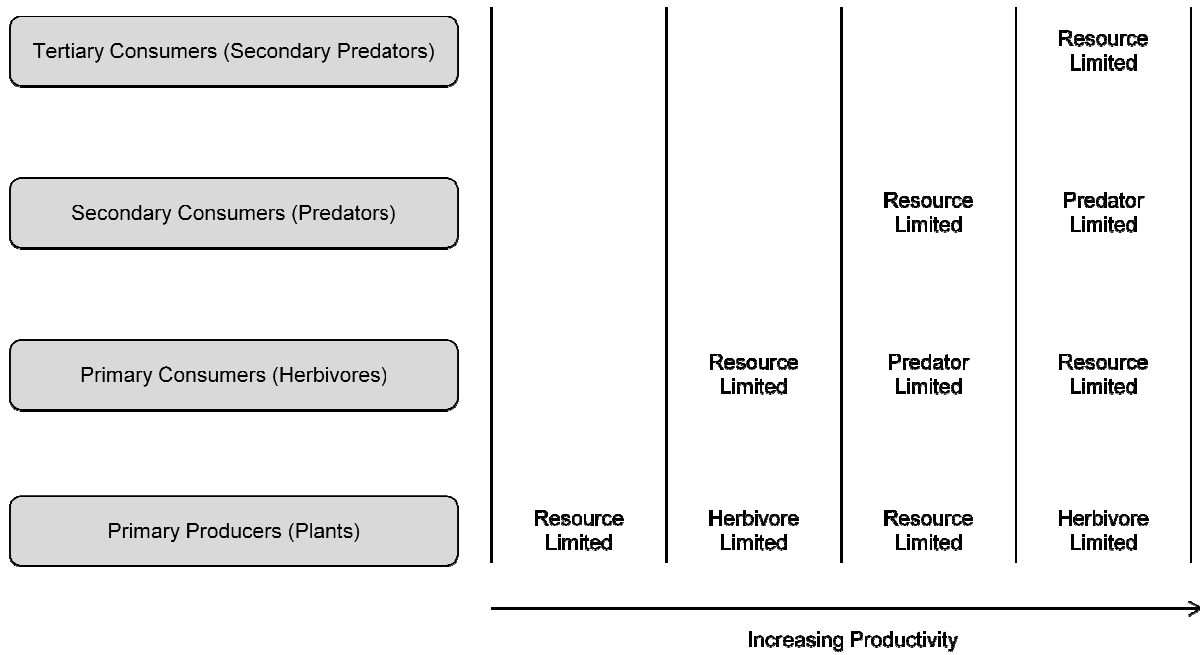


Figure 1.2.1. Fretwell's (1977) idea that increased productivity allows for the addition of higher trophic levels. Note how the highest trophic level is always resource limited and the effect this has lower in the food chain. In chains of an odd number of trophic levels, vegetation is always resource limited. Conversely, in chains with an even number of trophic levels, vegetation is always herbivore limited.

Fretwell further extended his ideas in collaboration with Oksanen *et al.* (1981) to develop the ecosystem exploitation hypothesis (EEH). Essentially, EEH predicts that primary productivity is the major determinant of food chain length, and that as food chain length changes, so too do the roles of top-down and bottom-up forcing in each trophic level (Oksanen *et al.* 1981; Oksanen & Oksanen 2000; Morris 2008). According to EEH, in three link ecosystems, plants and predators are resource limited, whereas herbivores are predator limited. This results in plant and predator biomass increasing with productivity, whilst herbivore biomass remains constant. Adding an additional trophic level (secondary predators) means that primary predators are then controlled via top-down forces. This in turn releases herbivores from primary predator control and results in plants then being subject to higher top-down control. Therefore, in four-link systems, secondary predator and herbivore biomass increases with productivity, while plant and primary predator biomass remains constant. Evidence corroborating EEH has been shown across productivity gradients in North America (Crête 1999) and Norway (Aunapuu *et al.* 2008), and by experimental manipulation of productivity in the UK (Fraser & Grime 1997; Fraser 1998).

Debate over the relative importance of top-down and bottom-up forcing, and the extent to which these processes structure ecological communities remains ongoing (Hunter & Price

1992; Power 1992; Closs, Balcombe & Shirley 1999; Menge 2000). Rather than think of these forcing effects as mutually exclusive, a more realistic view is that many (if not most) ecosystems are in a constant state of dynamic flux, whereby elements of top-down and bottom-up forcing occur simultaneously within each trophic level (Hunter & Price 1992; Andersen, Linnell & Solberg 2006; Terborgh, Holt & Estes 2010). For example, Power (1984) describes an interaction whereby armoured catfishes (Loricariidae) preferentially forage in deeper water, where food is in short supply, to avoid predation pressure in shallower water where food is more plentiful. In this way, the top-down effect of predation pressure forces fish into spatial refuges where they are more subject to the bottom-up effects of food availability. Furthermore, animal migrations such as those of many African ungulates may lead to spatial and/or temporal fluctuations in the effects of top-down and bottom-up forcing across multiple trophic levels (Fryxell & Sinclair 1988; Hopcraft, Olf & Sinclair 2010).

Clearly, the processes by which ecosystems are structured are strikingly dynamic and complex. The underlying assumption of the green world hypothesis and EEH, that trophic levels are the smallest ecosystem units and act as homogenous entities, is a drastic oversimplification of real world scenarios (Oksanen *et al.* 1981; Hunter & Price 1992; Polis & Strong 1996). Instead, factors such as body mass (Radloff & Du Toit 2004), diet breadth (Jiang & Morin 2005) and prey preferences of many predators (Hayward & Kerley 2005; Hayward *et al.* 2006a, b) mean that within each trophic level, different species fulfil separate ecological niches. As such, interactions between particular species within and between trophic levels may initiate top-down and/or bottom-up forces that cannot be generalized to entire trophic levels (Hunter & Price 1992). Therefore, rather than think of food chains as acting in a linear fashion, a more pragmatic view is that species within an ecosystem are all linked through intricate webs (Polis & Strong 1996).

The complexities of food webs become most apparent when a change in the abundance, distribution, or behaviour of particular species has both direct and/or indirect effects on seemingly unconnected species. Such effects are known as trophic cascades and have been demonstrated worldwide in terrestrial, freshwater and marine ecosystems (Terborgh & Estes 2010). For example, declines in pelagic fish stocks in the north Pacific Ocean during the 1980s were mirrored by pinniped population declines (Estes *et al.* 1998). Following this, killer whales (*Orcinus orca*) were forced to expand their diet to include sea otters (*Enhydra lutris*) (Estes *et al.* 1998). In turn, sea otter populations were depressed, allowing for an unregulated increase in sea urchin abundances. Consequently, kelp forests became severely overgrazed, which caused wide scale collapse in the coastal ecosystem of western Alaska (Estes *et al.* 1998). This link between pelagic fishes and coastal kelp forests serves

to highlight how unexpected and serious the effects of species declines can be. Therefore, trophic cascade effects clearly require further investigation if ecosystems are to be maintained in a healthy state.

1.3 The mesopredator release hypothesis

One type of trophic cascade that has received increasing attention during the last few decades is the mesopredator release hypothesis (MRH). Though they were not the first to demonstrate the phenomenon, the term ‘mesopredator release’ was first used by Soulé *et al.* (1988). Their work primarily aimed to gauge the effects of habitat fragmentation and isolation on native chaparral-requiring birds in San Diego, California, U.S.A. They found that habitat patch size and time since isolation had the most significant effects on chaparral-requiring bird diversity. However, inclusion of a mammalian predator variable showed some thought provoking results. They classified mammalian predator presence into three categories; 1) gray foxes (*Urocyon cinereoargenteus*) present, coyotes (*Canis latrans*) either present or absent; 2) foxes and coyotes absent, or; 3) coyotes present, foxes absent. Interestingly, chaparral habitats where coyotes were present, but foxes were not, generally exhibited higher bird diversity.

Soulé *et al.* (1988) likened this result to previous studies which had shown ‘explosions’ of spider numbers in the absence of lizards (Pacala & Roughgarden 1984; Schoener & Spiller 1987). They hypothesized that the presence of coyotes helped to control foxes and similar sized predators such as cats (*Felis catus*), raccoons (*Procyon lotor*), skunks (Mephitidae) and opossums (Didelphidae) which were more prolific predators of birds than coyotes. Therefore, in the absence of large predators, smaller predators could have become more abundant and may have increased local extinction rates of vulnerable prey species, a process which Soulé *et al.* (1988) called mesopredator release.

The MRH gained mathematical support with the models of Courchamp, Langlais & Sugihara (1999). Many insular ecosystems have suffered severe deleterious effects in many species, resulting from the introduction of non-native species (Hanna & Cardillo 2014). Courchamp, Langlais & Sugihara (1999) modelled such a situation where introduced cats (*Felis catus*) and rats (*Rattus* spp.) inflict a significant negative influence on local bird populations. Their somewhat simplified model incorporated intrinsic growth rates for super predator, mesopredator and prey populations. Further, they included values for predation rates of mesopredators on prey populations, and separate predation rates of super predators on both mesopredator and prey populations (Figure 1.3.1 A). Applying realistic values to these growth and predation rates, Courchamp, Langlais & Sugihara (1999) showed that super predators, mesopredators and prey could co-exist (Figure 1.3.1 B), whereas, removal of

super predators from the system drove the prey population to extinction (Figure 1.3.1 C), as predicted by MRH. Interestingly, their models also showed that in systems with no mesopredators, super predators and prey could co-exist, and that in systems with high super predator abundance, mesopredators were extirpated and super predators could then co-exist with prey populations.

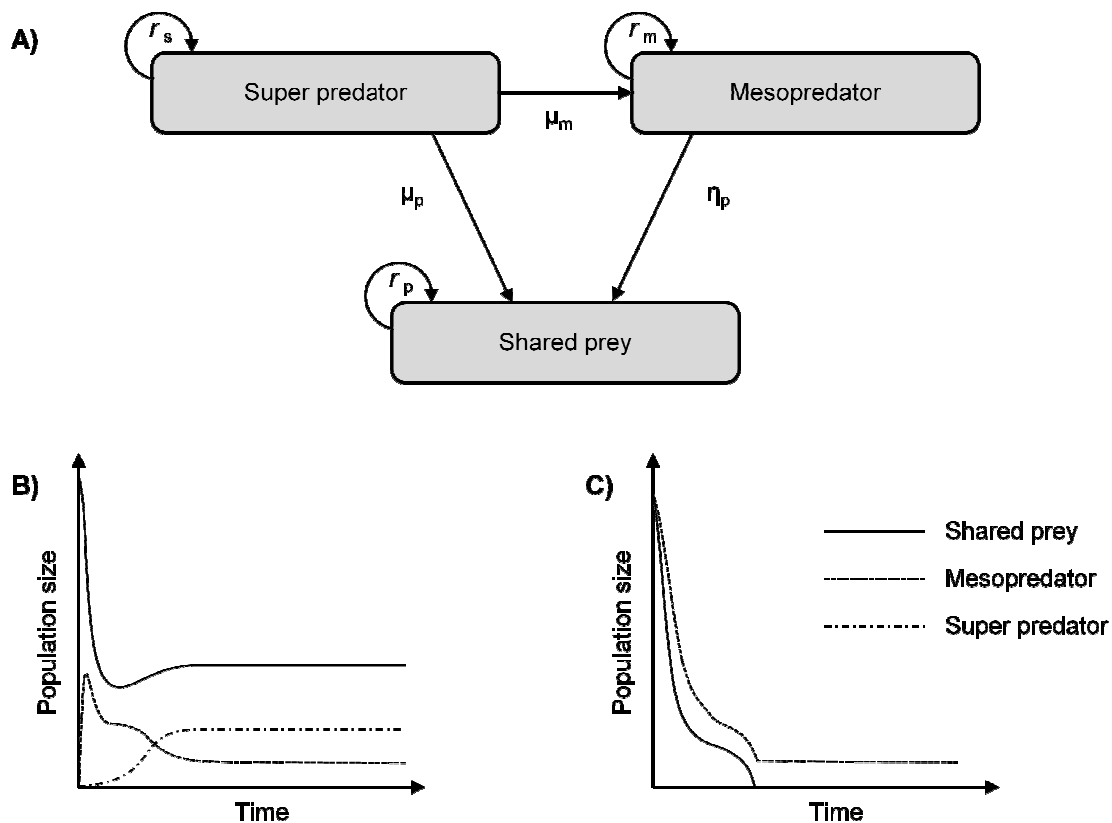


Figure 1.3.1. A) The model of Courchamp, Langlais & Sugihara (1999) whereby curved arrows indicate intrinsic growth rates of super predator, mesopredator and prey populations by r_s , r_m and r_p respectively, straight arrows indicate predation rates of super predators on mesopredators and prey by μ_m and μ_p respectively and predation rate of mesopredators on prey by η_p . B) Simulation results of a system containing super predators, mesopredators and prey showing that the system eventually stabilizes and all three populations can co-exist. C) Simulation results where super predators are absent and mesopredators drive the prey to extinction. Initial values for the simulations in B) and C) were 100,000 prey items, 100 mesopredators and 1 super predator. Prey, mesopredators and super predators are plotted on different scales. Figure modified from Courchamp, Langlais & Sugihara (1999).

Mesopredator release is often associated with habitat fragmentation (Crooks & Soulé 1999; Prugh *et al.* 2009). Large predators generally occur at low densities and require large home ranges, making them highly sensitive to habitat loss and fragmentation (Prugh *et al.* 2009; Balme, Slotow & Hunter 2010). Conversely, mesopredators normally require less space, and are therefore less affected by habitat fragmentation (Litvaitis & Villafuerte 1996; Crooks 2002). Moreover, many mesopredators may even benefit from habitat fragmentation and urbanization due to increased anthropogenic resources and/or spatial refuges from larger predators (Prange & Gehrt 2004; Cove *et al.* 2012).

The use of spatial refuges highlights that apex predators not only affect mesopredator abundances, but may also influence their distribution through 'landscape of fear' effects (Laundré, Hernández & Altendorf 2001; Ritchie & Johnson 2009). For example, in North America, coyotes preferentially disperse into, or through, areas where wolf (*Canis lupus*) abundance is relatively low (Berger, Gese & Berger 2008). Additionally, in Israel, apex predators have been shown to influence behaviour by altering foraging strategies of red foxes (*Vulpes vulpes*) (Mukherjee, Zelcer & Kotler 2009). Therefore, adding to the definition by Soulé *et al.* (1988), a more encompassing definition of mesopredator release is 'an increase in density, distribution or a behavioural change of middle ranked predators when the top-down forcing effects of larger predators are reduced or removed' (Prugh *et al.* 2009; Brashares *et al.* 2010). Importantly, it should be noted that carnivore species cannot be classified as mesopredators based solely on life history traits such as body mass, but instead must be classified in context of entire ecosystems. For example, in the presence of wolves, coyotes are mesopredators. Conversely, in areas where wolves are absent, coyotes may fulfil the role of an apex predator (Crooks & Soulé 1999; Berger & Conner 2008; Ritchie & Johnson 2009).

1.4 Motivation & Aims

The range of camera traps that are now commercially available is extensive, and design specifications are incredibly varied. Despite this, very few studies have assessed the effectiveness of different camera trap design features, and what effects they may have in ecological research (Meek & Pittet 2012; Rovero *et al.* 2013). Therefore, it is unclear how camera trap specifications may affect the quality and quantity of the data collected, and how accurately the data reflect animal populations. Ultimately, these issues may lead to false inference and promote inadequate management policies.

Land use changes in the Eastern Cape of South Africa have caused severe fragmentation and degradation of the Thicket Biome (La Cock 1992; Evans, Avis & Palmer 1997; Lloyd, van den Berg & Palmer 2002; Lechmere-Oertel, Kerley & Cowling 2005). Consequently,

many large predators such as lions (*Panthera leo*), leopards, (*P. pardus*) brown hyaenas (*Hyaena brunnea*), and cheetahs (*Acinonyx jubatus*) have been extirpated due to habitat loss or anthropogenic persecution (Woodroffe & Frank 2005; Balme, Slotow & Hunter 2010; Thorn *et al.* 2012). However, in recent years, many private land owners have re-introduced these species as a means to attract tourists (Lindsey *et al.* 2007; Hayward *et al.* 2007; Di Minin *et al.* 2013). Significantly, the introduction or removal of large predators has largely been driven by economic incentives, and the long term ecological effects may have been overlooked.

Numerous studies in South Africa have focused on large, charismatic species, such as lions (Hayward & Hayward 2006; Bissett, Bernard & Parker 2012) and leopards (Norton *et al.* 1986; Hunter *et al.* 2003; Owen, Niemann & Slotow 2010). Studies of smaller mesopredators such as black-backed jackals (*Canis mesomelas*) and caracals (*Caracal caracal*) are fewer, and focus mainly on their diets (Bussiahn 1997; Brassine 2011; Brassine & Parker 2011; Braczkowski *et al.* 2012). Consequently, the effects that apex predators may have on black-backed jackal and caracal abundance, distribution and diel activity patterns remain principally unknown. Therefore, further studies are pivotal for understanding how large predator manipulations may affect the health and balance of ecosystems.

The broad aims of my study were to explore how camera trap design features affect the quality and quantity of data collected for assessing vertebrate diversity and abundance. Additionally, I aimed to investigate MRH by comparing black-backed jackal and caracal relative abundance, occupancy, distribution and daily activity patterns at one site with, and one site without, apex predators.

Chapter 2

Study Sites & General Methods

2.1 Study sites

My study took place in the Fish-Kowie corridor (Figure 2.1.1). The Fish-Kowie corridor was identified by the 2000-2004 Subtropical Thicket Ecosystem Project (STEP) as an important area for maintaining Subtropical Thicket biodiversity (Cowling *et al.* 2003). The Fish-Kowie corridor, as defined by STEP, spans approximately 3,600 km² (Rouget *et al.* 2006) and falls within the Albany centre of floristic endemism (Victor & Dold 2003). My study, part of a larger research programme, included additional properties between the Great Fish River and Kowie River, increasing the corridor to nearly 5,200 km² (Figure. 2.1.1). The Fish-Kowie corridor is roughly delineated by the Great Fish and Kowie Rivers at the coast, and extends in a north westerly direction, ending approximately 25 km north west of Somerset East (Figure. 2.1.1).

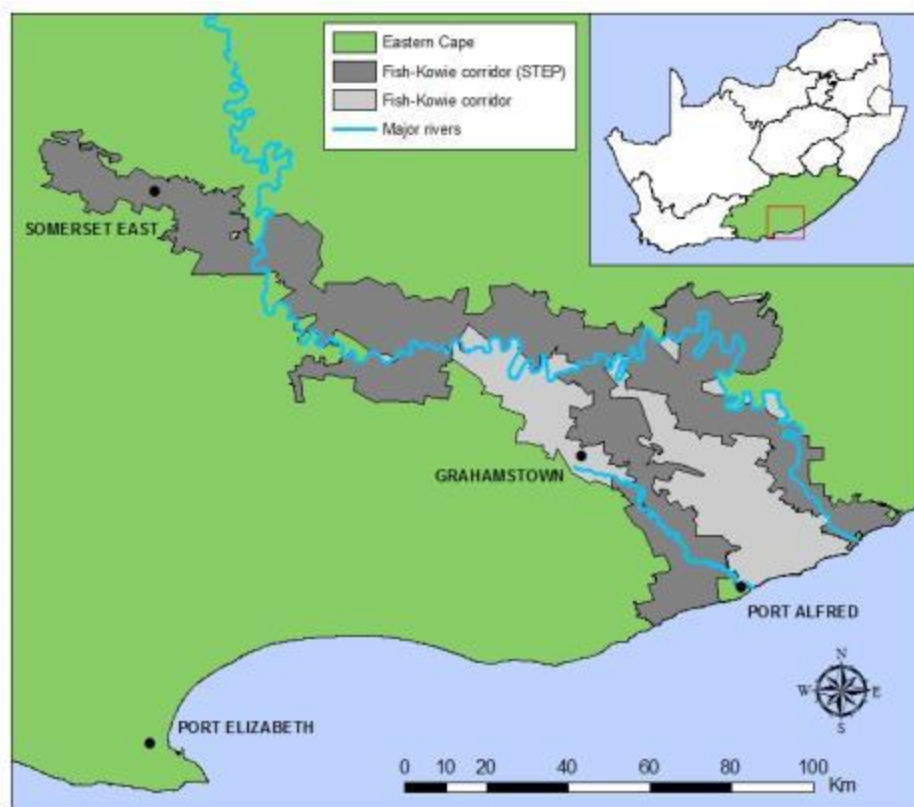


Figure 2.1.1 The location and extent of the Fish-Kowie corridor as defined by the Subtropical Thicket Ecosystem Project (STEP) (dark grey) and additional areas included in the corridor for my study (light grey).

Elevation in the Fish-Kowie corridor ranges from sea level in the south, to over 600m above sea level on valley ridges in the north. Mean annual temperature in Grahamstown (located centrally in the Fish-Kowie corridor) is ~16°C, with daily high temperatures of ~30°C during the summer months of January and February, and daily low temperatures of ~5°C in the winter months of June and July (Figure 2.1.2) (Lubke & de Moor 1998). Grahamstown receives a mean annual rainfall of 681mm, rainfall is aseasonal and highly variable with slight peaks during March and October (Figure 2.1.3) (Lubke & de Moor 1998).

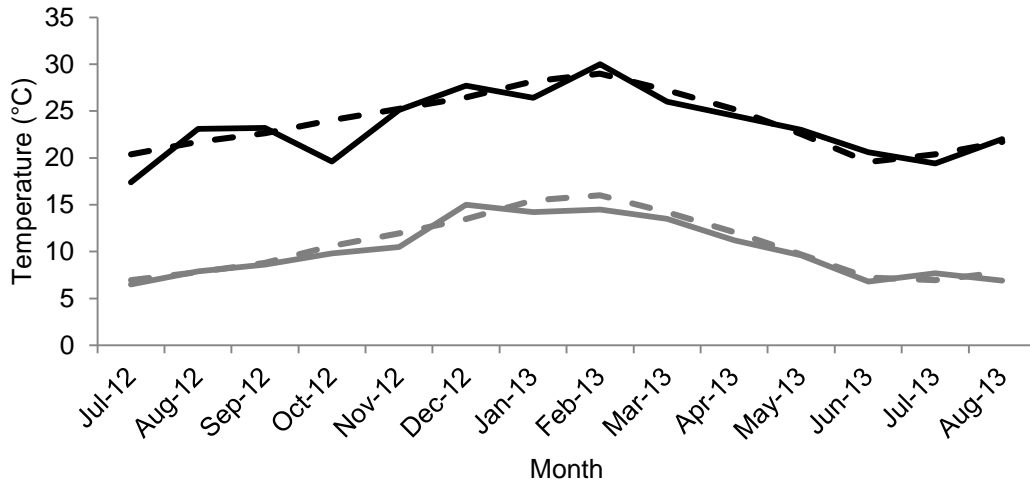


Figure 2.1.2 Mean monthly high (black) and low (grey) temperatures during my study period (solid lines), 10 year means (dashed lines) are included for comparison. Data recorded by Grahamstown weather station (<http://en.tutiempo.net/climate/ws-688490.html>). Accessed 16/10/2015.

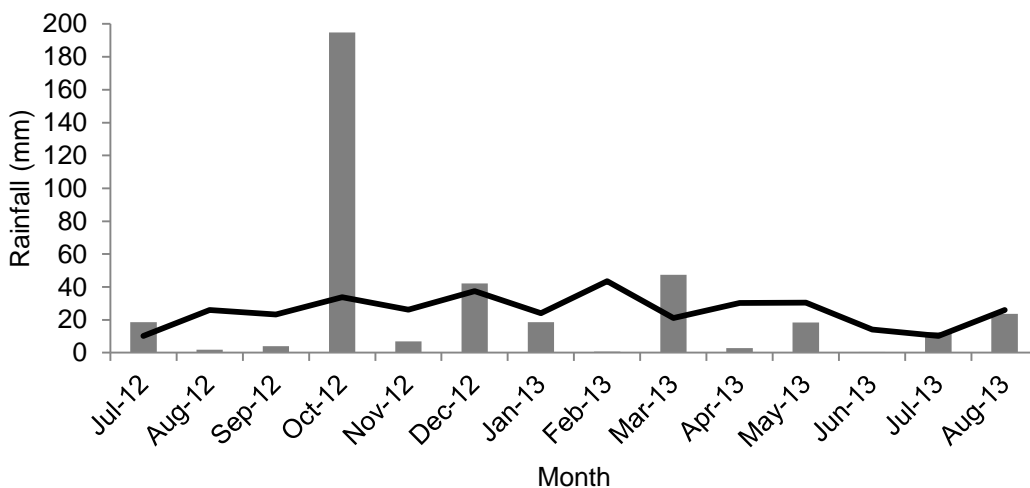


Figure 2.1.3 Total monthly rainfall during my study period (grey bars), 10 year mean monthly rainfall is included for comparison (black line). Data recorded by Grahamstown weather station (<http://en.tutiempo.net/climate/ws-688490.html>). Accessed 16/10/2015.

Much of the Fish-Kowie corridor is dominated by Albany Thicket, sometimes referred to as valley bushveld (Kerley, Boshoff & Knight 1999). The Thicket Biome is characterized by dense, evergreen, sclerophyllous or succulent trees and shrubs, many of which are spinescent (Evans, Avis & Palmer 1997). A total of 21 vegetation types are represented in the Fish-Kowie corridor (Mucina & Rutherford 2006). However, Great Fish Thicket, Kowie Thicket and Great Fish Noorsveld comprise a combined total of over 60% of the vegetation (Mucina & Rutherford 2006). Great Fish Thicket forms clumped vegetation of short, medium and tall types, centred on areas of high zoogenic activity (Mucina & Rutherford 2006). *Portulacaria afra* is the dominant species, giving way to *Euphorbia bothae* in more arid areas. Moister areas such as south-facing slopes and riparian zones allow for *P. afra* to be replaced by woody elements and tall *Euphorbia* spp. (Mucina & Rutherford 2006). Areas with deeper soils support long lived woody shrubs and trees including *Pappea capensis* and *Boscia oleoides*. Kowie Thicket is a tall thicket type, found mainly on dry, north-facing slopes (Mucina & Rutherford 2006). Kowie Thicket is dominated by succulent *Euphorbia* and *Aloe* spp. with a thick understory of spinescent shrubs, woody lianas, shrubby succulents and a poorly developed herbaceous layer (Mucina & Rutherford 2006). Great Fish Noorsveld is mostly found on plateaus and gentle slopes (Mucina & Rutherford 2006). *Euphorbia bothae* is the dominant species, interspersed with both sclerophyllous and succulent shrubs including *Grewia*, *Euclea*, *Gymnosporia* and *Crassula* spp. and a rich variety of grasses (Mucina & Rutherford 2006).

The Fish-Kowie corridor comprises a mosaic of stock farming ventures including domestic sheep (*Ovis* spp.), goats (*Capra* spp.), and cattle (*Bos* spp.), often internally fenced to manage grazing pressures (Knight & Cowling 2011). Conversely, many conservation areas and private game reserves within the Fish-Kowie corridor have removed internal fences to allow natural movement of wildlife. However, these properties require 2.4m perimeter fencing, often electrified, to obtain a certificate of adequate enclosure needed for hunting and/or introductions of large and dangerous species such as African elephants (*Loxodonta africana*), black rhinoceroses (*Diceros bicornis*), white rhinoceroses (*Ceratotherium simum*) and large carnivores (Knight & Cowling 2011). My study utilised two field sites within the Fish-Kowie corridor, Kwandwe Private Game Reserve and E-Zulu Private Game Reserve (Figure 2.1.4). These sites were chosen based on their similar size, topography, vegetation types and central location within the Fish-Kowie corridor.

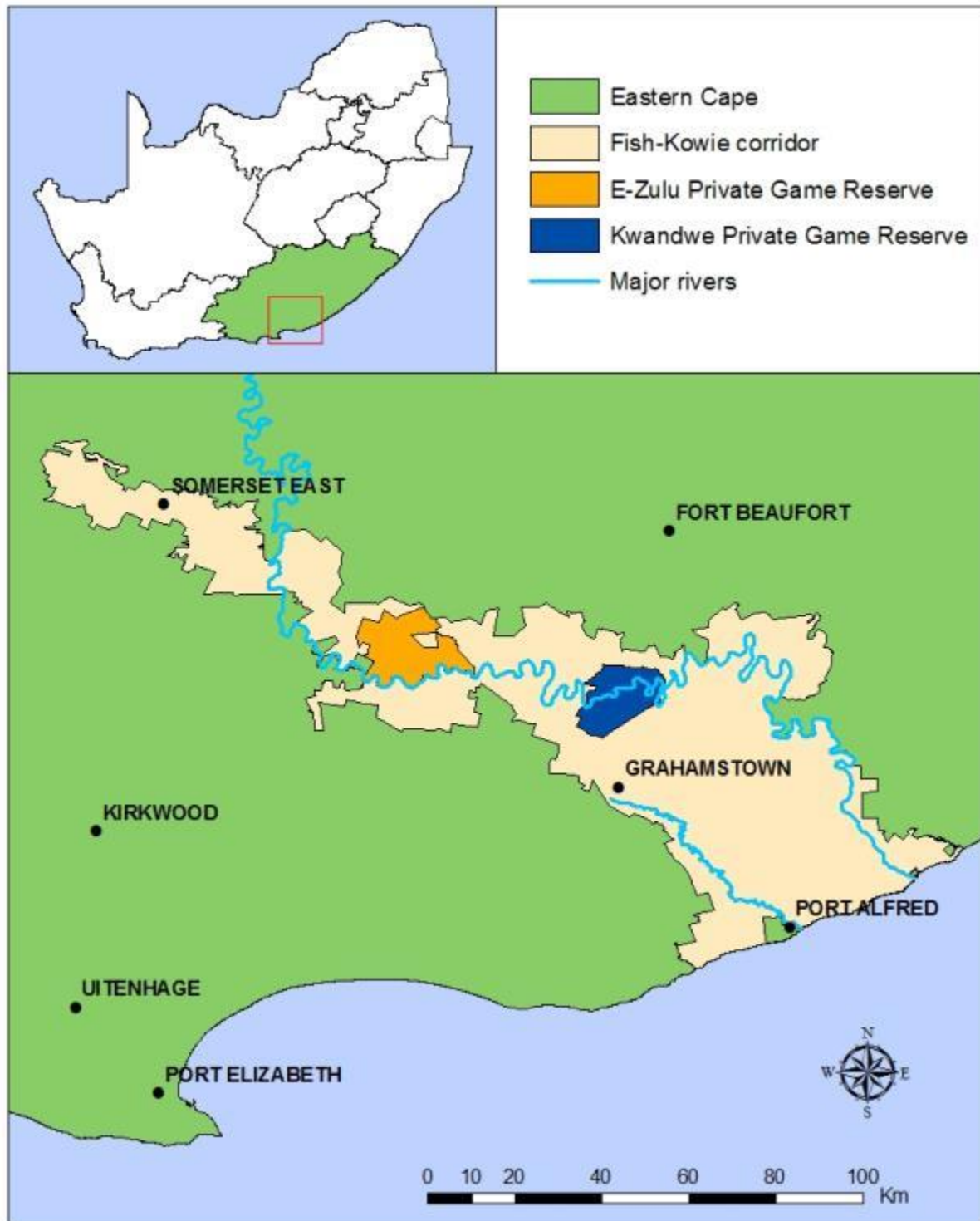


Figure 2.1.4 The central location of Kwandwe Private Game Reserve and E-Zulu Private Game Reserve within the Fish-Kowie corridor, Eastern Cape, South Africa.

Kwandwe Private Game Reserve

Kwandwe Private Game Reserve (hereafter 'Kwandwe') is an eco-tourism based 'big 5' reserve situated 20km north of Grahamstown and spans approximately 21,000 Ha. The Great Fish River meanders through the reserve for roughly 25km, flowing from west to east, with the Bothas River branching off to the south (Figure 2.1.5). The area north of the Great Fish river is characterized by deep valleys with steep slopes, dominated by Great Fish Thicket (Mucina & Rutherford 2006). South of the river is characterized by lower lying, more open plains. Great Fish Noorsveld comprises the majority of vegetation, although small areas of Great Fish Thicket, Kowie Thicket and Albany broken veld also occur (Figure 2.1.5). Albany broken veld is fairly open, with many scattered low trees, grasses and dwarf shrubs of karroid origin (Mucina & Rutherford 2006). The land surrounding Kwandwe is predominantly privately owned small stock and game farms (Bissett 2004).

Prior to Kwandwe being established in 1999, the land was used mainly for Ostrich (*Struthio camelus*) and small stock farming, with indigenous wild game including greater kudu (*Tragelaphus strepsiceros*), bushbuck (*T. scriptus*), grey duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*), bushpig (*Potamochoerus larvatus*), and warthog (*Phacochoerus africanus*) occurring in the area (Bissett 2004). Installation of 2.4m electrified game fencing allowed for the re-introduction of large game such as white rhinoceros, black rhinoceros, giraffe (*Giraffa camelopardalis*), and elephant between 1999 and 2001 (Bissett 2004). Carnivore introductions during this time included four lions (*Panthera leo*), nine cheetahs (*Acinonyx jubatus*), two leopards (*Panthera pardus*), and six brown hyaenas (*Hyaena brunnea*) (Bissett 2004; Hayward *et al.* 2007). Six African wild dogs (*Lycaon pictus*) were also introduced in 2004 and their numbers increased to 14 by 2005. However, two adult females were sold in December 2005 and a further two male cubs were sold in February 2006 (Bissett 2007). Later in 2006, one pup was found dead and two pups went missing. The remaining pack contracted canine distemper and all but the alpha pair died. Four new adult females were introduced in November 2006, but all wild dogs were removed from Kwandwe when they learned to chase game animals into the fence as a hunting strategy (Bissett 2007; Bissett pers. comm. 2013).

At the time of my study, there were 11 lions at Kwandwe. The Great Fish River separated the territories of two adult males, although they occasionally spent time together. Two adult females stayed together with four cubs, and two adult females wandered alone, one with a single cub. Six cheetahs were also present during my study, a mother with two sub-adult sons, a single adult female and a coalition of two brothers, all to the south of the Great Fish River. The elusive nature of the leopards and brown hyaenas meant their numbers and

population structure were not known. Black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*) numbers were also unknown, but staff members at Kwandwe reported that these two species were most often seen south of the Great Fish River.

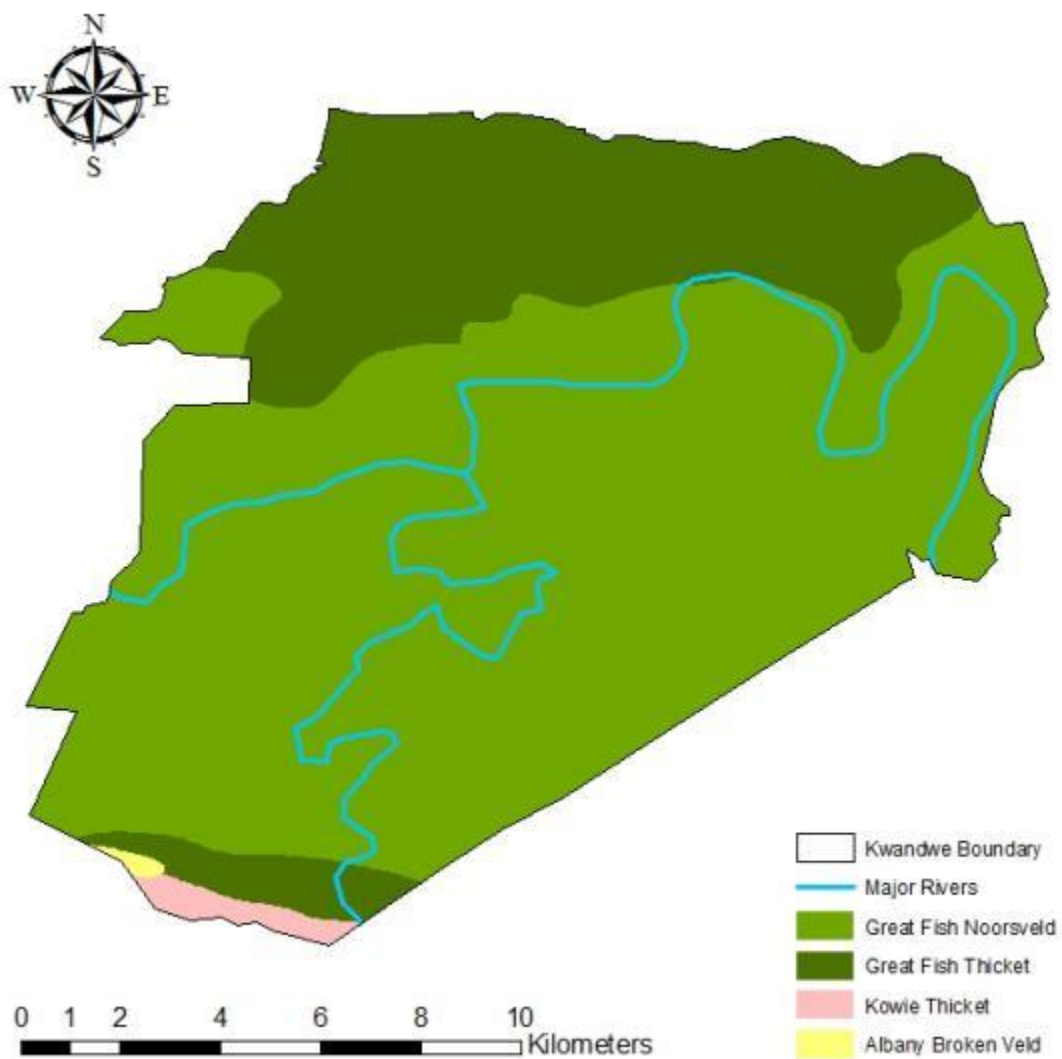


Figure 2.1.5 The vegetation and major rivers of Kwandwe. Descriptions of each vegetation type are provided in the text.

E-Zulu Private Game Reserve

E-Zulu Private Game Reserve (hereafter 'E-Zulu') is a privately owned game reserve centred on commercial trophy hunting. The reserve lies 45km north west of Grahamstown and is approximately 25,500 Ha. Much of the reserve is covered by Great Fish Thicket, with small areas of Bedford dry grassland occurring in the far north (Figure 2.1.6). Bedford dry grassland is characterised by short (10-100cm) grasses, interspersed with *Acacia karroo* and dwarf karroid shrubs (Mucina & Rutherford 2006). Small belts of Albany broken veld and Southern karoo riviere follow the Great Fish River that forms the southern border of the reserve (Figure 2.1.6) (Mucina & Rutherford 2006). Southern karoo riviere is characterised by a complex of *A. karroo*, *Tamarix usneoides* and *Salsola* spp., with *Stipagrostis namaquensis* also occurring in particularly sandy areas (Mucina & Rutherford 2006). More arid areas of E-Zulu support high levels of invasive cacti, particularly *Opuntia* spp. (pers. obs).

Before E-Zulu was established in 2007, the land was mainly used for game farming, as well as cattle and small stock farming and lucerne (*Medicago sativa*) cultivation. Similar to Kwandwe, indigenous ungulates such as greater kudu, bushbuck, grey duiker, and steenbok were present before E-Zulu acquired the land. Since 2007, game introductions at E-Zulu have included white rhinoceros, buffalo (*Syncerus caffer*), sable (*Hippotragus niger*), and roan (*H. equinus*). Large predators (i.e. those >21.5kg indicating obligate carnivory; Carbone *et al.* 1999) were extirpated from the area before E-Zulu purchased the land and none have been introduced since. Smaller predators, particularly black-backed jackals and caracals are lethally controlled ~2-3 times per week. In addition, a 'shoot on sight' policy has been implemented across the reserve in an attempt to protect high value game species such as sable and roan (trophy fees for these species in 2013 were \$15,800 and \$18,800, respectively). An estimated figure of 250-300 predators are lethally controlled per annum, mostly black-backed jackals (Price pers. comm. 2013). A privately owned farm of mixed game and small stock remains completely enclosed by E-Zulu (Figure 2.1.6) and the land surrounding E-Zulu is comprised mainly of private small stock and game farms.

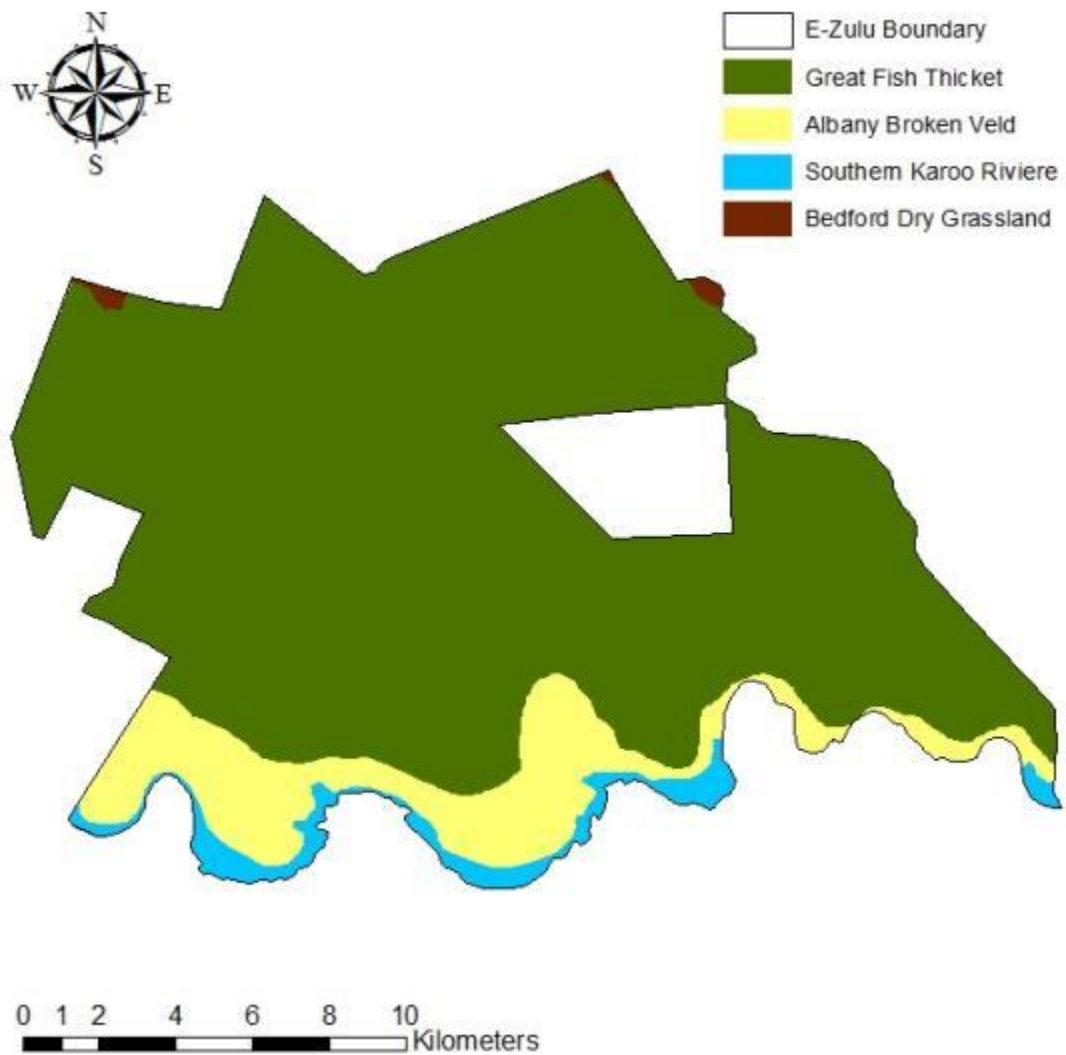


Figure 2.1.6 The vegetation of E-Zulu. Descriptions of each vegetation type are provided in the text. Note the mixed small stock and game farm completely enclosed by the reserve.

2.2 Camera trap specifications

My study utilised two different models of camera trap, the Cuddeback® 'Attack'® (hereafter 'Cuddeback'), and Wildview® 'Xtreme 5'® (hereafter 'Wildview') (Figure 2.2.1). Both models house 5 megapixel digital cameras, are triggered by passive infrared (PIR) sensors and produce a white Xenon gas flash.

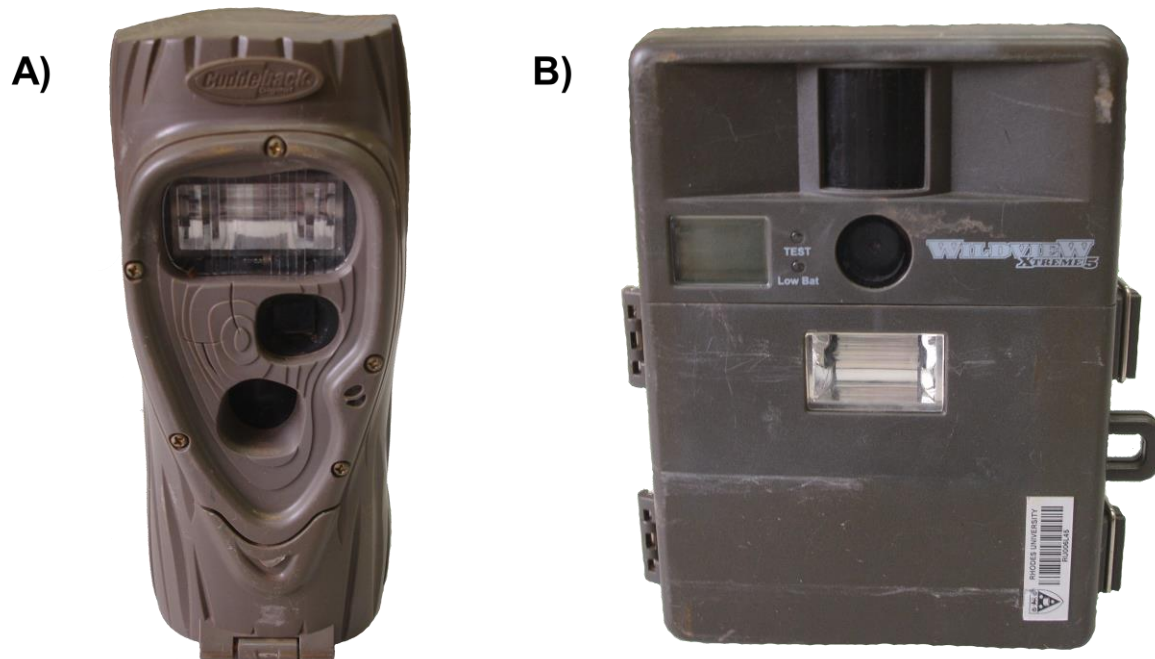


Figure 2.2.1 The two models of camera trap used during my study, the Cuddeback 'Attack' (A) and the Wildview 'Xtreme5' (B).

Both the Cuddeback and Wildview cameras have several features that can be programmed by the user (Wildview 2010; Cuddeback 2012a). These include a delay between pictures, changeable from 5 seconds to 30 minutes for the Cuddeback cameras and from 1 minute to 20 minutes for the Wildview cameras. Longer delays prevent multiple pictures of large herds of animals, therefore prolonging battery life and saving memory space. Shorter delays (e.g. < 1 minute) may result in numerous pictures of the same group of animals. This may be useful if animal demographics are being assessed, but reduces battery life and uses more memory. As data storage was not an issue for my study (I used 16GB SD cards, Transcend® SDHC), Cuddeback cameras were set to a relatively short delay of 30 seconds. Wildview cameras were set to their shortest possible delay, 1 minute.

Both camera models allow for the picture quality to be altered and were set to their highest quality picture settings for my study. Further, the Cuddeback cameras allow for the flash intensity to be changed from a 10-40 metre range. For my study, the flash range was set to 10m as the dense vegetation at most camera sites would have caused pictures to become over exposed at higher flash settings. The Wildview cameras can be set to take either one, three or five picture ‘bursts’ when the motion sensor is triggered. For my study, cameras were set to take single pictures to allow for better comparison between camera types (see chapter 3). The physical specifications of each camera model, fixed during manufacturing, are outlined in Table 2.2.1.

Table 2.2.1 Comparison of physical design features of the Cuddeback and Wildview cameras used during my study.

	Cuddeback	Wildview
Dimensions (mm)	210 x 90 x 90	176 x 155 x 45
Batteries	4 x 'D' cell ¹	4 x 'C' cell ²
Angle of detection	28° ³	48° ⁴
Trigger speed	0.25 seconds ⁵	1.37 seconds ⁶
Internal memory (MB)	120 ⁷	32 ⁴

¹Energizer® max® ²GP® 350 CHC ³ Cuddeback (2012b) ⁴Wildview (2010)
⁵<http://cuddeback.com/cameras/attack.aspx> ⁶(Meek, Ballard & Fleming 2012) ⁷Cuddeback (2012a)

2.3 Overall study design

To avoid bias towards any particular vertebrate species, cameras were deployed to random positions at each site (O'Brien 2011; Rowcliffe *et al.* 2011). Using ARCGIS v.9 (ESRI, Redlands, CA, USA), a grid of 3600 Ha was randomly placed over each of the study sites to define an effective trapping area (ETA). To ensure even coverage of the ETA, the 3600 Ha grid was further divided into nine grid cells of 400 Ha each. This grid size was chosen as an attempt to adequately survey both small and large carnivores that have drastically different home ranges. For example, gray mongoose (*Galerella pulverulenta*) home ranges are in the region of 0.2 – 0.6 Km² (Cavallini & Nel 1990), while lion home ranges can be in excess of 100 Km² (Bissett 2007). At E-Zulu, the grid had to be modified to accommodate the mixed game and small stock farm enclosed by E-Zulu. However, the ETA remained continuous and was the same size as at Kwandwe (Figure. 2.3.1). Coincidentally, at both sites, grid cells one

to three were characterised by deep valleys with steep, densely vegetated slopes, while grid cells four to nine were flatter and more open (Figure 2.3.1).

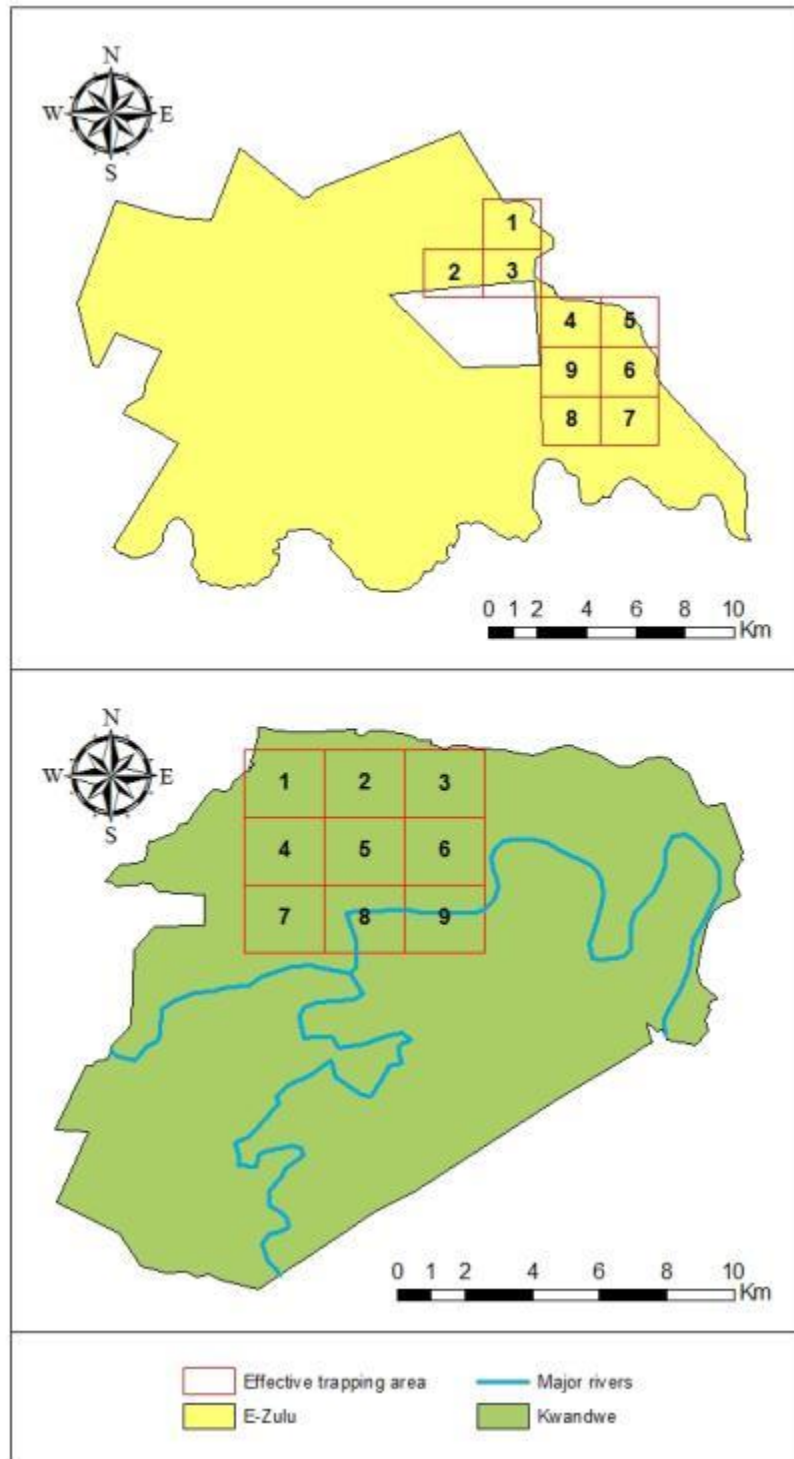


Figure 2.3.1 The 3,600 Ha effective trapping areas (ETA's) at E-Zulu (above) and Kwandwe (below). Despite the irregular ETA grid at E-Zulu, grid cells three and four remained connected by a corridor of roughly 125m width allowing animals to move freely through. Grid cell numbers referred to in text.

Random points were then generated within each of the nine sub-grids and subsequently uploaded to a handheld GPS unit (Garmin® GPSmap 60CSx). Using the handheld GPS unit, the random points were located in the field and a suitable site for camera placement was found within a 'buffer zone' of 100m around each random point. This was possible for all but one camera station, which was 102.4m from the random point. Suitable sites were those with a sturdy tree or similar structure (e.g. a fence post) that the camera could be attached to, and were in close proximity to a relatively open area (e.g. a clearing, road, game trail or drainage line) as animals generally prefer these paths of least resistance (Karanth, Nichols & Kumar 2010; Mann, O'Riain & Parker 2014; Cusack *et al.* 2015). Once a suitable site had been established, cameras were mounted at a height of ~30cm from the ground, facing an open area to maximise capture probability (Meek, Ballard & Fleming 2012). A height of ~30cm was chosen as it minimised the chance of animals passing under the PIR beam undetected, but was still high enough to produce good quality pictures of larger animals. Cameras were angled so that the detection beam was parallel with the ground to maximise the area covered by the PIR sensor.

As far as possible, the facing of cameras due east and due west was avoided to prevent pictures becoming over exposed by the rising and/or setting sun. Occasionally, small shrubs, grasses and overhanging branches had to be removed to allow a clear field of view for the camera and PIR sensor. Vegetation clearance was kept to a minimum as the scent of freshly chopped vegetation may have altered the behaviour of herbivores, possibly in turn influencing predator behaviour and movement past the cameras. Cameras at Kwandwe were placed in protective metal casings to prevent large and aggressive animals such as elephants, black rhinoceroses and lions from damaging the cameras (Figure. 2.3.2).

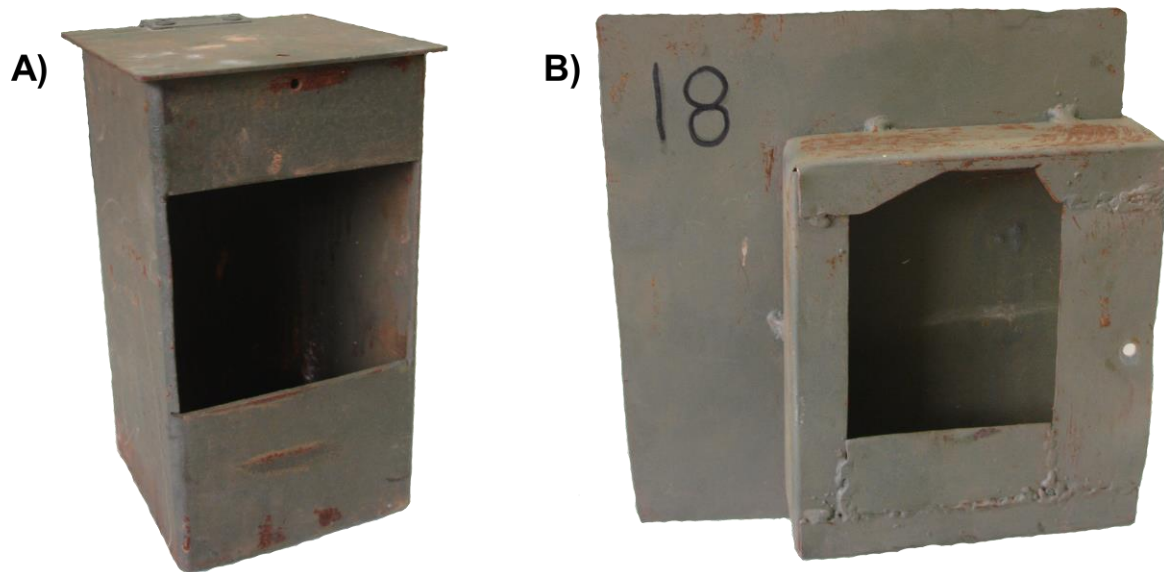


Figure 2.3.2 Metal casings used at Kwandwe for the Cuddeback A) and Wildview B) cameras.

Once cameras had been deployed, they were left in the field for 90 days (Linkie *et al.* 2013). Cameras were re-visited on a regular (~30 day) basis to replace batteries as necessary and download data from the SD memory cards. All images were processed using PhotoGoFer (Rapid Imaging Inc. Albuquerque, NM, USA). PhotoGoFer extracts metadata such as the date and time images were taken, and allows images to be ‘tagged’ with multiple fields such as species names, number of individuals, identifiable animals, and any other comments. Tags can later be queried, images can be reviewed, and data files can be exported for use with additional software programs. Non-independent events were discarded from analyses. Independent events were those for which one hour or more had passed since the last photograph of the same species, unless it was clearly a different individual (e.g. male/female, adult/juvenile or had distinct markings) (Gómez *et al.* 2005; Tobler *et al.* 2008). Using only independent events removes bias that may be introduced by re-counting the same individual multiple times if it remains in front of the camera for an extended period (Tobler *et al.* 2008). All analyses were performed using STATISTICA v.10 (StatSoft Inc. Tulsa, OK, USA) unless otherwise stated.

Chapter 3

Evaluating the Effectiveness of Camera Trap Design Features for Estimating Species Diversity and Abundances

3.1 Introduction

In the late 1890s, George Shiras III made ground breaking developments in wildlife photography by experimenting with levers and trip wires to activate cameras. Although his work was never used for scientific purposes, Shiras later published over 950 of his photographs in the two volume series 'Hunting wild life with camera and flashlight' (Shiras III 1935a, b). Later, it was realised that remote photography may have useful applications in wildlife research, and several authors began to use this technique for data collection (e.g. Pearson 1959, 1960; Osterberg 1962; Cowardin & Ashe 1965; Winkler & Adams 1968). Early remote photography systems consisted of separate camera units, flash units, battery packs, trigger systems, and electric motors, often totalling in excess of 21kg (Abbott & Coombs 1964). Technological advances have permitted modern day remote cameras (camera traps) to conveniently incorporate all the necessary components in a single housing, allowing for simple deployment in the field.

Camera traps have been used as security and surveillance tools (Kastek, Sosnowski & Piątkowski 2008; Sosnowski *et al.* 2008), often by private land owners wishing to identify culprits of stock theft and/or poaching (Rovero *et al.* 2013). Further, numerous land owners use camera traps to monitor and manage game species important to the hunting industry. Additionally, camera traps are increasingly being used as recreational tools by wildlife enthusiasts wishing to observe animals in their local area (Rovero *et al.* 2013). Moreover, the compact and unobtrusive nature of camera traps makes them suitable for a wide range of applications in ecological research (McCallum 2012). Following this, the number of camera trap publications in the scientific literature has increased dramatically during the past two decades (Figure 3.1.1)

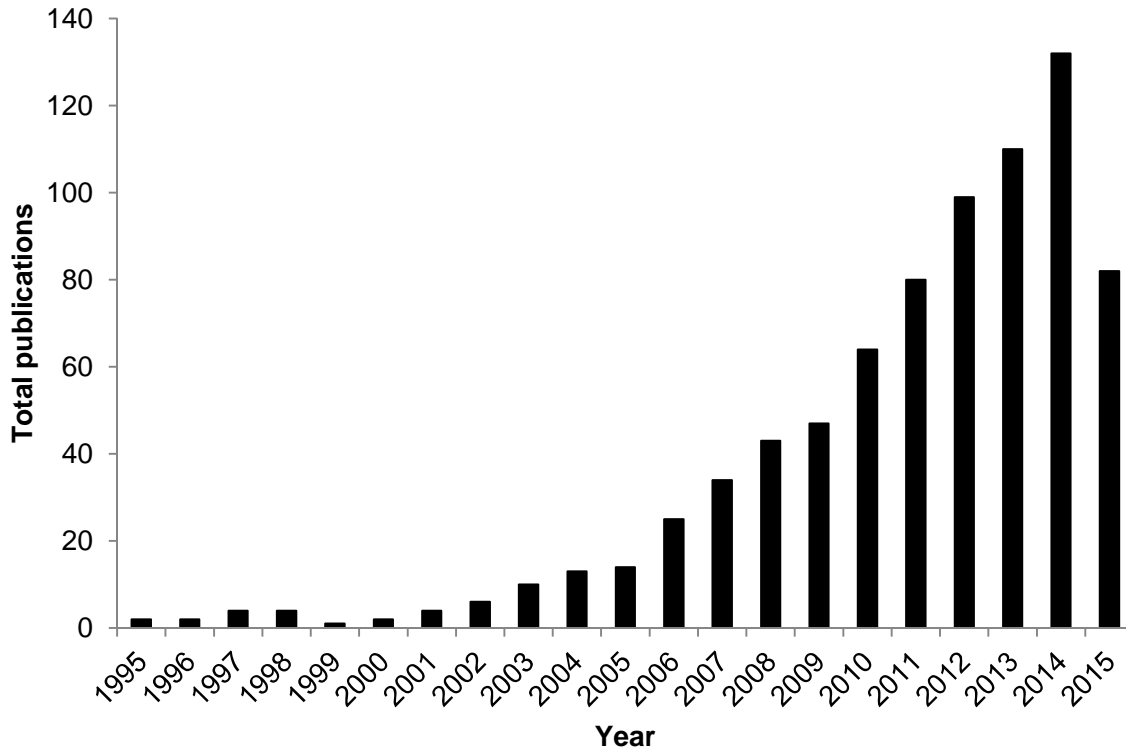


Figure 3.1.1 Total camera trap publications per year from 1995-2015. Extracted from ISI Web of Science categories biology, ecology, and zoology using the query term 'camera trap'. 2015 total accurate as of 22/09/2015.

Camera traps have been used to conduct species inventories in Africa (Rovero & De Luca 2007; Stein, Fuller & Marker 2008), South America (Trolle 2003; Tobler *et al.* 2008), and Asia (Giman *et al.* 2007; Shek, Chan & Wan 2007). Camera traps are well suited to these studies as they can remain in the field for long periods, are permanently active, and cause minimal disturbance (McCallum 2013). Consequently, camera traps have often recorded the presence of rare and/or elusive animals (Sanderson & Trolle 2005), and have documented previously undescribed species such as the Annamite striped rabbit (*Nesolagus timminsii*) (SurrIDGE *et al.* 1999).

Camera traps have also seen extensive use in studying animal density and abundance. For instance, camera traps have been used in conjunction with a capture-recapture framework to estimate abundance of individually marked species such as tigers (*Panthera tigris*) (Karanth 1995; Karanth & Nichols 1998), jaguars (*P. onca*) (Salom-Pérez *et al.* 2007; Tobler & Powell 2013), and leopards (*P. pardus*) (Odden & Wegge 2005; Chapman & Balme 2010; Grant 2012; Gray & Prum 2012). Further, camera traps have also been used to estimate density and abundance of non-individually marked species by using relative abundance indices

(Carbone *et al.* 2001; Rovero & Marshall 2009; Gerber *et al.* 2010; Jenks *et al.* 2011), and more robust approaches including random encounter models (REM) (Rowcliffe *et al.* 2008, 2011; Carbajal-borges, Godínez-gómez & Mendoza 2014) and occupancy models (MacKenzie *et al.* 2002; Royle & Nichols 2003; Cove *et al.* 2013; Schuette *et al.* 2013).

In addition to species inventories and density and abundance estimates, camera traps have been implemented in many behavioural studies. For example, activity profiles of many species have been constructed by using the time of day that animals are recorded (van Schaik & Griffiths 1996; Tobler, Carrillo-Percestequi & Powell 2009; Blake *et al.* 2012; Meek, Zewe & Falzon 2012). Following this, it is possible to assess the degree of overlap between species activity profiles and possibly highlight temporal separation of species activity (Lynam *et al.* 2013; Monterroso, Alves & Ferreras 2013). Behavioural studies using camera traps have also assessed habitat preferences, such as those of forest ungulates in Tanzania (Bowkett, Rovero & Marshall 2008) and various carnivores in the U.S.A (Kelly & Holub 2008). Further, camera traps have been used to monitor plant-animal interactions such as fruit consumption by various species (Jayasekara *et al.* 2007) and foraging frequency of the Yakushima macaque (*Macaca fuscata yakui*) (Otani 2001). Additionally, a combination of camera trapping and scat analysis has allowed for the investigation of seed dispersal by the Japanese marten (*Martes melampus*) (Otani 2002). Similarly, several studies have used camera trapping to estimate prey availability, followed by scat analysis, to determine the proportions of which each prey species occur in carnivore diets (Weckel, Giuliano & Silver 2006; Braczkowski *et al.* 2012).

Moreover, camera traps have also proven useful in tackling several conservation issues. For instance, camera traps have been used to monitor the success of wildlife crossings and green bridges (Foster & Humphrey 1995; Clevenger, Ford & Sawaya 2009). Additionally, the World Wildlife Fund (WWF) and many other conservation based Non-Government Organisations (NGOs) often publish camera trap images and/or video on social media websites to raise public awareness.

Camera traps have clearly proven useful for a wide range of applications. Reflecting this is the extensive range of camera trap models that are now commercially available. Camera traps are manufactured in a multitude of shapes and sizes, with a vast and varied array of technical specifications that can be adjusted by the user. For example, many models allow the user to specify whether the camera records still photography and/or video, and whether the camera takes set-interval time lapse photographs or is activated by a detector. Further, the delay between triggers can often be changed to prevent multiple images of herds that may move past the camera, and many cameras include a 'burst mode' option that allows for

several still images to be recorded in quick succession. However, several features of camera traps are often constrained by the components used, or are set during the manufacturing process. Typically, these include flashes, detection mechanisms and trigger speeds.

Flashes

Some camera traps are now available with modular flashes that can be changed to suit the needs of the user (e.g. the Cuddeback 'C' series). However, the majority of camera traps have a built in white or infrared (IR) flash that cannot be changed. White flashes are produced by either Xenon gas or light emitting diodes (LEDs). Xenon flashes are generally effective over a further range than LED flashes, but can take ≥ 30 seconds to recharge (Rovero *et al.* 2013). Conversely, white LED flashes recharge almost instantly, making them suitable for collecting a rapid succession of nocturnal photographs. All white flashes are visible to animals and may alter their natural behaviour. After encountering the flash, animals may then avoid the area, an effect known as 'trap shyness' (Wegge, Pokheral & Jnawali 2004). IR flashes are produced by LEDs. They are almost invisible to wildlife and can be activated for long periods. This makes them particularly useful for nocturnal studies, allowing for photographs and video to be recorded without disturbing natural behaviour. Unfortunately, in darkness, IR flashes can only produce monochrome images. Thus, for studies of uniquely marked animals, white flashes may be preferred as they produce pictures in true colour (Rovero *et al.* 2013).

Detection mechanisms

Mechanical triggers used by early camera traps are still in use today and can allow for very precise actions to activate the camera (Figure 3.1.2). Mechanical triggers are well suited to nest predation studies, where movement of a false egg activates a camera (e.g. Reitsma, Holmes & Sherry 1990; Picman & Schriml 1994; Danielson, Degraaf & Fuller 1996; Anthony *et al.* 2004). Similarly, active infrared (AIR) sensors create an invisible 'trip wire' that can be set to target very precise areas (Figure 3.1.2) and have also been used in nest predation studies (Sawin *et al.* 2003). However, AIR systems require accurate alignment of the emitter and receiver to function effectively, and these systems can be prone to false triggers in severe weather, or by vegetation interrupting the IR beam (Swann, Kawanishi & Palmer 2010). Furthermore, many AIR systems require external batteries and cables to power and connect their various components, making them somewhat cumbersome in the field.

Many camera traps now use passive infrared (PIR) sensors integrated in a single unit with the camera (Figure 3.1.2). PIR sensors emit no radiation, but monitor infrared signatures given off by other objects. PIRs are triggered when detecting movement of an object that

differs by $>2.7\text{ }^{\circ}\text{C}$ from background temperature (Meek, Ballard & Fleming 2012; Rovero *et al.* 2013). Unfortunately, this means that PIR sensors can fail to detect animals when ambient temperature is similar to the target's body temperature (Sosnowski *et al.* 2008; Meek *et al.* 2014). However, PIR systems are more practical in the field and can detect animals over a wider area than AIR systems (Swann, Kawanishi & Palmer 2010). The detection area of a PIR system is largely determined by a Fresnel lens that focuses IR energy onto the PIR sensor. Single Fresnel lenses result in narrow detection zones, while multifaceted lenses or lens arrays focus IR energy from a wider area. Unfortunately, the IR rays focussed towards the PIR sensor by multifaceted lenses and lens arrays are generally less intense than those focussed by a single lens (Meek & Pittet 2012). Consequently, single lens systems are generally more sensitive to heat and movement than systems that incorporate multifaceted lenses or lens arrays, but the detection zone is much smaller (Meek & Pittet 2012).

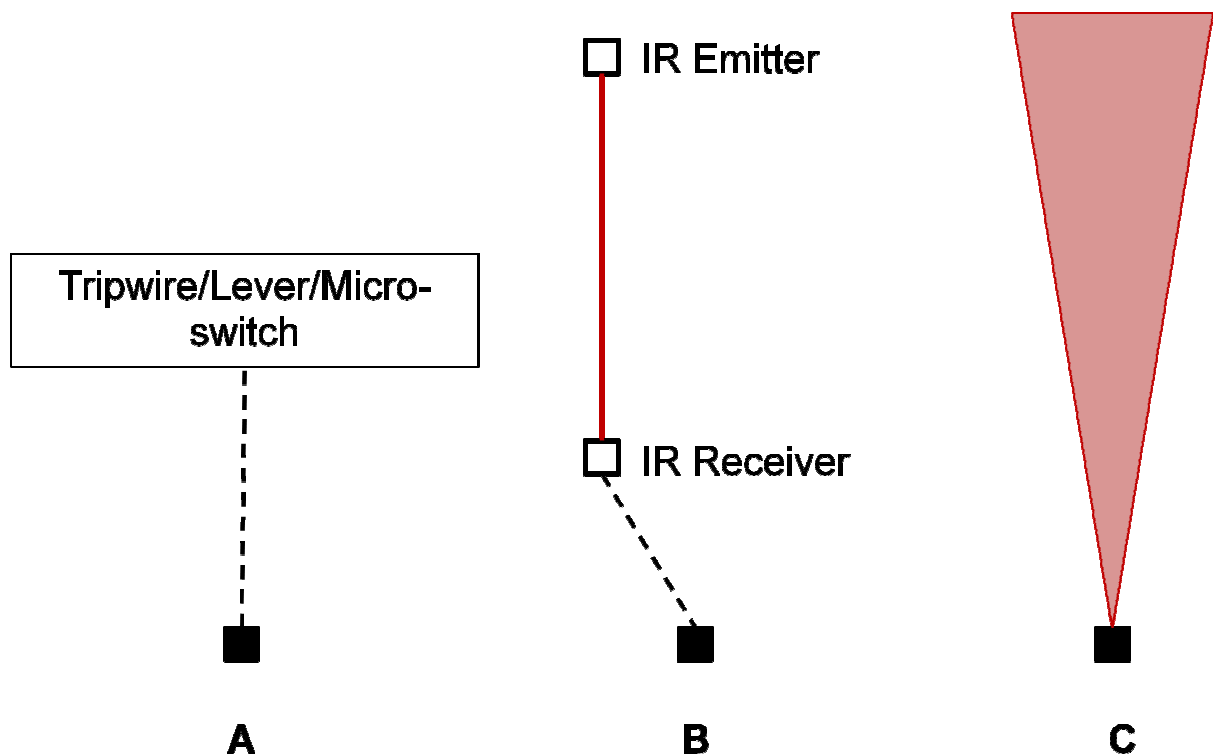


Figure 3.1.2. Mechanical (A), active infrared (AIR) (B), and passive infrared (PIR) (C) detection methods. Filled squares represent cameras, dashed lines represent hard wired and/or wireless connections, and shaded area for the PIR system represents detection zone. Note that for mechanical and AIR systems, cameras can be placed anywhere relative to the detector. Descriptions of how each system works are provided in the text.

Trigger speeds

The 'trigger speed' or 'trigger delay' refers to the delay between detection and the camera being activated. Trigger speeds can vary from 0.1 seconds in models such as the Bushnell Trophy Cam Essential (Rovero *et al.* 2013; Bushnell 2014) to over 4 seconds for the Stealth Cam Rogue IR (Meek, Ballard & Fleming 2012; Trollet *et al.* 2014). Slow trigger speeds may result in empty photographs if animals move too quickly through the cameras field of view. This may be minimized by using lures, or placing cameras near waterholes and feeding stations. Faster trigger speeds increase the chance of recording animals, particularly of fast moving species that may only be in the cameras field of view for a brief moment.

When selecting camera traps for research, it is important to select models with design features that are best suited to the type of data to be collected. For example, as previously eluded to, IR flashes are excellent for nocturnal behavioural studies, but are less applicable when individual recognition of identifiable animals is needed. Arguably, detection area and trigger speed are the most important features in determining the quantity and quality of images obtained (Rowcliffe *et al.* 2011; Meek & Pittet 2012). Therefore in this chapter I aimed to assess the effects of PIR detection angles and trigger speeds when estimating species diversity and relative abundances for both carnivores and non-carnivores. Further, I aimed to investigate how these factors may affect the quality of images recorded in terms of subject positioning in the cameras field of view. I hypothesized that wider PIR detection angles would increase diversity and relative abundance estimates because animals are more likely to encounter larger detection zones. Additionally, I hypothesized that slower trigger speeds may decrease diversity and relative abundance estimates due to animals leaving the cameras field of view before images are recorded. I further hypothesized that slow trigger speeds would produce fewer images with subjects in the centre of the cameras field of view due to the longer delay between detection and camera activation.

3.2 Materials & Methods

Sampling procedure and point randomization for camera locations followed the protocol outlined in chapter 2. At both sites, Cuddeback Attack cameras (hereafter 'Cuddeback') (n=18) were deployed first and left in position at each camera station for 90 days (810 trap nights) (Table 3.2.1). Following this first 90 day sampling period, Wildview Xtreme 5 cameras (hereafter 'Wildview') (n=18) were deployed to the same locations, facing the same directions, and also left in position for 90 days (Table 3.2.1). Battery life of the Wildview cameras was considerably shorter than that of the Cuddeback cameras and needed to be changed circa every two weeks, as opposed to roughly every three months for the Cuddeback cameras. Occasionally, even with two week battery changes, the Wildview cameras ran out of battery life. On such occasions, the number of trap nights was calculated from when the batteries were replaced until the camera took its last photograph (Blake *et al.* 2012). This led to a loss of 177 trap nights for the Wildview cameras at Kwandwe and 83 trap nights for the Wildview cameras at E-Zulu (Table 3.2.1).

Table 3.2.1. The dates, total number of days and total number of trap nights that Cuddeback Attack and Wildview Xtreme 5 cameras were active between 09/01/2013 – 08/07/2013 for Kwandwe, and 21/11/12 – 21/05/2013 for E-Zulu. Battery failures in Wildview Xtreme 5 cameras led to a loss of trap nights at both sites.

	Kwandwe			E-Zulu		
	Dates	Days	Trap nights	Dates	Days	Trap nights
Cuddeback Attack	09/01/2013 - 09/04/2013	90	810	21/11/2012 - 19/02/2013	90	810
Wildview Xtreme 5	09/04/2013 - 08/07/2013	90	633	19/02/2013 - 21/05/2013	91	736

Camera locations at Kwandwe were a mean distance of $76.28 \pm 21.54\text{m}$ (range = 39.41 - 106.42m) from the randomly generated points (Figure 3.2.1). At E-Zulu, camera locations were a mean distance of $19.74 \pm 11.78\text{m}$ (range = 7.24 - 37.58m) from the randomly generated points (Figure 3.2.2).

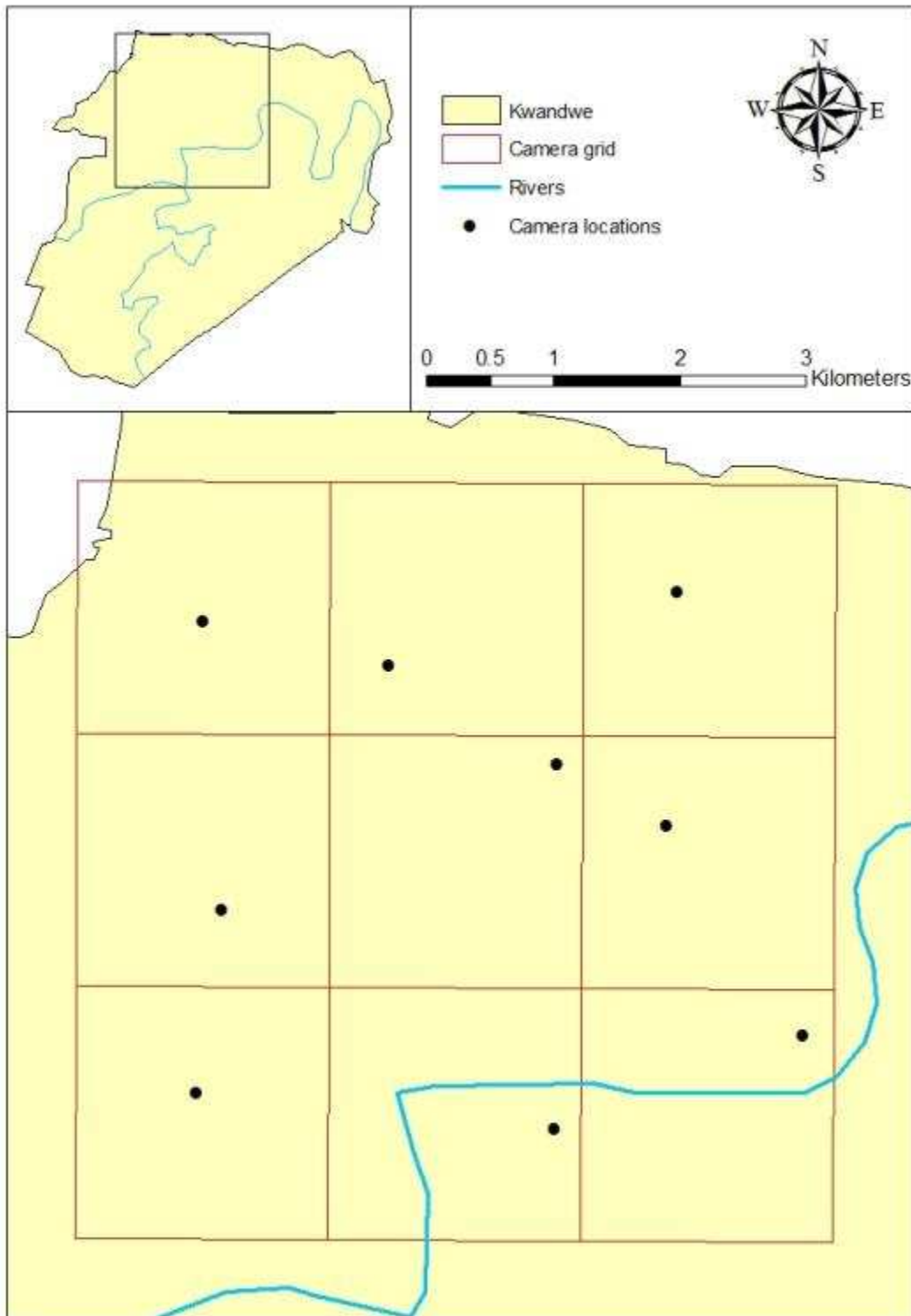


Figure 3.2.1. The positions of each of the nine cameras within the 3,600 Ha trapping grid at Kwandwe. Cuddeback cameras were placed first and left for 90 days before being replaced with Wildview cameras.

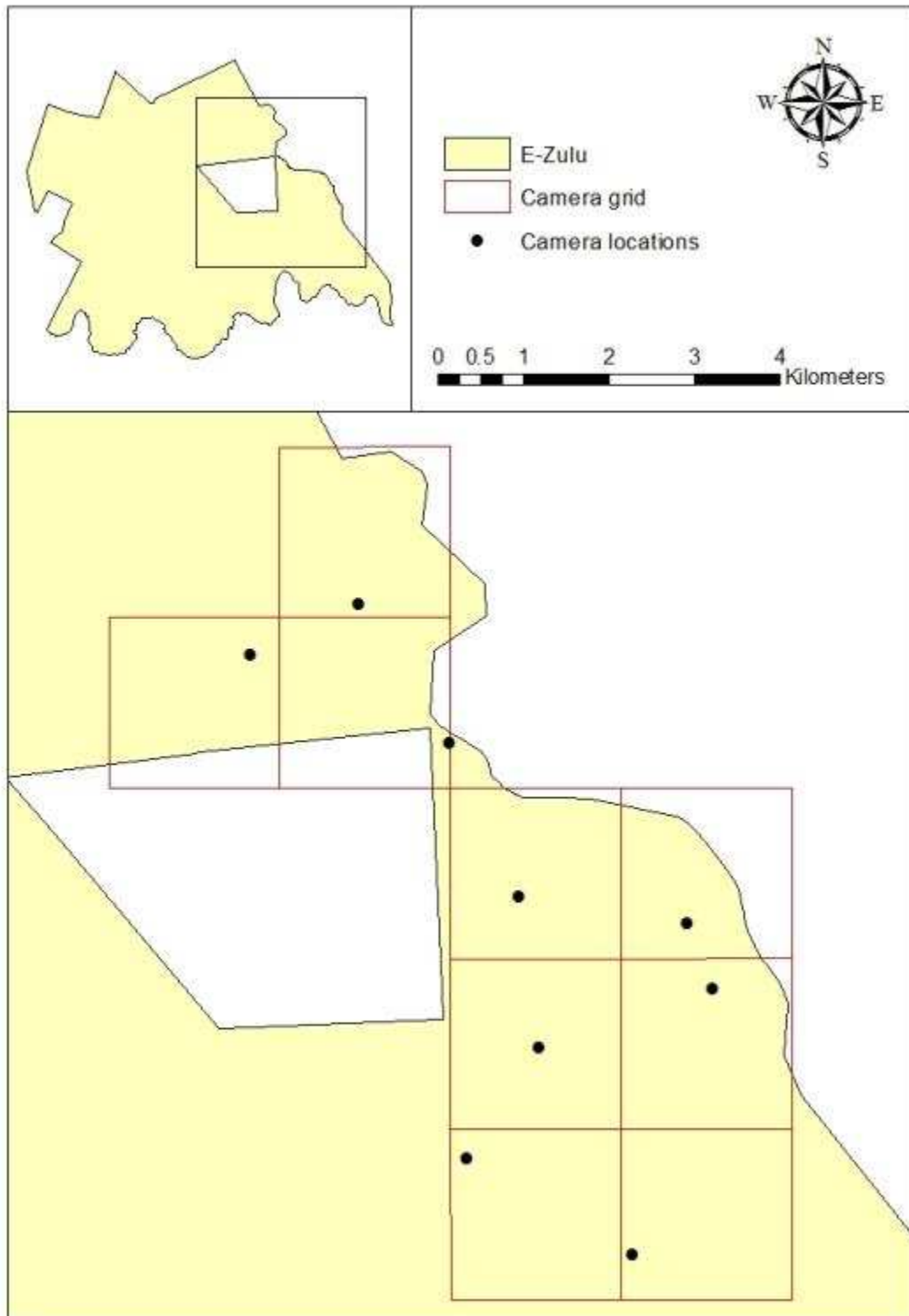


Figure 3.2.2. The positions of each of the nine cameras within the 3,600 Ha trapping grid at E-Zulu. Cuddeback cameras were placed first and left for 90 days before being replaced with Wildview cameras.

Data analysis

Only independent mammal events were used for analyses (Gómez *et al.* 2005). Using only independent events removes bias that may be introduced by re-counting the same individual multiple times if it remains in the detection zone for an extended period, hence giving an over estimate of relative abundance. Independent events were those for which one hour or more had passed since the last photograph of the same species, unless it was clearly a different individual (e.g. male/female, adult/juvenile or had distinct markings) (Gómez *et al.* 2005). Carnivore species (of the order Carnivora, regardless of diet) were analysed separately to non-carnivore species. This was done because carnivore abundance is generally lower than non-carnivore abundance, carnivores are often more territorial, and often behave in different ways to non-carnivore species (Wallach *et al.* 2015).

Relative abundance was calculated for each mammal species (Kwandwe Cuddeback N=32, Kwandwe Wildview N=29, E-Zulu Cuddeback N=30, E-Zulu Wildview N=25) at each camera station (n=9 per site) by dividing the number of independent events for a carnivore species at a camera station by the total number of days that camera was active. This was then multiplied by 100 to give a relative abundance as the number of carnivore events per 100 trap days (Jenks *et al.* 2011; Sollmann *et al.* 2013). For mammal species that were photographed by both camera types at each site (Kwandwe N=28, E-Zulu N= 24), a Mann-Whitney U-test was performed using Statistica v.10 (StatSoft. Inc. Tulsa, OK, USA) to test for significant differences in the relative abundance of each mammal species as determined by each camera type.

Capture histories were constructed collectively for all cameras of each camera type at each site and for each mammal species (Table 3.2.2). Sampling occasions were classified as each 24 hour period from 00:00-23:59 (Gray & Prum 2012; Lazenby & Dickman 2013; Mann 2014). Capture histories were analysed using Estimate S v9.1 (Colwell 2013) to produce species rarefaction curves. Species rarefaction curves are produced by randomly re-sampling the cumulative number of species present at each sampling occasion and plotting the means to give an estimate of species richness (Colwell 2013). As the rarefaction curve approaches an asymptote, it suggests that the sampling period has been sufficient to record all species present. Estimate S was also used to calculate a Chao 1 estimate (Chao 1984) for each camera type at each site. The Chao 1 estimator takes into account rare species (i.e. those recorded only once or twice), and based on those rare species, estimates species richness that includes species that may have been present but remained unrecorded (Chao 1984; Colwell & Coddington 1994). Shannon diversity indices were also calculated for each

camera type at each site to give a diversity estimate that incorporates not only species richness, but also species evenness (Tuomisto 2010; Zar 2010).

Table 3.2.2. Hypothetical photographic capture histories for five species across five sampling occasions. In this example, aardwolves were only photographed once, on the fifth sampling occasion. Baboons were photographed a total of 10 times, twice on the first sampling occasion (collectively across all cameras), four times on the second sampling occasion and once on the third etc.

	Sampling occasion				
	1	2	3	4	5
Aardwolf	0	0	0	0	1
Baboon	2	4	1	3	0
Kudu	4	2	1	3	4
Scrub hare	1	0	0	1	0
Warthog	5	4	4	3	1

To assess picture quality, photographs from both study sites were pooled for each camera type and classified as containing only the front of the subject (i.e. entering the frame), only the back of the subject (i.e. leaving the frame) or centred (i.e. the whole subject visible in the frame) (Figure 3.2.3). Photographs that contained more than one subject were excluded from this analysis as they often contained individuals that were centred, and individuals that were entering and/or leaving the frame. Moreover, for photographs that contained multiple subjects, it was often unclear as to which individual had triggered the camera. Pictures in which the subject was too close to the camera were also discarded as they could be classified into any or all of the subject position categories. Subjects were deemed too close to the camera if they extended above the top of the frame (see Figure 3.2.3). Once the subjects of all valid pictures had been categorised as front only, centred or back only, the data were arcsine square-root transformed (Zar 2010) and a 2-way ANOVA was performed using Statistica v.10 (StatSoft. Inc. Tulsa, OK, USA) to test for differences in the positioning of subjects between the two camera types.



Figure 3.2.3. The position of subjects in photographs were classified as (A) entering the frame (front only), (B) entirely within the frame, or (C) leaving the frame (back only). Photographs with multiple subjects (D) and photographs in which the subject was too close to the camera (E) were removed from the analysis.

3.3 Results

Total sampling effort for the Cuddeback cameras at Kwandwe was 810 trap nights, resulting in a combined total of 2863 photographs of wildlife, anthropogenic events and false triggers. A total of 32 mammal species and seven bird species were photographed (Table 3.3.1). Total sampling effort at Kwandwe for the Wildview cameras was 633 trap nights, resulting in a total of 1757 photographs of wildlife, anthropogenic events and false triggers. The Wildview cameras recorded three fewer mammal species and five fewer bird species than the Cuddeback cameras (Table 3.3.1).

Total sampling effort for the Cuddeback cameras at E-Zulu was 810 trap nights, yielding a total of 4179 photographs of wildlife, anthropogenic events and false triggers. A total of 30 mammal species, eight bird species, and one reptile species were photographed (Table 3.3.1). Total sampling effort for the Wildview cameras at E-Zulu was 736 trap nights, resulting in a total of 4153 photographs of wildlife, anthropogenic events and false triggers. A total of 25 mammal species and three bird species were photographed (Table 3.3.1). A complete species list with number of photographs for both camera types is provided in appendix A.

Table 3.3.1. The total number of trap nights, number of photographs and number of species of mammals, birds, and reptiles taken by each camera type at each site between 21/11/2012 and 08/07/2013. The blank and other category incorporates false triggers, camera failures, over-exposed photographs, and photographs where animals could not be identified.

	Kwandwe		E-Zulu	
	Cuddeback	Wildview	Cuddeback	Wildview
	Attack	Xtreme 5	Attack	Xtreme 5
Trap nights	810	633	810	736
Total Photographs	2863	1757	4179	4153
Mammal photographs	819	1216	1524	2296
Mammal spp.	32	29	30	25
Bird photographs	36	4	40	13
Bird spp.	7	2	8	3
Reptile photographs	0	0	4	0
Reptile spp.	-	-	1	-
Anthropogenic photographs	133	99	223	98
Blank & other	1875	438	2388	1746

*Carnivore relative abundance**Kwandwe*

Cuddeback cameras photographed nine carnivore species and determined that black-backed jackals, followed by aardwolves, had the highest mean relative abundances (Table 3.3.2). Wildview cameras photographed seven carnivore species, missing the two genet species which the Cuddeback cameras had recorded (Table 3.3.2). Aardwolves had the highest mean relative abundance as determined by the Wildview cameras, very closely followed by brown hyaenas (Table 3.3.2). There were no significant differences in the relative abundances of any carnivore species as determined by each camera type. Interestingly, however, the only three carnivore species for which Wildview cameras produced higher mean relative abundances than Cuddeback cameras (aardwolves, brown hyaenas and leopards) were also the three largest carnivore species recorded (species weights from Stuart & Stuart (2007)).

Table 3.3.2. The number of independent events (n) (total photographs in parentheses) recorded by each camera type, mean relative abundance index (mean RAI) determined by each camera type and standard deviation (S.D) of the mean RAI for all carnivore species recorded at Kwandwe between 09/01/2013 and 08/07/2013.

	Cuddeback			Wildview		
	n	Mean RAI	S.D	n	Mean RAI	S.D
Aardwolf	20 (20)	2.47	4.99	38 (45)	4.72	12.87
Bat-eared fox	4 (4)	0.49	1.48	1 (1)	0.21	0.62
Black-backed jackal	46 (54)	6.05	18.15	14 (14)	1.74	4.78
Brown hyaena	6 (6)	0.74	1.11	33 (36)	4.60	5.64
Gray mongoose	7 (7)	0.86	1.82	3 (3)	0.61	1.82
Large-spotted genet	5 (5)	0.62	1.85	0	-	-
Leopard	3 (3)	0.37	0.56	15 (16)	2.06	2.27
Small-spotted genet	3 (3)	0.37	0.56	0	-	-
Striped polecat	3 (3)	0.37	1.11	1 (1)	0.14	0.41

E-Zulu

Cuddeback cameras recorded nine carnivore species, of which aardwolves had the highest mean relative abundance (Table 3.3.3). Wildview cameras recorded only three carnivore species. However, it must be noted that the leopard recorded by Cuddeback cameras had been removed from the property before Wildview cameras were active. Bat-eared foxes had the highest mean relative abundance as determined by the Wildview cameras (Table 3.3.3). The relative abundances of each carnivore species determined by Wildview cameras were lower than those determined by the Cuddeback cameras (Table 3.3.3). Cuddeback cameras produced a significantly higher relative abundance of black-backed jackal across all cameras compared to the Wildview cameras ($Z=2.08$, $df=16$, $p<0.05$).

Table 3.3.3. The number of independent events (n) (total photographs in parentheses) recorded by each camera type, mean relative abundance index (mean RAI) determined by each camera type and standard deviation (S.D) of the mean RAI for all carnivore species recorded at E-Zulu between 21/11/2012 and 21/05/2013.

	Cuddeback			Wildview		
	n	Mean RAI	S.D	n	Mean RAI	S.D
Aardwolf	18 (18)	2.22	3.09	0	-	-
Bat-eared fox	13 (13)	1.60	1.93	6 (6)	0.84	1.30
Black-backed jackal	13 (13)	1.60	1.13	2 (2)	0.26	0.78
Gray mongoose	2 (2)	0.25	0.49	0	-	-
Leopard	1 (1)	0.12	0.37	0	-	-
Small-spotted genet	4 (4)	0.49	0.98	0	-	-
Striped polecat	4 (6)	0.49	1.13	0	-	-
Suricate	2 (3)	0.25	0.74	0	-	-
Yellow mongoose	4 (4)	0.49	1.13	2 (2)	0.26	0.52

*Non-carnivore relative abundance**Kwandwe*

Warthog, closely followed by kudu, were the most photographed species by both camera types (Table 3.3.4). For Cuddeback cameras, warthog also had the highest mean relative abundance across all cameras, with kudu having the second highest mean relative abundance (Table 3.3.4). For the Wildview cameras, however, this trend was reversed with kudu having the highest mean relative abundance, and warthog the second highest mean relative abundance (Table 3.3.4). Wildview cameras produced a significantly higher mean relative abundance for kudu than the Cuddeback cameras ($Z=2.16$, $df=16$, $p<0.05$). There were no other significant differences in the relative abundances of any of the other non-carnivore species as determined by each camera type. However, Wildview cameras produced a near significant higher relative abundance of elephants ($Z=1.94$, $df=16$, $p=0.052$). Among species that were recorded by both camera types, Wildview cameras produced equal or higher mean relative abundances for all species except red rock rabbits and scrub hares (Table 3.3.4). Interestingly, these two species were also the two smallest species that were recorded by both camera types (species weights from Stuart & Stuart (2007)).

Table 3.3.4. The number of independent events (n) (total photographs in parentheses) recorded by each camera type, mean relative abundance index (mean RAI) determined by each camera type and standard deviation (S.D) of the mean RAI for all non-carnivore species recorded at Kwandwe between 09/01/2013 and 08/07/2013. Continues on next page.

	Cuddeback			Wildview		
	n	Mean RAI	S.D	n	Mean RAI	S.D
Aardvark	1 (1)	0.12	0.37	1 (1)	0.12	0.37
African elephant	9 (39)	1.11	2.94	15 (17)	2.20	2.01
Black rhinoceros	1 (1)	0.12	0.37	1 (1)	0.12	0.37
Bushbuck	39 (44)	4.81	8.66	83 (101)	14.31	26.36
Bushpig	5 (8)	0.62	1.13	5 (6)	0.70	1.19
Cape buffalo	2 (3)	0.25	0.74	11 (20)	1.80	2.40
Cape porcupine	12 (19)	1.48	1.47	16 (18)	2.37	2.31
Chacma baboon	29 (65)	3.58	4.57	52 (83)	8.81	7.09
Common duiker	42 (49)	5.19	8.33	46 (50)	6.61	11.35

Table 3.3.4. Continued.

	Cuddeback			Wildview		
	n	Mean RAI	S.D	n	Mean RAI	S.D
Eland	2 (2)	0.25	0.74	4 (4)	1.06	2.17
Gemsbok	2 (2)	0.25	0.74	13 (13)	1.69	4.01
Giraffe	1 (1)	0.12	0.37	9 (13)	1.11	3.33
Greater kudu	75 (107)	9.26	7.54	168 (381)	29.83	22.06
Impala	8 (9)	0.99	2.96	9 (14)	1.13	2.94
Mountain reedbuck	0	-	-	2 (2)	0.28	0.84
Plains zebra	9 (10)	1.11	1.84	18 (36)	2.91	3.12
Pouched mouse	1 (1)	0.12	0.37	0	-	-
Red hartebeest	1 (1)	0.12	0.37	0	-	-
Red rock rabbit	9 (10)	1.11	2.36	5 (5)	0.82	1.62
Scrub hare	21 (23)	2.59	4.58	19 (24)	2.58	4.02
Steenbok	9 (10)	1.11	3.33	13 (14)	1.60	4.81
Warthog	197 (290)	24.32	50.96	185 (261)	27.10	47.63
Waterbuck	1 (1)	0.12	0.37	12 (13)	1.58	2.14
White rhinoceros	7 (19)	0.86	1.91	19 (23)	2.41	5.09

E-Zulu

Warthog were the most photographed species by Cuddeback cameras and also had the highest mean relative abundance (Table 3.3.5). Kudu were the second most photographed species and had the second highest mean relative abundance as determined by the Cuddeback cameras (Table 3.3.5). For the Wildview cameras, kudu were the most photographed species and had the highest mean relative abundance (Table 3.3.5). Warthog were the second most photographed species and also had the second highest mean relative abundance (Table 3.3.5). Wildview cameras produced a significantly higher relative abundance of aardvark across all cameras than the Cuddeback cameras ($Z=2.08$, $df=16$, $p<0.05$). Wildview cameras also produced a near significant higher relative abundance of buffalo compared to Cuddeback cameras ($Z=1.98$, $df=16$, $p=0.063$). There were no significant differences in the relative abundances of any of the other non-carnivore mammal species as determined by each camera type. However, Wildview cameras determined higher mean relative abundances for all species except eland, nyala, scrub hares and vervet monkeys (Table 3.3.5).

Table 3.3.5. The number of independent events (n) (total photographs in parentheses) recorded by each camera type, mean relative abundance index (mean RAI) determined by each camera type and standard deviation (S.D) of the mean RAI for all non-carnivore species recorded at E-Zulu between 21/11/2012 and 21/05/2013.

	Cuddeback			Wildview		
	n	Mean RAI	S.D	n	Mean RAI	S.D
Aardvark	2 (2)	0.25	0.49	9 (9)	1.22	1.19
Blue wildebeest	6 (8)	0.74	2.22	14 (28)	1.88	4.69
Bontebok	1 (2)	0.12	0.37	13 (42)	1.90	5.70
Bushbuck	5 (8)	0.62	1.48	7 (9)	0.95	2.85
Bushpig	4 (6)	0.49	0.81	8 (10)	1.09	1.93
Cape buffalo	4 (4)	0.49	0.98	19 (25)	2.79	3.55
Cape porcupine	9 (9)	1.11	2.55	11 (12)	1.48	2.05
Chacma baboon	61 (86)	7.53	6.50	86 (132)	11.70	10.84
Common duiker	134 (186)	16.54	12.66	131 (160)	18.19	14.15
Eland	16 (26)	1.98	4.04	9 (16)	1.21	2.38
Gemsbok	6 (11)	0.74	1.47	18 (24)	2.52	4.33
Giraffe	0	-	-	4 (6)	0.52	1.57
Greater kudu	248 (435)	30.62	19.04	496 (802)	70.28	38.48
Impala	12 (17)	1.48	1.67	42 (79)	5.83	9.30
Nyala	3 (13)	0.37	0.79	1 (2)	0.13	0.40
Sable	1 (2)	0.12	0.37	3 (10)	0.42	0.92
Scrub hare	7 (8)	0.86	1.34	6 (7)	0.79	1.95
Spring hare	1 (1)	0.12	0.37	1 (1)	0.15	0.44
Steenbok	18 (22)	2.22	4.30	35 (37)	5.01	12.00
Vervet monkey	21 (25)	2.59	2.89	7 (7)	0.97	1.72
Warthog	280 (499)	34.57	14.26	392 (696)	53.93	30.31
Waterbuck	59 (91)	7.28	7.01	117 (170)	16.00	14.07

*Carnivore species rarefaction curves and diversity indices**Kwandwe*

For the Wildview cameras, carnivore species accumulation was initially quicker than for that of the Cuddeback cameras (Figure 3.3.1). However, after roughly two weeks of sampling, the number of species recorded by the Cuddeback cameras surpassed the number of species recorded by the Wildview cameras (Figure 3.3.1). At the end of sampling, Cuddeback cameras had reached an asymptote and the observed species rarefaction curve had converged with the Chao 1 estimator (Figure 3.3.1), suggesting that all species present had been recorded. Conversely, observed species for the Wildview cameras never reached an asymptote during the 90 day sampling period. Furthermore, the difference between the observed species rarefaction curve and the Chao 1 estimator suggests that one species was present, yet remained undetected (Figure 3.3.1). Shannon diversity indices for the two camera types were very similar at $H' = 1.5$ and $H' = 1.47$ for Cuddeback and Wildview cameras respectively.

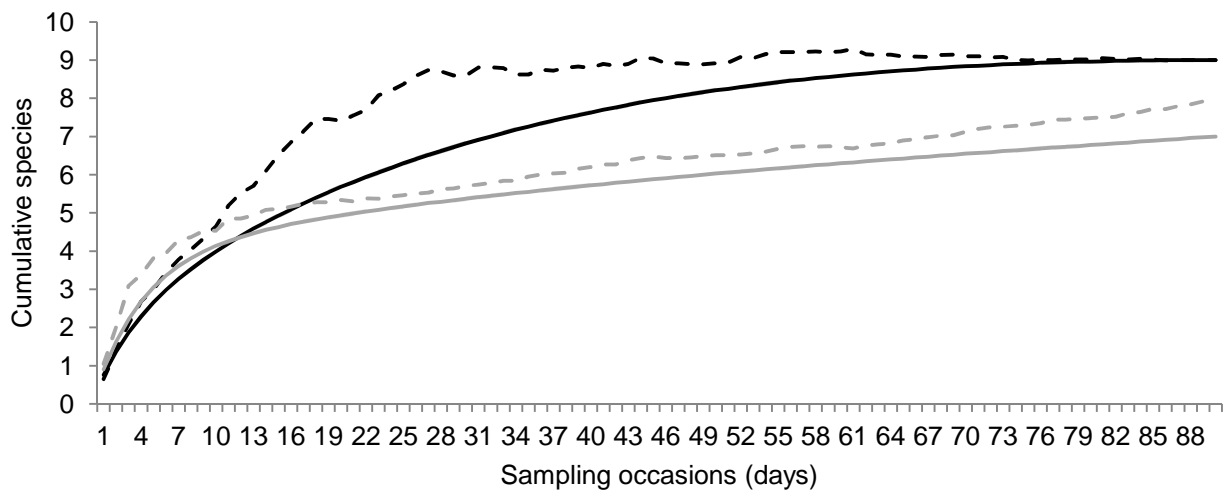


Figure 3.3.1. Observed species rarefaction curves (solid lines) and Chao 1 estimates (dashed lines) for Cuddeback cameras (black) and Wildview cameras (grey) for carnivore species at Kwandwe.

E-Zulu

Carnivore species accumulation for the Wildview cameras occurred at a relatively slow rate, and remained fairly constant for the entire 91 day sampling period (Figure 3.3.2). Species accumulation for the Cuddeback cameras was initially much higher, and then occurred at a similar rate to the Wildview cameras from roughly 45 days of sampling onwards (Figure 3.3.2). Species rarefaction curves for both camera types converged with their Chao 1 estimates by the end of sampling, suggesting that all species present were recorded (Figure 3.3.2). As might be expected from the sparsity of species recorded by the Wildview cameras, the Shannon diversity index for Cuddeback cameras was higher than that for the Wildview cameras at $H'=1.85$ and $H'=1.05$ respectively.

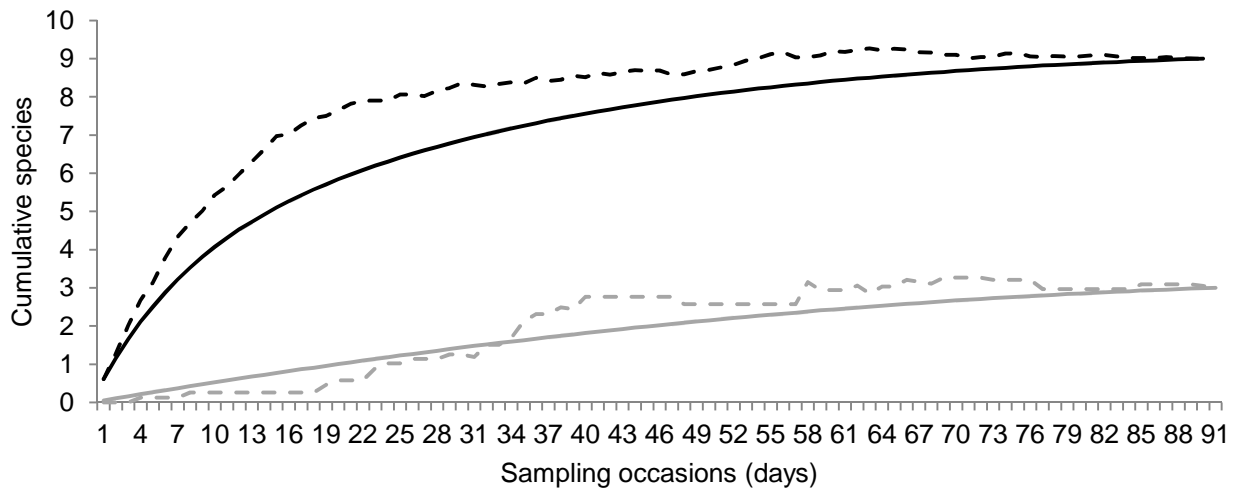


Figure 3.3.2. Observed species rarefaction curves (solid lines) and Chao 1 estimates (dashed lines) for Cuddeback cameras (black) and Wildview cameras (grey) for carnivore species at E-Zulu.

*Non-carnivore species rarefaction curves and diversity indices**Kwandwe*

Species accumulation initially occurred at a higher rate for the Wildview cameras than for the Cuddeback cameras (Figure 3.3.3). By roughly 70 days of sampling, the Wildview cameras approached an asymptote and the number of species observed by the Wildview cameras was surpassed by that of the Cuddeback cameras (Figure 3.3.3). At the end of the sampling period, the Chao 1 estimator had almost converged with the species rarefaction curve, suggesting that only one species was present but remained undetected (Figure 3.3.3). For the Cuddeback cameras, however, there was a larger difference between the rarefaction curve and the Chao 1 estimator, which predicted that four species were present but remained undetected (Figure 3.3.3). Although the Cuddeback cameras detected one more species than the Wildview cameras, the Wildview cameras produced a higher Shannon index of $H' = 2.3$, compared to $H' = 2.07$ for the Cuddeback cameras. This suggests that even though species richness was slightly higher for the Cuddeback cameras, species evenness was higher for the Wildview cameras, hence producing a higher Shannon diversity index.

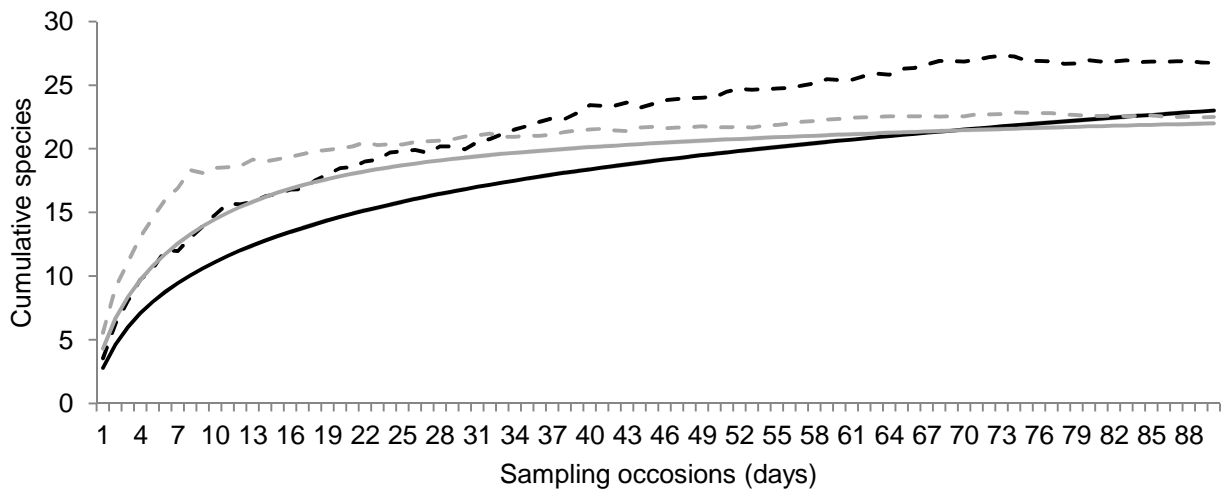


Figure 3.3.3. Observed species rarefaction curves (solid lines) and Chao 1 estimates (dashed lines) for Cuddeback cameras (black) and Wildview cameras (grey) for 'non-carnivore' species at Kwandwe.

E-Zulu

For the first four days of sampling, species accumulation occurred at a similar rate for both camera types (Figure 3.3.4). Following this, species accumulation for the Cuddeback cameras was slightly lower than for the Wildview cameras (Figure 3.3.4). However, after 90 days of sampling, the Wildview cameras were closer to approaching an asymptote than the Cuddeback cameras (Figure 3.3.4). Neither of the camera type rarefaction curves converged with their Chao 1 estimator, suggesting that the Wildview cameras failed to detect one species and the Cuddeback cameras failed to detect two species that were present (Figure 3.3.4). Shannon diversity indices were similar for both camera types. The Cuddeback cameras produced a Shannon index of $H'=1.94$, compared to the slightly higher $H'=1.99$ for the Wildview cameras.

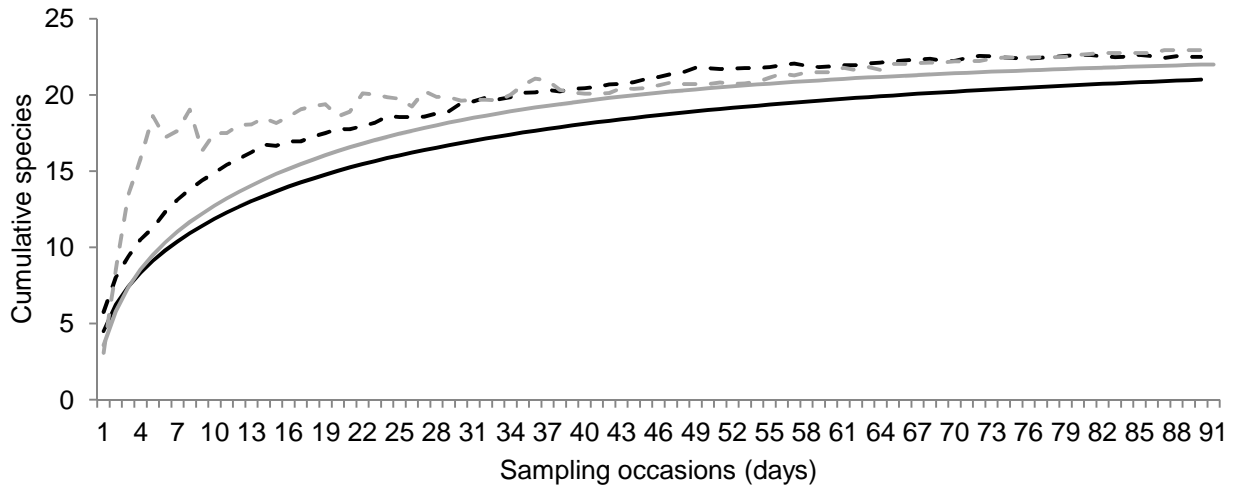


Figure 3.3.4. Observed species rarefaction curves (solid lines) and Chao 1 estimates (dashed lines) for Cuddeback cameras (black) and Wildview cameras (grey) for 'non-carnivore' species at E-Zulu.

*Picture quality**Carnivore species*

Following the removal of photographs in which there were multiple subjects or the subject was too close to the camera, a total of 153 photographs for Cuddeback cameras and 110 photographs for the Wildview cameras remained for analysis (Table 3.3.6). Across both camera types, there were significantly more centred subjects than front only or back only subjects ($F_{2,60} = 83.3$, $p < 0.001$). When comparing the positioning of subjects between the two camera types, Cuddeback cameras produced a significantly higher proportion of centred subjects than the Wildview cameras ($F_{2,60} = 4.4$, $p < 0.05$). Although not significant, the proportion of back only photographs produced by the Wildview cameras was almost five-fold higher than those produced by the Cuddeback cameras. Interestingly, this difference was attributable to the positions of apex and mesocarnivore species (Table 3.3.6). With the exception of small-spotted genets, all microcarnivore species were centred in 100% of photographs for both camera types (Table 3.3.6).

Table 3.3.6. The number of events (percentage of total events per species, per camera type in parentheses) in which only the front of the subject was photographed, the subject was centred in the frame, or only the back of the subject was photographed for all carnivore species recorded by each camera type combined across both sites.

	Cuddeback			Wildview		
	Front only	Centred	Back only	Front only	Centred	Back only
Aardwolf	0 (0%)	35 (94.6%)	2 (5.4%)	1 (2.6%)	31 (81.6%)	6 (15.8%)
Bat-eared fox	0 (0%)	15 (100%)	0 (0%)	0 (0%)	6 (100%)	0 (0%)
Black-backed jackal	1 (1.7%)	55 (91.7%)	4 (6.7%)	0 (0%)	13 (81.3%)	3 (18.8%)
Brown hyaena	0 (0%)	5 (100%)	0 (0%)	0 (0%)	21 (67.7%)	10 (32.3%)
Large-spotted genet	0 (0%)	5 (100%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Leopard	2 (50%)	2 (50%)	0 (0%)	1 (7.1%)	11 (78.6%)	2 (14.3%)
Small gray mongoose	0 (0%)	9 (100%)	0 (0%)	0 (0%)	3 (100%)	0 (0%)
Small-spotted genet	1 (14.3%)	6 (85.7%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Striped polecat	0 (0%)	6 (100%)	0 (0%)	0 (0%)	1 (100%)	0 (0%)
Suricate	0 (0%)	1 (100%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Yellow mongoose	0 (0%)	4 (100%)	0 (0%)	0 (0%)	1 (100%)	0 (0%)
Total	4 (2.6%)	143 (93.5%)	6 (3.9%)	2 (1.8%)	87 (79.1%)	21 (19.1%)

Non-carnivore species

A total of 845 photographs for the Cuddeback cameras and 1573 photographs for the Wildview cameras remained for analysis after the removal of photographs containing multiple subjects, or when the subject was too close to the camera (Table 3.3.7). There were significantly more centred subjects across both camera types ($F_{2,162} = 60.8$, $p < 0.001$) than subjects entering or exiting the field of view. However, there was no significant difference in the positioning of subjects between camera types. While not significant, the Wildview cameras had a slightly higher proportion of photographs containing only the front of the subject, and twice the proportion of photographs containing only the back of the subject (Table 3.3.7). The higher proportion of Wildview photographs containing only the back of subjects was mainly attributable to the positions of baboons, duikers, kudu, and warthogs, the four most commonly photographed species (Table 3.3.7).

Table 3.3.7. The number of events (percentage of total events per species, per camera type in parentheses) in which only the front of the subject was photographed, the subject was centred in the frame or only the back of the subject was photographed for all non-carnivore species recorded by each camera type combined across both sites. Continues on next page.

	Cuddeback			Wildview		
	Front only	Centred	Back only	Front only	Centred	Back only
Aardvark	1 (50%)	1 (50%)	0 (0%)	0 (0%)	9 (100%)	0 (0%)
Black rhinoceros	1 (100%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Blue wildebeest	0 (0%)	2 (100%)	0 (0%)	2 (33.3%)	2 (33.3%)	2 (33.3%)
Bontebok	0 (0%)	1 (100%)	0 (0%)	1 (12.5%)	5 (62.5%)	2 (25%)
Bushbuck	7 (19.4%)	27 (75%)	2 (5.6%)	18 (22.8%)	58 (73.4%)	3 (3.8%)
Bushpig	3 (50%)	3 (50%)	0 (0%)	1 (8.3%)	10 (83.3%)	1 (8.3%)
Cape buffalo	1 (33.3%)	2 (66.7%)	0 (0%)	9 (42.9%)	12 (57.1%)	0 (0%)
Cape porcupine	1 (6.3%)	14 (87.5%)	1 (6.3%)	0 (0%)	18 (90%)	2 (10%)
Chacma baboon	2 (3.6%)	52 (94.5%)	1 (1.8%)	2 (1.9%)	90 (84.9%)	14 (13.2%)
Common duiker	23 (14.4%)	133 (83.1%)	4 (2.5%)	12 (7.5%)	130 (80.7%)	19 (11.8%)
Eland	2 (25%)	5 (62.5%)	1 (12.5%)	4 (57.1%)	3 (42.9%)	0 (0%)
Gemsbok	0 (0%)	2 (100%)	0 (0%)	4 (19%)	13 (61.9%)	4 (19%)
Greater kudu	21 (15.9%)	100 (75.8%)	11 (8.3%)	127 (23.6%)	369 (68.7%)	41 (7.6%)
Impala	1 (7.1%)	12 (85.7%)	1 (7.1%)	4 (14.8%)	22 (81.5%)	1 (3.7%)
Mountain reedbuck	0 (0%)	0 (0%)	0 (0%)	0 (0%)	2 (100%)	0 (0%)
Nyala	1 (100%)	0 (0%)	0 (0%)	0 (0%)	1 (100%)	0 (0%)

Table 3.3.7. Continued.

	Cuddeback			Wildview		
	Front only	Centred	Back only	Front only	Centred	Back only
Plains zebra	0 (0%)	4 (100%)	0 (0%)	4 (28.6%)	8 (57.1%)	2 (14.3%)
Pouched mouse	0 (0%)	1 (100%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Red hartebeest	0 (0%)	1 (100%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Red rock rabbit	0 (0%)	9 (100%)	0 (0%)	0 (0%)	4 (80%)	1 (20%)
Sable	0 (0%)	0 (0%)	1 (100%)	1 (50%)	1 (50%)	0 (0%)
Scrub hare	0 (0%)	26 (96.3%)	1 (3.7%)	0 (0%)	19 (90.5%)	2 (9.5%)
Spring hare	0 (0%)	1 (100%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Steenbok	3 (11.5%)	23 (88.5%)	0 (0%)	2 (4.3%)	41 (89.1%)	3 (6.5%)
Vervet monkey	0 (0%)	13 (86.7%)	2 (13.3%)	0 (0%)	6 (100%)	0 (0%)
Warthog	39 (13.9%)	234 (83.3%)	8 (2.8%)	39 (11%)	275 (77.9%)	39 (11%)
Waterbuck	11 (28.2%)	23 (59%)	5 (12.8%)	22 (20.8%)	76 (71.7%)	8 (7.5%)
White rhinoceros	1 (100%)	0 (0%)	0 (0%)	2 (66.7%)	1 (33.3%)	0 (0%)
Total	118 (14%)	689 (81.5%)	38 (4.5%)	254 (16.1%)	1175 (74.7%)	144 (9.2%)

3.4 Discussion

At E-Zulu, the Wildview cameras produced lower relative abundance estimates for all carnivore species than the Cuddeback cameras. Similarly, Wildview cameras determined the relative abundances to be lower for all carnivore species except brown hyaenas, leopards, and aardwolves at Kwandwe. Interestingly, with the exception of the leopard that was removed from E-Zulu, carnivore species that were recorded by the Cuddeback cameras but not by the Wildview cameras were all relatively small ($\leq 11\text{kg}$ (Stuart & Stuart 2007)). Furthermore, the three carnivore species for which the Wildview cameras produced higher relative abundance estimates were the three largest species recorded (Stuart & Stuart 2007).

These results could be interpreted in several ways. It may simply be that temporal differences in carnivore abundances between deployments of the two camera types led to the different relative abundances that were recorded. Alternatively, the PIR sensitivity may have been decreased in warmer temperatures (Swann *et al.* 2004). At E-Zulu, average daily temperatures were higher during Wildview camera deployment, possibly reducing the sensitivity of Wildview camera PIRs. Conversely, at Kwandwe, average daily temperatures were lower during Wildview camera deployment. However, this suggests that ambient temperature had little effect on PIR sensitivities, and that differences in carnivore relative abundance estimates recorded by the two camera types may be due to other reasons. For example, the Wildview cameras contain slightly older technology than the Cuddeback cameras. Therefore, it may be that the PIRs in the Wildview cameras were less effective at detecting smaller carnivore species with less obvious infrared signatures (Swann *et al.* 2004; Damm, Grand & Barnett 2010). If so, this may account for the higher relative abundance estimates of large carnivore species, and the lower relative abundance estimates of smaller carnivore species recorded by the Wildview cameras.

Species diversity estimates and accumulation curves for the carnivore species suggest similar conclusions. At both sites, Shannon diversity of carnivores was lower for the Wildview cameras, possibly due to not recording species for reasons described above. Moreover, the carnivore species accumulation curve for the Cuddeback cameras at Kwandwe converged with the Chao 1 estimator, but this was not the case for Wildview cameras. This result suggests that there were carnivore species present, but which remained unrecorded by the Wildview cameras at Kwandwe. Again, this may possibly be because of differences in PIR sensitivity between the two camera types.

Relative abundance and diversity estimates of non-carnivore species showed contrasting patterns to carnivore species. For the Wildview cameras, non-carnivore species accumulation curves were closer to converging with the Chao 1 estimators, and Shannon diversity estimates were higher at both sites. Further, at Kwandwe, relative abundance estimates from the Wildview cameras were higher for all except the two smallest non-carnivore species (scrub hares and red rock rabbits) compared to the Cuddeback cameras. Likewise, the Wildview cameras produced higher relative abundance estimates for the majority of non-carnivore species at E-Zulu. Similar to the carnivore data, these results may be due to temporal differences in non-carnivore species abundances between deployments of the two camera types. Alternatively, detection area has been suggested as the most important determinant of animal detection rates in camera trapping studies (Rowcliffe *et al.* 2011; Trollet *et al.* 2014). Therefore, it may be that animals encountered the larger detection zone of Wildview cameras more frequently, leading to inflated relative abundance estimates of non-carnivore species.

If it were possible to remove confounding factors and assume that; 1) there were no temporal differences in species abundances between deployment of different camera types; 2) PIRs of each camera type were equally sensitive, regardless of age or environmental conditions and; 3) encounter rates are determined by detection area, then it may be possible to interpret the influence of trigger speed. The contrasting patterns of diversity and relative abundances produced by each camera type suggest that regardless of detection area, trigger speed affects carnivore and non-carnivore data collection differently.

Feeding opportunities may be more spatially and temporally ephemeral for carnivore species compared to non-carnivore species. Therefore, it may be that carnivores move at a greater average speed to cover larger areas when attempting to locate food. Faster movement speeds may lead to blank photographs if animals move outside the cameras field of view during longer trigger delays, such as in the Wildview cameras. Conversely, feeding opportunities for non-carnivore species are likely to exhibit a more uniform distribution across space and time. Coupled with instinctive caution, many non-carnivore species may move at slower average speeds than carnivores as food is more readily available. If so, animals may remain in the camera's field of view for longer, and the effects of slower trigger speeds may possibly be negated. This may explain why Wildview cameras produced lower relative abundance for carnivores but higher relative abundance of non-carnivores compared to the Cuddeback cameras.

Picture quality analyses corroborated the idea that trigger speed affects carnivore and non-carnivore data collection differently. For carnivore species, Cuddeback cameras recorded

significantly more subjects in the centre of the cameras field of view than the Wildview cameras. Further, although not significant, the Wildview cameras recorded a fivefold higher proportion of images in which carnivores were exiting the cameras field of view. This highlights that for carnivores, fast trigger speeds are important to ensure that the whole subject is photographed. Such data may be essential when studying individually marked species such as tigers, leopards, and African wild dogs (*Lycaon pictus*) (Karanth 1995; Balme, Hunter & Slotow 2009; Ramnanan, Swanepoel & Somers 2013). Trigger speeds proved less important to obtain centred images of non-carnivore species. Across both camera types, a significant proportion of images contained the whole subject, but there was no significant difference between camera types. However, Wildview cameras did produce a slightly higher proportion of photographs of non-carnivore species exiting the field of view. This shows that slow trigger speeds may also result in lower quality data of non-carnivore species.

Summary and implications

Considering all mammal, bird, and reptile species together, the Wildview cameras recorded more photographs at both study sites compared to the Cuddeback cameras. However, the total number of mammal, bird, and reptile species recorded by the Wildview cameras was fewer at both sites compared to the Cuddeback cameras. This suggests that wider detection areas increase encounter rates, but slow trigger speeds may fail to record faster moving species. Therefore, wider detection areas may provide larger data sets when studying demographics, or when using approaches such as occupancy modelling and random encounter models (REM). However, fast trigger speeds are essential for accurate identification of individual marked animals when using capture-recapture models. Further, faster trigger speeds recorded a higher number of species and may perform better than slow trigger speeds when constructing species inventories. Interestingly, wider detection areas led to a higher initial rate of species accumulation for Wildview cameras in all cases except carnivores at E-Zulu. This suggests that wider detection areas are better for short term studies, particularly if coupled with fast to moderate trigger speed to reduce blanks and improve quality of photos.

Unfortunately, as my study assessed only two camera trap models, the interactive effects of detection area and trigger speed are hard to discern. Therefore, further studies using a wider range of camera traps is essential for better understanding of how camera trap design features affect the quality and quantity of data collected.

Chapter 4

Testing the Mesopredator Release Hypothesis on Two Enclosed Reserves in the Eastern Cape, South Africa

4.1 Introduction

Subsequent to the top-down forcing ideas of Hairston, Smith & Slobodkin (1960), many authors noted that in the absence of large predators, intermediate level predators can become more abundant (e.g. Schoener & Toft 1983; Pacala & Roughgarden 1984; Schoener & Spiller 1987). Later, this 'explosion' of intermediate level predators in the absence of larger predators was referred to as 'mesopredator release' (Soulé *et al.* 1988). A more recent and more encompassing definition of the mesopredator release hypothesis (MRH) is 'an increase in abundance, or changes in the distribution or behaviour of middle ranked predators when the top-down forcing effects of larger predators are reduced or removed' (Prugh *et al.* 2009; Brashares *et al.* 2010). Furthermore, decreases in mesopredator abundances associated with apex predator reintroductions, 're-wilding' programs and population recoveries are often cited as indications of historical mesopredator release (McDonald, O'Hara & Morrish 2007; Elmhagen *et al.* 2010).

Often, changes in mesopredator distribution and behaviour are interrelated (Palomares *et al.* 1996; Heithaus & Dill 2002; Berger, Gese & Berger 2008; Sergio & Hiraldo 2008; Salo *et al.* 2008). For example, Berger, Gese & Berger (2008) observed the interactions between grey wolves (*Canis lupus*) and coyotes (*Canis latrans*) in the Grand Teton National Park, Wyoming, USA. They found that wolf presence/absence had no significant effect on resident coyote abundance. However, abundance of transient coyotes was significantly higher in areas not utilized by wolves, suggesting that wolves alter the dispersal behaviour of coyotes, which may ultimately influence coyote distribution (Berger, Gese & Berger 2008). Similarly, it has been suggested that behavioural responses to reduce predation risk by Iberian lynx (*Lynx pardinus*) affects the distribution of smaller predators including Egyptian mongooses (*Herpestes ichneumon*) and common genets (*Genetta genetta*) in south-western Spain (Palomares *et al.* 1996). However, it could be argued that the distributions of these smaller predators are a result of habitat preferences rather than predation risk (Litvaitis & Villafuerte 1996).

Detecting changes in mesopredator distribution requires long-term observations or comparisons of recent data with historical data. One example is that of the fisher (*Martes*

pennanti) in North America (LaPoint, Belant & Kays 2015). Following severe range contractions due to land conversion, fishers were reintroduced back into areas of their historic range. In areas with no large predators such as coyotes, cougars (*Puma concolor*), or Canadian lynxes (*Lynx canadensis*), fisher range expansion was as high as 119%. Conversely, in areas where these large predators were present, the distribution of fishers remained relatively unchanged with only a 15-18% range expansion (LaPoint, Belant & Kays 2015).

Behavioural changes in mesopredators can manifest themselves as altered foraging strategies (Mukherjee, Zelcer & Kotler 2009; Dunphy-Daly *et al.* 2010). For instance, in the north-central Negev Desert, Israel, red foxes (*Vulpes vulpes*) altered their time spent foraging in response to perceived predation risk from striped hyaenas (*Hyaena hyaena*) and Indian wolves (*Canis lupus pallipes*) (Mukherjee, Zelcer & Kotler 2009). Similarly, in areas of high tiger shark (*Galeocerdo cuvier*) density in the Eastern Gulf of Shark Bay, Australia, Pied Cormorants (*Phalacrocorax varius*) increased dive durations to minimize time spent at the surface where predation risk is highest (Dunphy-Daly *et al.* 2010). Altered feeding strategies such as these are not strictly indicative of mesopredator release. However, they serve to highlight the complex interactions between many apex and mesocarnivores. Only when these interactions are fully understood can management strategies be best tailored towards maintaining healthy ecosystems.

Possibly the most numerous examples of MRH are those which correlate increased mesopredator abundance with decreased or zero apex predator abundance (e.g. Mittelbach *et al.* 1995; Fedriani *et al.* 2000; Ward & Myers 2005; Burkepile & Hay 2007; Trewby *et al.* 2008; Chakarov & Krüger 2010). For instance, Burkepile & Hay (2007) were able to exclude large predatory fishes from particular areas of coral reefs in the Florida Keys, Florida, USA. In predator exclusion zones, the normally rare flamingo tongue snail (*Cyphoma gibbosum*) showed a 19-fold increase in abundance during their ten month experiment (Burkepile & Hay 2007). In turn, gorgonian corals were more frequently and extensively grazed by *C. gibbosum* in areas of predator exclusion than in areas where predatory fish were present. Similarly, dramatic declines in tuna (Tribe: Thunnini), billfish (Istiophoridae), and large elasmobranch species between the 1950s and 1990s are correlated with significant increases in catch rates of pelagic mesopredatory fishes in the Pacific (Ward & Myers 2005; Baum & Worm 2009).

Ritchie & Johnson (2009) indicated that among terrestrial examples of MRH, there is a strong bias towards North American systems, particularly those involving the Canidae family (e.g. Berger & Conner 2008; Berger, Gese & Berger 2008; Cove *et al.* 2012; Miller *et al.*

2012; Levi & Wilmers 2012; Ripple *et al.* 2013). Further, many North American studies have also investigated non-canid predators including cougars (Ackerman, Lindzey & Hemker 1984; Koehler & Hornocker 1991), skunks (Mephitidae) (Prange & Gehrt 2007), bobcats (*Lynx rufus*) (Fedriani *et al.* 2000), and raccoons (*Procyon* spp.) (Gehrt & Clark 2003; Gehrt & Prange 2007).

Numerous examples of MRH have also been published in Australia. For example, dingoes (*Canis lupus dingo*) have been shown to influence the abundance and behaviour of feral cats (*Felis catus*) (Kennedy *et al.*, 2012; Brook, Johnson & Ritchie, 2012) and red foxes (Johnson & VanDerWal, 2009; Letnic & Dworjanyn, 2011). However, results from other studies in Australia do not support these findings. For instance, Allen *et al.* (2013) conducted predator manipulation experiments whereby dingo populations were reduced using poisoned baits. Their results showed no significant difference in the abundances of feral cats, red foxes, or monitor lizards (*Varanus* spp.) between sites with high or low dingo abundance.

In Europe, MRH has been shown by way of Eurasian lynx (*Lynx lynx*) limiting red fox abundance in Sweden (Helldin, Liberg & Glöersen 2006; Elmhagen & Rushton 2007; Pasanen-Mortensen, Pyykönen & Elmhagen 2013), Iberian lynx controlling Egyptian mongoose populations and ultimately benefiting rabbits (*Oryctolagus cuniculus*) in Spain (Palomares *et al.*, 1995), and the culling of European badgers (*Meles meles*) has led to increased red fox abundance in the UK (Trewby *et al.* 2008). Additionally, tigers (*Panthera tigris*) and leopards (*P. pardus*) have been shown to control dhole (*Cuon alpinus*) populations through predation on the Indian subcontinent (Johnsingh 1992; Karanth & Sunquist 1995).

Evidently, mesopredator release is widespread and common in terrestrial ecosystems. However, only a handful of studies have investigated the role of mesopredators in African ecosystems (e.g. Maina & Jackson 2003; Lloyd 2007; van der Merwe *et al.* 2009; Brassine & Parker 2011; Yarnell *et al.* 2013). Among these studies, evidence for mesopredator release is sparse. For example, the findings of Lloyd (2007) do not support the idea that nest predators such as mongooses (Herpestidae) are released from top down forcing in areas where larger predators are lethally controlled. Also, in similar nest predation studies in Kenya, mesopredator release has been proposed as an explanation for differing levels of nest predation, but cannot be proven as mesopredator abundance was not measured (Maina & Jackson 2003). Further, the presence/absence of apex predators such as lions (*P. leo*) has been shown to influence the diet of brown hyaenas (*Hyaena brunnea*), possibly through altered scavenging opportunities (van der Merwe *et al.* 2009; Yarnell *et al.* 2013). However, apex predators induce little change in the diets of other mesopredator species

such as black-backed jackals (*Canis mesomelas*) (Brassine & Parker 2011; Yarnell *et al.* 2013).

Excluding the predominantly aquatic Cape clawless otter (*Aonyx capensis*) and spotted-necked otter (*Lutra maculicollis*), the southern African subregion is home to 37 species of terrestrial carnivores, spanning seven families and 29 genera (Skinner & Chimimba 2005). As might be expected in such a diverse predator assemblage, classification of which species constitute a mesopredator has varied from study to study (e.g. mongooses in Lloyd (2007), black-backed jackals in Brassine & Parker (2011) and brown hyaenas in Yarnell *et al.* (2013)).

Significantly, competition between predators can often follow a linear hierarchy based on body size (Gehrt & Clark 2003). Therefore, predators present at my study sites were classified by weight. Apex predators were those above the 21.5 kg threshold that leads to obligate carnivory (Carbone *et al.* 1999), and this included lions, leopards and brown hyaenas, all of which were intentionally re-introduced at Kwandwe (Bissett 2004). Carnivores <5kg are likely to be in little competition with apex carnivores and were classed as microcarnivores, and included the Cape fox (*Vulpes chama*) and several species from the Herpestidae, Viverridae and Mustelidae families. Species weighing between 5 and 21.5kg included black-backed jackals, caracals (*Caracal caracal*), African wildcats (*Felis silvestris*), bat-eared foxes (*Otocyon megalotis*) and aardwolves (*Proteles cristatus*). Of these species, bat-eared foxes and aardwolves are primarily insectivores (Koop & Velimirov 1982; Kuntzsch & Nel 1992; Matsebula *et al.* 2009; Yarnell & MacTavish 2013). By contrast, black-backed jackals and caracals readily consume mammalian prey (Skinner & Chimimba 2005) and were the mesopredators of focus for my study. Interestingly, these two species are also reported as having the highest levels of conflict with land owners in South Africa (Thorn *et al.* 2012).

Black-backed jackals are roughly 38cm tall at the shoulder and weigh 6-10kg (Stuart & Stuart 2007). Black-backed jackals have an overall reddish-brown colour with a white flecked, but predominantly black saddle running from the base of the neck to the base of the tail. The muzzle is long and pointed, the ears are large, erect and pointed and the tail is bushy with dark colouration (Skinner & Chimimba 2005). Black-backed jackals are generalist predators with a broad diet consisting of large and small mammals, invertebrates, birds, reptiles, fruits, seeds, and anthropogenic items (Skinner & Chimimba 2005; Stuart & Stuart 2007; Brassine 2011). Caracals are slightly larger, roughly 45cm tall at the shoulder and weigh 7-19kg (Stuart & Stuart 2007). Caracals exhibit obvious sexual dimorphism, with males being significantly larger than females (Skinner & Chimimba 2005). Caracal colour

varies geographically from a reddish-fawn in arid areas to sandy-brown in areas of higher rainfall. Caracals have a relatively short tail and large pointed ears with distinctive black tufts (Nowell & Jackson 1996; Skinner & Chimimba 2005). The diet of caracals is generally restricted to birds and small to medium sized mammals, however, reptiles and invertebrates are occasionally eaten (Skinner 1979; Melville, Bothma & Mills 2004; Skinner & Chimimba 2005; Braczkowski *et al.* 2012).

In this chapter, I aimed to assess meso and micropredator relative abundances at two sites, one with and one without apex predators. Additionally, for species with sufficient data, I aimed to use the more robust approach of occupancy modelling to further investigate the effects that apex predators may have on meso and micropredator abundances. Furthermore, I aimed to use the number of photographs of each carnivore species at each camera station (see chapter 2) to determine crude spatial distribution patterns for each predator species. Moreover, using the time of day that each carnivore photograph was taken, I aimed to assess daily activity patterns of each carnivore species. I hypothesized that where apex predators were absent, mesopredators would be more abundant due to a lack of top-down forcing, as predicted by MRH (Soulé *et al.* 1988; Prugh *et al.* 2009; Brashares *et al.* 2010). In addition, I hypothesized that mesopredators would be spatially displaced in the presence of apex predators due to competitive exclusion and/or interspecific killing (Caro & Stoner 2003; Donadio & Buskirk 2006). I further hypothesized that apex predators would induce a temporal shift in the daily activity patterns of mesopredators, possibly minimizing predation risk by being active at different times of day (Steinmetz, Seuaturien & Chutipong 2013).

4.2 Materials & Methods

The sampling procedure was as outlined in chapter 2 and only Cuddeback “Attack” cameras (n=18) were used, as they performed better when photographing carnivores (see chapter 3). Cameras were left in place at each sampling station for 90 days before being relocated to a new randomly generated point (see chapter 2 for details). One camera at Kwandwe was inactive for 32 days, leading to a loss of 32 trap nights of data. Further, a software malfunction occurred when downloading photographs to a handheld tablet (Samsung Galaxy note 10.1) on 21/11/2012, and this led to a loss of 42 days of data for each camera station (378 trap nights) at E-Zulu. To compensate for this, the 90 day sampling period was restarted after the loss of data, hence the gap between the end of rotation 1 and the start of rotation 2 at E-Zulu (Table 4.2.1).

Table 4.2.1. The dates for each camera station rotation, number of days each station was active and number of trap nights at Kwandwe and E-Zulu between 03/07/2012 and 19/08/2013. One camera station during rotation 1 at Kwandwe was not active for 32 days, hence the lower than expected number of trap nights for that rotation.

	Kwandwe			E-Zulu		
	Dates	Days	Trap nights	Dates	Days	Trap nights
Rotation 1	03/07/2012 - 04/10/2012	93	805	11/07/2012 - 10/10/2012	91	819
Rotation 2	04/10/2012 - 09/01/2013	97	873	21/11/2012 - 19/02/2013	90	810
Rotation 3	09/01/2013 - 09/04/2013	90	810	19/02/2013 - 21/05/2013	91	819
Rotation 4	09/04/2013 - 08/07/2013	90	810	21/05/2013 - 19/08/2013	90	810
Total	03/07/2012 - 08/07/2013	370	3298	11/07/2012 - 19/08/2013	362	3258

Camera placement at Kwandwe was a mean distance of $39.02 \pm 32.13\text{m}$ (range = 0.34 - 102.42m) away from the randomly generated points (Figure 4.2.1). At E-Zulu, camera placement was a mean distance of $15.06 \pm 12.81\text{m}$ (range = 0.41 - 51.03m) from the randomly generated points (Figure 4.2.2). Exact GPS co-ordinates of all cameras are provided in appendix B.

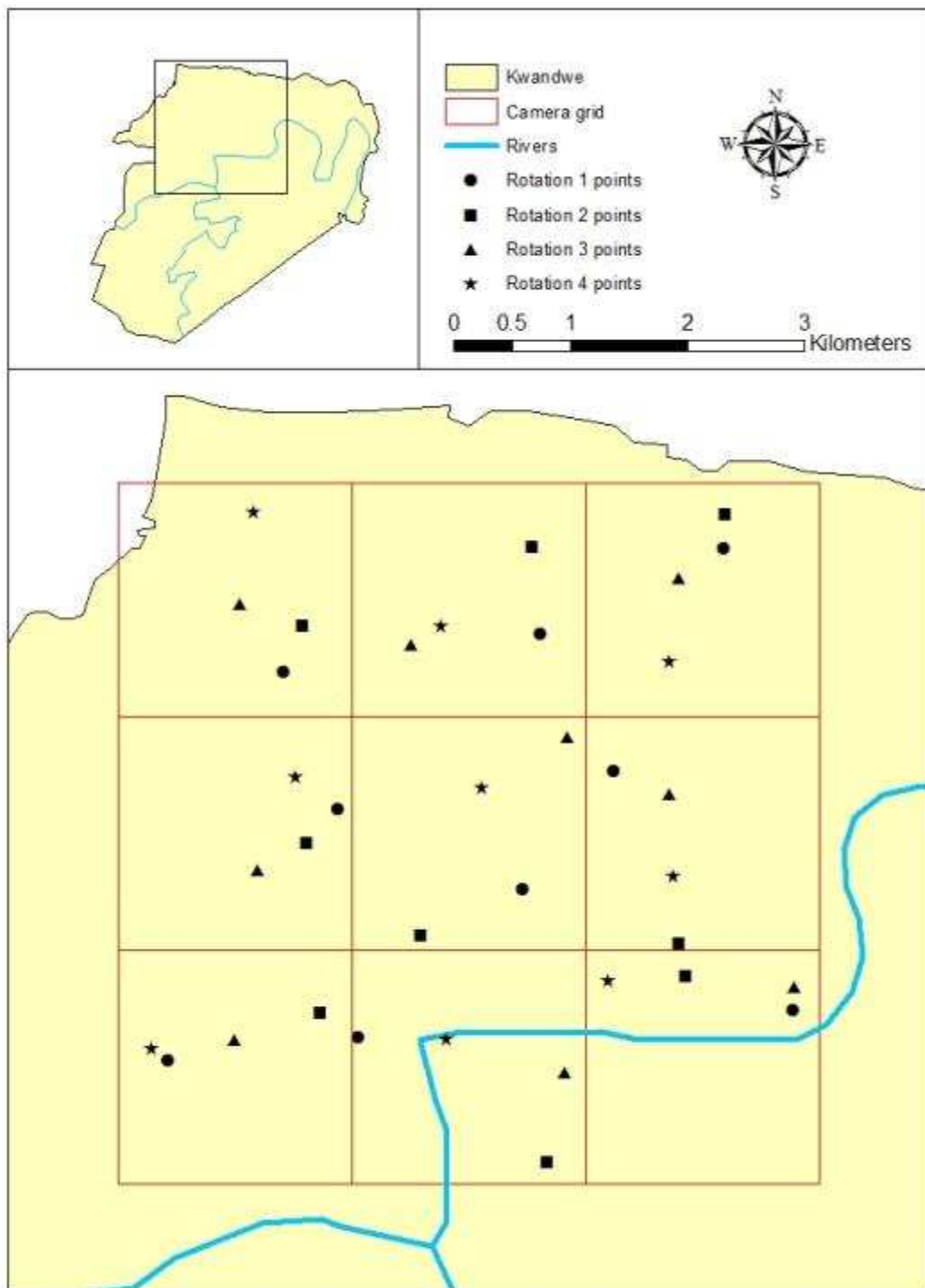


Figure 4.2.1. The position of each of the nine camera stations within the 3,600 Ha trapping grid at Kwandwe. Symbol type indicates camera positions for each rotation. Cameras were rotated to new positions on the dates outlined in Table 4.2.1.

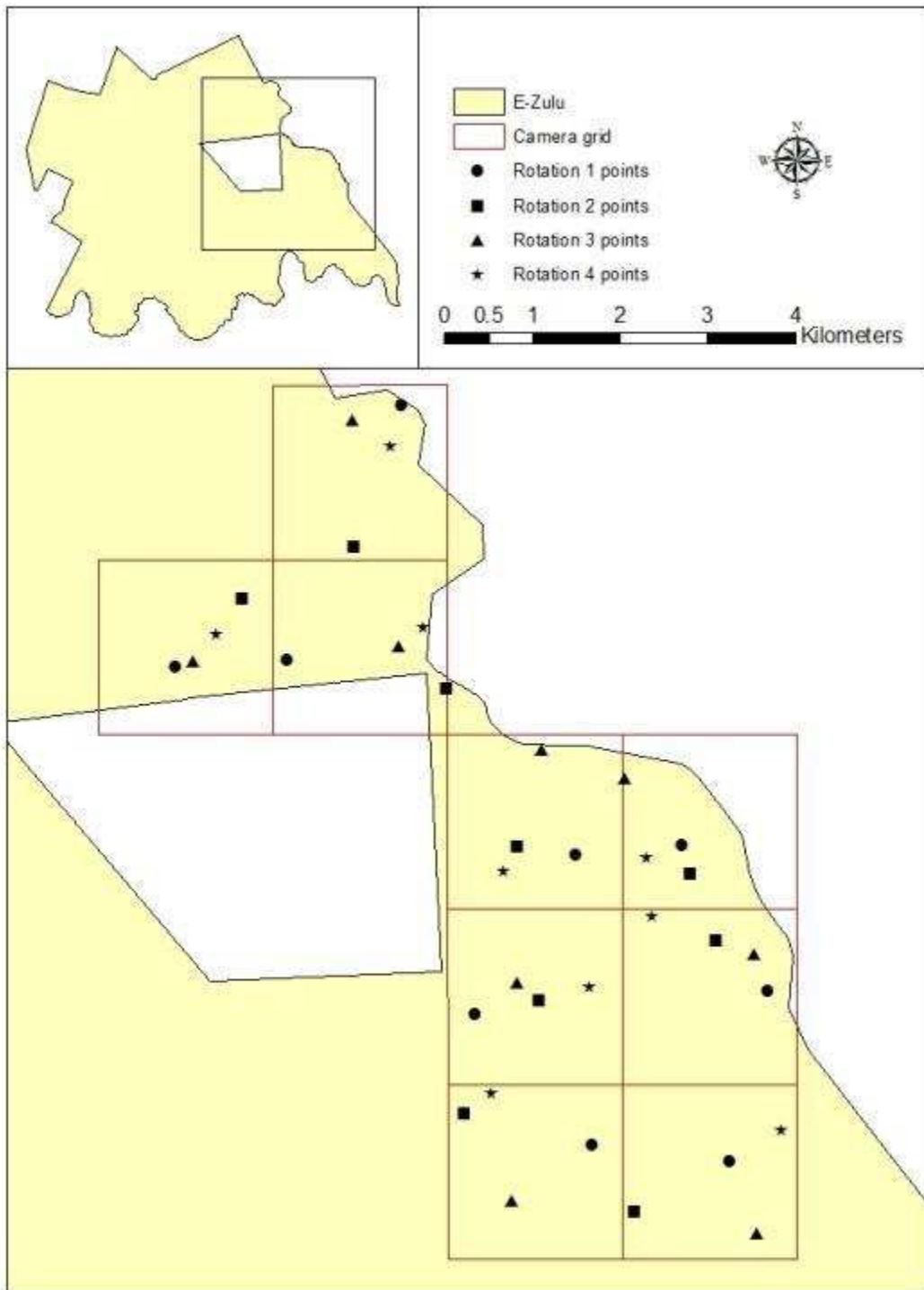


Figure 4.2.2. The position of each of the nine camera stations within the 3,600 Ha trapping grid at E-Zulu. Symbol type indicates camera positions for each rotation. Cameras were rotated to new positions on the dates outlined in Table 4.2.1.

Data analysis

To remove bias that may be introduced by re-counting the same individual multiple times if it remains in front of the camera for an extended period, only independent carnivore events were used for analyses (Gómez *et al.* 2005). Independent events were those as described in chapters 2 and 3.

Relative abundance

Relative abundance was calculated for each carnivore species (Kwandwe n=11, E-Zulu n=12) at each camera station (n=36 per site). This was done by dividing the number of independent events for a carnivore species at a camera station by the total number of days that camera was active and multiplied by 100 to give a relative abundance as the number of carnivore events per 100 trap days (Jenks *et al.* 2011; Sollmann *et al.* 2013). A Mann-Whitney U-test was then performed using Statistica v.10 (StatSoft. Inc. Tulsa, OK, USA) to test for any significant differences in the relative abundances of the carnivore species at Kwandwe and E-Zulu.

Carnivore occupancy and detection

An assumption of occupancy modelling is that species do not colonise or become extinct from sites during the study period (i.e. population closure), and that each camera station is independent of all others (i.e. geographic closure) (MacKenzie *et al.* 2006). It is fairly reasonable to assume that during each rotation of camera placements (~90 days), population closure assumptions were met for the largest carnivore species such as lions, leopards and brown hyaenas. However, large home ranges of these species were likely to incorporate several camera stations, and long periods may have been spent outside the effective trapping area, therefore violating geographic closure assumptions (Gittleman & Harvey 1982). Further, smaller carnivores such as genets and mongooses may satisfy geographic closure assumptions, yet 90 days may be too long to guarantee population closure, particularly as these species may be prey items for larger carnivores (Hayward *et al.* 2006a). However, although closure assumptions were likely violated, random placement of cameras removes any possible bias (O'Brien 2011; Rowcliffe *et al.* 2011; Midlane *et al.* 2014). This means that an occupancy modelling framework can still be applied, but that results must be interpreted as probability of site usage and not probability of site occupancy (Midlane *et al.* 2014).

All occupancy analyses were conducted using software PRESENCE v9.3 (Hines 2006). Candidate models were ranked using Akaike's information criterion (AIC), adjusted for small

sample sizes (AIC_c) (Burnham & Anderson 2002; MacKenzie *et al.* 2006). Camera station specific covariates (Table 4.2.2) were derived using ArcGIS v.9 (ESRI, Redlands, CA, USA), and continuous covariates were standardized using a Z-transformation (Zar 2010; Linkie *et al.* 2013). There was no co-linear relationship between any covariates.

Table 4.2.2. Description of each covariate used in occupancy models, their type (categorical or continuous), the abbreviations used in model titles and a rationale for each covariate's inclusion.

Covariate description	Type	Abbreviation	Rationale
No covariates	-	(.)	Probability of detection and/or site use remains constant, i.e. not a function of site specific covariates.
Site - Kwandwe or E-Zulu	Categorical	(Site)	Differences in abundance, distribution, or behaviour at Kwandwe and E-Zulu may affect site usage and/or probability of detection.
Rotation - Position 1-4 of cameras within each grid cell. Dates of each rotation are provided in table 4.2.1.	Categorical	(Rot)	Seasonal differences in abundance, distribution, or behaviour may affect site usage and/or probability of detection.
Percentage cover - The percentage of vegetation cover in a 50m buffer zone around each camera. Values were calculated from satellite imagery using ARCGIS v.9 (ESRI, Redlands, CA, USA).	Continuous	(Cov)	Vegetation cover may affect site use and/or probability of detection due to ease of movement through the bush and cover available for hunting or predator avoidance.
Normalized difference vegetation index (NDVI) - NDVI gives a simple indication vegetation productivity via the 'condition' and photosynthetic capability of vegetation. Data obtained from MODIS ¹	Continuous	(NDVI)	Different levels of vegetation productivity may affect prey distribution, ultimately influencing predator site use and/or detection probability.
Distance to water - Distance to the closest permanent water source. Values were calculated from satellite imagery using ARCGIS v.9 (ESRI, Redlands, CA, USA).	Continuous	(DW)	Proximity to water may affect the proportion of time spent in particular areas or animal density, hence affecting site use and/or detection probability.

¹ Moderate Resolution Imaging Spectroradiometer (MODIS) (<http://reverb.echo.nasa.gov/reverb/>).

Detection/non-detection histories (Table 4.2.3) were created for each carnivore species where there was sufficient data. Sampling occasions were defined as each 24 hour period from 00:00 – 23:59 (Gray & Prum 2012; Lazenby & Dickman 2013). Each rotation was treated as a concurrent replicate, resulting in a capture history matrix of 72 camera stations (n=36 per site) and consisting of ~90 days. Missing data due to differences in the number of days cameras were active were represented by a period (.) in capture history matrices.

Holding probability of site use constant ($\psi(\cdot)$), camera station covariates that may have affected survey specific detection probabilities (p_i) were each assessed in univariate form for each species. Those that had a non-significant effect (i.e. 95% CI of β -values included zero) were excluded from further models for that species (Midlane *et al.* 2014). Remaining covariates were modelled in all possible multivariate combinations to produce a suite of detection models for each species. The detection model with the lowest AIC_c score for each species was then carried forward to conduct univariate analysis of factors that may have affected site usage (ψ). Again, those factors which showed non-significance were discarded, and remaining factors were considered in all possible multivariate combinations to produce a final set of candidate models. For each species, model fit was assessed with 10,000 parametric bootstraps of the best performing model to give an overdispersion factor (\hat{c}). Where $\hat{c} > 1$, a quasi-corrected AIC_c (QAIC_c) was used to rank candidate models (Burnham & Anderson 2002; MacKenzie *et al.* 2006; Cove *et al.* 2012).

Table 4.2.3. Hypothetical capture history showing that the species was not photographed at camera station one, was photographed on sampling occasions two and five at camera station two and sampling occasions one, four and five at camera station three etc. Similar capture histories were constructed for each carnivore species.

	Sampling occasion				
	1	2	3	4	5
Camera station 1	0	0	0	0	0
Camera station 2	0	1	0	0	1
Camera station 3	1	0	0	1	1
Camera station 4	0	0	1	0	0
Camera station 5	0	1	0	1	0

Spatial distribution

To give a crude indication of the spatial distribution of carnivores at each site, total independent events for each carnivore species at each camera station (n=36 per site) were plotted in ArcGIS 9 (ESRI, Redlands, CA, USA) as a proportion of total events for that species. Furthermore, the mean number of events across all rotations, for each carnivore species, in each grid cell (n=9 per site) was tested against a random distribution of points using a Chi square goodness-of-fit test in Statistica v.10 (StatSoft. Inc. Tulsa, OK, USA). Expected values were calculated as mean number of events per species, per rotation, divided by the number of grid cells (n=9 per site).

Activity patterns

Daily activity patterns for each carnivore species were calculated, per rotation, by summing independent events in each 1 hour time period throughout the day for each species and converting these counts to a proportion of total events for that species (Carbajal-borges, Godínez-gómez & Mendoza 2014). These data were arcsine square root transformed and a 2-way ANOVA was then applied to test for differences in activity patterns between study sites and between time periods using Statistica v.10 (StatSoft. Inc. Tulsa, OK, USA). Carnivore species with fewer than 10 independent photographs at each site were not included in the analysis of daily activity patterns (Blake *et al.* 2012).

4.3 Results

Total sampling effort at Kwandwe was 3298 trap nights, yielding 9665 photographs of wildlife, anthropogenic events, and false triggers. A total of 41 mammal species were photographed, including 11 carnivore species (Table 4.3.1). Total sampling effort at E-Zulu was 3258 trap nights, resulting in 9994 photographs of wildlife, anthropogenic events, and false triggers. A total of 39 mammal species were photographed, of which 12 were carnivores (Table 4.3.1). African wildcat, Cape fox, and leopard were each only recorded on a single occasion at E-Zulu (Table 4.3.2). The leopard at E-Zulu was removed from the property by the owner five days after being photographed. A complete species list, with the number of photographs of each species, is provided in Appendix C.

Table 4.3.1. The total number of trap nights and number of species and photographs for mammals, birds and reptiles taken at each site between 03/07/2012 and 19/08/2013. The blank and other category incorporates false triggers, camera failures, over-exposed photographs, and photographs where animals could not be identified.

	Kwandwe		E-Zulu	
	n	%	n	%
Trap nights	3298		3258	
Total photographs	9665	100	9994	100
Mammal spp.	41	-	39	-
Mammal photographs	3408	35.26	5795	57.98
Carnivore photographs	415	4.29	417	4.17
Independent carnivore events	396	4.10	387	3.87
Carnivore spp.	11	-	12	-
Bird photographs	90	0.93	101	1.01
Bird spp.	10	-	17	-
Reptile photographs	4	0.04	4	0.04
Reptile spp.	1	-	1	-
Anthropogenic photographs	795	8.23	1030	10.31
Blank & other	5368	55.54	3064	30.66

Relative abundance

Brown hyaenas were photographed more than any other carnivore species at Kwandwe, closely followed by black-backed jackals. Bat-eared foxes, followed by black-backed jackals, were the most photographed carnivores at E-Zulu (Table 4.3.2). Gray mongooses were photographed almost three times more at Kwandwe compared to E-Zulu, whereas bat-eared foxes were photographed twice as often at E-Zulu compared to Kwandwe (Table 4.3.2). Aardwolves and striped polecats had a relatively high and fairly similar number of photographs at both sites. The only apex predator photographed at both sites was the leopard, however there was only a single leopard photograph at E-Zulu (Table 4.3.2). Brown hyaenas had the highest mean relative abundance of all carnivore species across all cameras at Kwandwe. Bat-eared foxes had the highest mean relative abundance across all cameras at E-Zulu (Table 4.3.2).

Table 4.3.2. The total number of independent events (n) for each carnivore species photographed at Kwandwe and E-Zulu between 03/07/2012 and 19/08/2013. Mean relative abundance index (RAI) was calculated as number of independent events per 100 trap nights. Standard deviation (S.D) is of the mean RAI for each carnivore species.

	Kwandwe (Apex present)			E-Zulu (Apex absent)		
	n	Mean RAI	S.D	n	Mean RAI	S.D
Total carnivore events	396			387		
Aardwolf	49	1.48	3.22	67	2.06	3.33
African wildcat	0	-	-	1	0.03	0.18
Bat eared fox	47	1.41	3.02	122	3.74	7.35
Black-backed jackal	68	2.09	8.66	70	2.15	3.23
Brown hyaena	75	2.22	5.21	0	-	-
Cape fox	0	-	-	1	0.03	0.19
Caracal	5	0.15	0.46	6	0.18	0.49
Gray mongoose	61	1.83	3.53	22	0.67	1.45
Large spotted genet	14	0.42	1.26	3	0.09	0.40
Leopard	26	0.77	1.82	1	0.03	0.19
Lion	4	0.12	0.43	0	-	-
Small spotted genet	19	0.57	1.12	32	0.98	1.85
Striped polecat	25	0.75	1.77	29	0.89	1.39
Suricate	0	-	-	7	0.22	0.64
Water mongoose	3	0.09	0.56	0	-	-
Yellow mongoose	0	-	-	26	0.80	1.88

Kwandwe had a significantly higher relative abundance of leopards ($Z=2.04$, $d.f.=70$, $P<0.05$) and brown hyaenas ($Z=3.85$, $d.f.=70$, $P<0.01$) compared to E-Zulu. By contrast, E-Zulu had significantly higher black-backed jackal relative abundance ($Z=3.65$, $d.f.=70$, $P<0.01$) and significantly higher bat-eared fox relative abundance ($Z=1.98$, $d.f.=70$, $P<0.05$) compared to Kwandwe. There was no significant difference in the relative abundances of any other carnivore species at Kwandwe or E-Zulu.

As expected, apex carnivores tended to be more abundant at Kwandwe compared to E-Zulu. Furthermore, in the absence of apex predators, mesopredators such as black-backed jackals and bat-eared foxes were more abundant at E-Zulu compared to Kwandwe. Interestingly, however, the increased relative abundance of some mesopredator species at E-Zulu had no significant negative effect on the relative abundances of micropredators (i.e. genets and mongooses) (Table 4.3.2). In fact, micropredators such as yellow mongooses, African wildcats, suricates and Cape foxes were only recorded at E-Zulu (Table 4.3.2).

Detection and site usage models

Top performing models for aardwolves, black-backed jackals and large-spotted genets fit the data well, each with \hat{c} values of marginally less than one, allowing for the use of AIC_c values to rank candidate models (Burnham & Anderson 2002; MacKenzie *et al.* 2006). Percentage of vegetation cover and NDVI were significant predictors in the detection (p) models for all of these species, and the only significant predictors for large-spotted genet detection models (Table 4.3.3). Distance to water also proved significant in the detection models for aardwolves and black-backed jackals, featuring in all of the 95% confidence set of models for black-backed jackals, and all but one of the 95% confidence set of models for aardwolves (Table 4.3.3). The rotation covariate was significant for black-backed jackals, and featured in both detection models that comprise the 95% confidence set (Table 4.3.3). Furthermore, the site covariate also proved significant for black-backed jackals and featured in the second ranked model of the 95% confidence set (Table 4.3.3). No covariates had a significant effect on site usage (ψ) for black-backed jackals or large-spotted genets (Table 4.3.3). However, percentage vegetation cover was significant in predicting aardwolf site usage and featured in the top ranked model (Table 4.3.3).

Table 4.3.3. Minus twice the log likelihood score and the number of parameters (K) for occupancy models of aardwolves, black-backed jackals, and large-spotted genets. Models presented for each species comprise the 95% CI set of models based on Akaike weight (w_i), and were ranked according to differences in AIC_c values (ΔAIC_c).

Model	$-2 \times \text{Log likelihood}$	K	AIC_c	ΔAIC_c	w_i
Aardwolf					
$\psi(\text{Cov}), \rho(\text{Cov}+\text{NDVI}+\text{DW})$	1019.60	6	1032.89	0.00	0.473
$\psi(\cdot), \rho(\text{Cov}+\text{NDVI}+\text{DW})$	1023.94	5	1034.85	1.96	0.178
$\psi(\cdot), \rho(\text{Cov}+\text{NDVI})$	1026.57	4	1035.17	2.28	0.151
$\psi(\cdot), \rho(\text{NDVI}+\text{DW})$	1027.98	4	1036.58	3.69	0.075
$\psi(\cdot), \rho(\text{Cov}+\text{DW})$	1028.30	4	1036.90	4.01	0.064
Black-backed jackal					
$\psi(\cdot), \rho(\text{Rot}+\text{Cov}+\text{NDVI}+\text{DW})$	999.28	8	1017.57	0.00	0.743
$\psi(\cdot), \rho(\text{Site}+\text{Rot}+\text{Cov}+\text{NDVI}+\text{DW})$	998.86	9	1019.76	2.19	0.249
Large-spotted genet					
$\psi(\cdot), \rho(\text{Cov}+\text{NDVI})$	182.76	4	191.36	0.00	0.748
$\psi(\cdot), \rho(\text{Cov})$	187.97	3	194.32	2.96	0.170
$\psi(\cdot), \rho(\text{NDVI})$	189.43	3	195.78	4.42	0.082

Covariates abbreviations are (Site) = Kwandwe or E-Zulu, (Rot) = position 1-4 of cameras during my study period, (Cov) = percentage of vegetation cover at camera stations, (NDVI) = normalized difference vegetation index at each camera station and (DW) = distance from camera to closest permanent water.

Data for bat-eared foxes, gray mongooses, small-spotted genets and striped polecats were over-dispersed, meaning candidate models were ranked using quasi- AIC_c ($QAIC_c$) (Burnham & Anderson 2002; MacKenzie *et al.* 2006). Percentage of vegetation cover was the only significant predictor in the detection (ρ) models for bat-eared foxes, and featured in many of the 95% confidence set of models for gray mongooses and small-spotted genets (Table 4.3.4). Site was also significant in the detection models for gray mongooses and small-spotted genets, featuring in the top performing models and several other models in the 95% confidence set for both species (Table 4.3.4). For gray mongooses and small-spotted genets, rotation was also a significant predictor in several detection models (Table 4.3.4), suggesting possible seasonal differences in detection probability. Similarly, rotation featured in detection models for striped polecats, however distance to water and NDVI were better predictors (Table 4.3.4). Site and percentage cover proved significant in the site usage (ψ)

models for bat-eared foxes (Table 4.3.4). There were no significant predictors in site usage models for gray mongooses, small-spotted genets or striped polecats.

Table 4.3.4. Minus twice the log likelihood score and the number of parameters (K) for occupancy models of bat-eared foxes, gray mongooses, small-spotted genets, and striped polecats. Models presented for each species comprise the 95% CI set of models based on Akaike weight (w_i), and were ranked according to differences in QAIC_c values (Δ QAIC_c).

Model	-2*Log likelihood	K	QAIC _c	Δ QAIC _c	w_i
Bat-eared fox					
$\psi(\text{Site}), \rho(\text{Cov})$	1273.44	4	977.66	0.00	0.296
$\psi(\text{Cov}), \rho(\text{Cov})$	1273.45	4	977.66	0.00	0.296
$\psi(\text{Site+Cov}), \rho(\text{Cov})$	1271.40	5	978.42	0.76	0.203
$\psi(\cdot), \rho(\text{Cov})$	1278.00	3	978.88	1.22	0.161
Gray mongoose					
$\psi(\cdot), \rho(\text{Site+Cov})$	786.10	4	401.65	0.00	0.250
$\psi(\cdot), \rho(\text{Cov})$	791.55	3	402.13	0.48	0.197
$\psi(\cdot), \rho(\text{Site})$	793.08	3	402.89	1.24	0.135
$\psi(\cdot), \rho(\text{Site+Rot+Cov})$	774.50	7	403.00	1.35	0.127
$\psi(\cdot), \rho(\cdot)$	798.45	2	403.40	1.75	0.104
$\psi(\cdot), \rho(\text{Site+Rot})$	781.36	6	403.97	2.32	0.078
$\psi(\cdot), \rho(\text{Rot+Cov})$	781.75	6	404.17	2.52	0.071
Small-spotted genet					
$\psi(\cdot), \rho(\text{Site+Cov})$	549.38	4	454.12	0.00	0.572
$\psi(\cdot), \rho(\text{Site+Rot+Cov})$	544.07	7	456.97	2.85	0.138
$\psi(\cdot), \rho(\text{Cov})$	555.79	3	457.08	2.96	0.130
$\psi(\cdot), \rho(\text{Rot+Cov})$	548.15	6	457.82	3.70	0.090
$\psi(\cdot), \rho(\text{Site+Rot})$	548.75	6	458.31	4.19	0.070
Striped polecat					
$\psi(\cdot), \rho(\text{DW})$	577.71	3	208.88	0.00	0.366
$\psi(\cdot), \rho(\text{NDVI})$	579.86	3	209.64	0.76	0.250
$\psi(\cdot), \rho(\text{NDVI+DW})$	574.65	4	209.81	0.93	0.230
$\psi(\cdot), \rho(\text{Rot+DW})$	571.15	6	212.58	3.70	0.058
$\psi(\cdot), \rho(\text{Rot})$	577.50	5	212.81	3.93	0.051

Covariates abbreviations are (Site) = Kwandwe or E-Zulu, (Rot) = position 1-4 of cameras during my study period, (Cov) = percentage of vegetation cover at camera stations, (NDVI) = normalized difference vegetation index at each camera station and (DW) = distance from camera to closest permanent water.

In relation to MRH, the most relevant covariate in my occupancy analyses was the site covariate. While there may be several differences between Kwandwe and E-Zulu, in the context of my study, the site covariate essentially represents the presence or absence of apex predators. Therefore, the occurrence of the site covariate in models for black-backed jackals and bat-eared foxes may corroborate the observed differences in the relative abundances of these species at each site. Furthermore, inclusion of the site covariate in models for gray mongooses and small-spotted genets suggest that apex predators may also somehow affect site usage or detection probabilities for these species. However, percentage of vegetation cover appeared in the top performing models for all predator species except striped polecats. This suggests that many predator species show habitat preferences for either open or densely vegetated areas, likely affecting their spatial distribution.

Spatial patterns

Kwandwe

Brown hyaena photographs were distributed across most of the study area. However, only a small number of photographs were taken in the centre, and a higher number of photographs in the north and south-west of the study grid. Consequently, brown hyaena spatial distribution was significantly different from random ($\chi^2=25.1$, d.f.=8, $P<0.01$) (Figure 4.3.1). Leopard photographs were also well distributed across the camera grid (Figure 4.3.1), yet there were slightly more photographs in the southern section of the camera grid compared to the northern section (Figure 4.3.1). Lions and caracals were only photographed at three and four sites respectively. Neither of these species were confined to particular areas of the camera grid (Figure 4.3.1). Black-backed jackal and small-spotted genet photographs were heavily concentrated in the south of the trapping grid, and this distribution was significantly different from random for black-backed jackals ($\chi^2=98.8$, d.f.=8, $P<0.01$) (Figure 4.3.1). Aardwolf and gray mongoose photographs were well distributed across the grid, though aardwolves tended to be photographed more in the eastern areas, and gray mongooses in the west and south-western areas (Figure 4.3.1). Large-spotted genets were concentrated in the north-east portion of the trapping grid ($\chi^2=23.8$, d.f.=8, $P<0.01$). Conversely, bat-eared foxes were photographed mainly in the west and south-west ($\chi^2=26.6$, d.f.=8, $P<0.01$). Striped polecats were also photographed mainly in the west and south-west, with a small number of photographs towards the east of the trapping area. Water mongooses were only photographed at a single camera station near the Great Fish River in the south-east of the trapping grid (Figure 4.3.1).

There was spatial overlap of all apex predator species with the mesopredators. However, 84% of all black-backed jackal events were at two camera stations south of the Great Fish River. The same two camera stations only photographed 4% of leopard events, 7% of brown hyaena events and did not record any lion events. Among the micropredators, only large-spotted genets and water mongooses did not overlap with black-backed jackals in terms of where they were photographed. However, a small amount of overlap was observed between large-spotted genets and caracals (Figure 4.3.1).

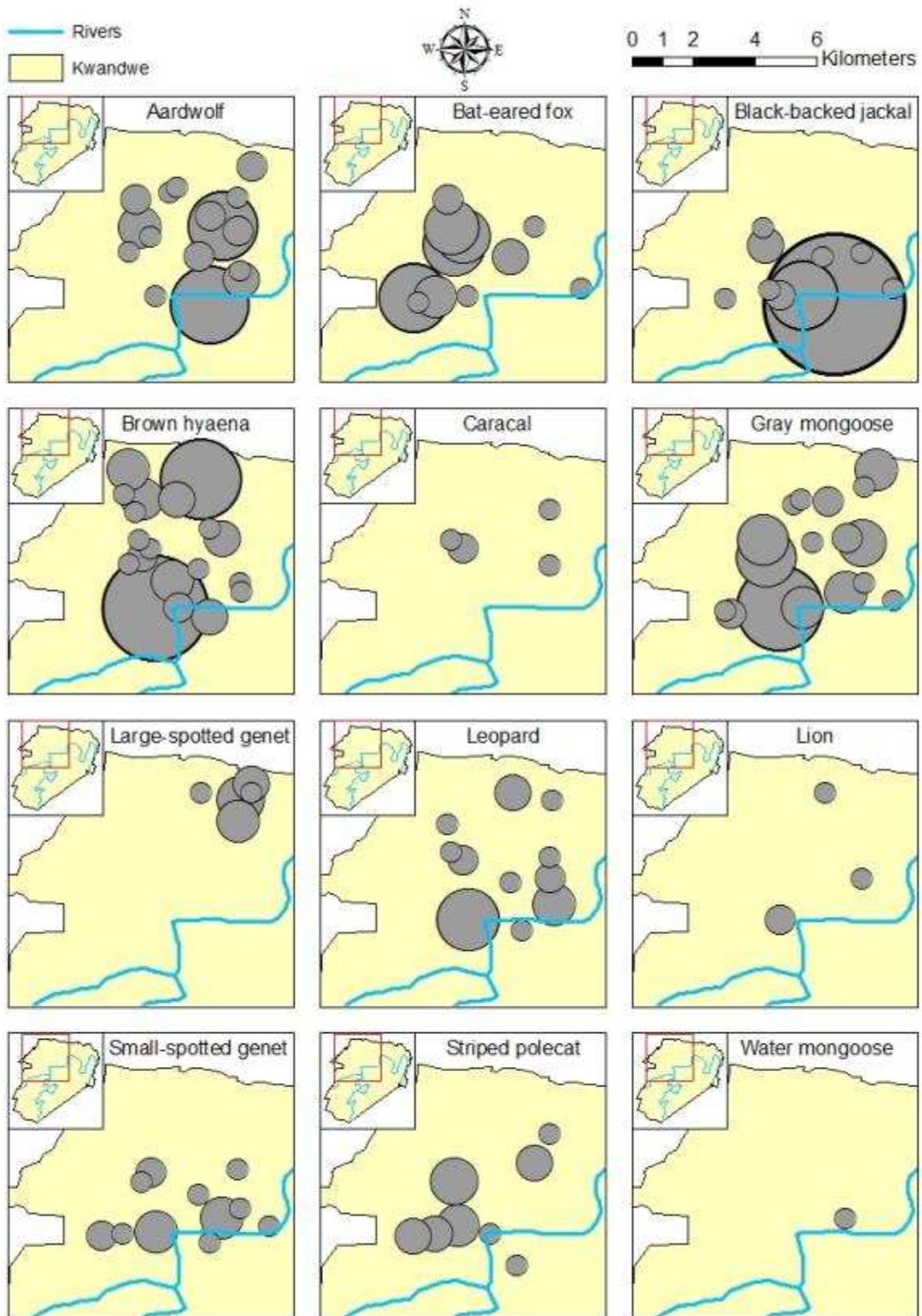


Figure 4.3.1. The camera stations at which each of the carnivore species were photographed at Kwandwe. Circle size indicates proportion of total independent events for each species.

E-Zulu

African wildcats, Cape foxes and leopards were each only photographed once at E-Zulu and all three photographs were in the north of the trapping area (Figure 4.3.2). Large-spotted genet photographs were also concentrated in the north of the trapping grid. Both gray mongooses and yellow mongooses were photographed in the northern and southern reaches of the trapping area and there were no photographs for either species in the central section of the grid (Figure 4.3.2). Caracals showed a similar pattern, with the majority of photographs in the north, fewer in the south and none in the central portion of the trapping grid (Figure 4.3.2). Aardwolves were photographed throughout the grid, though photographs in the north were concentrated at three cameras, whereas photographs in the south were spread over 11 camera stations (Figure 4.3.2). Bat-eared foxes and black-backed jackals were photographed throughout the trapping grid, though bat-eared fox photographs were significantly higher in the central area of the trapping grid ($\chi^2=22.5$, d.f.=8, $P<0.01$) compared to a random distribution (Figure 4.3.2). Small-spotted genet and striped polecat photographs were relatively uniformly distributed across the entire trapping grid. Suricates were only photographed in the south with the exception of a single photograph in the far north of the trapping grid (Figure 4.3.2).

There was spatial overlap of all the mesopredator species, both with each other and with the micropredators (Figure 4.3.2). There was also overlap between most of the micropredators with each other. However, large-spotted genets did not overlap with suricates or yellow mongooses in terms of where they were photographed (Figure 4.3.2).

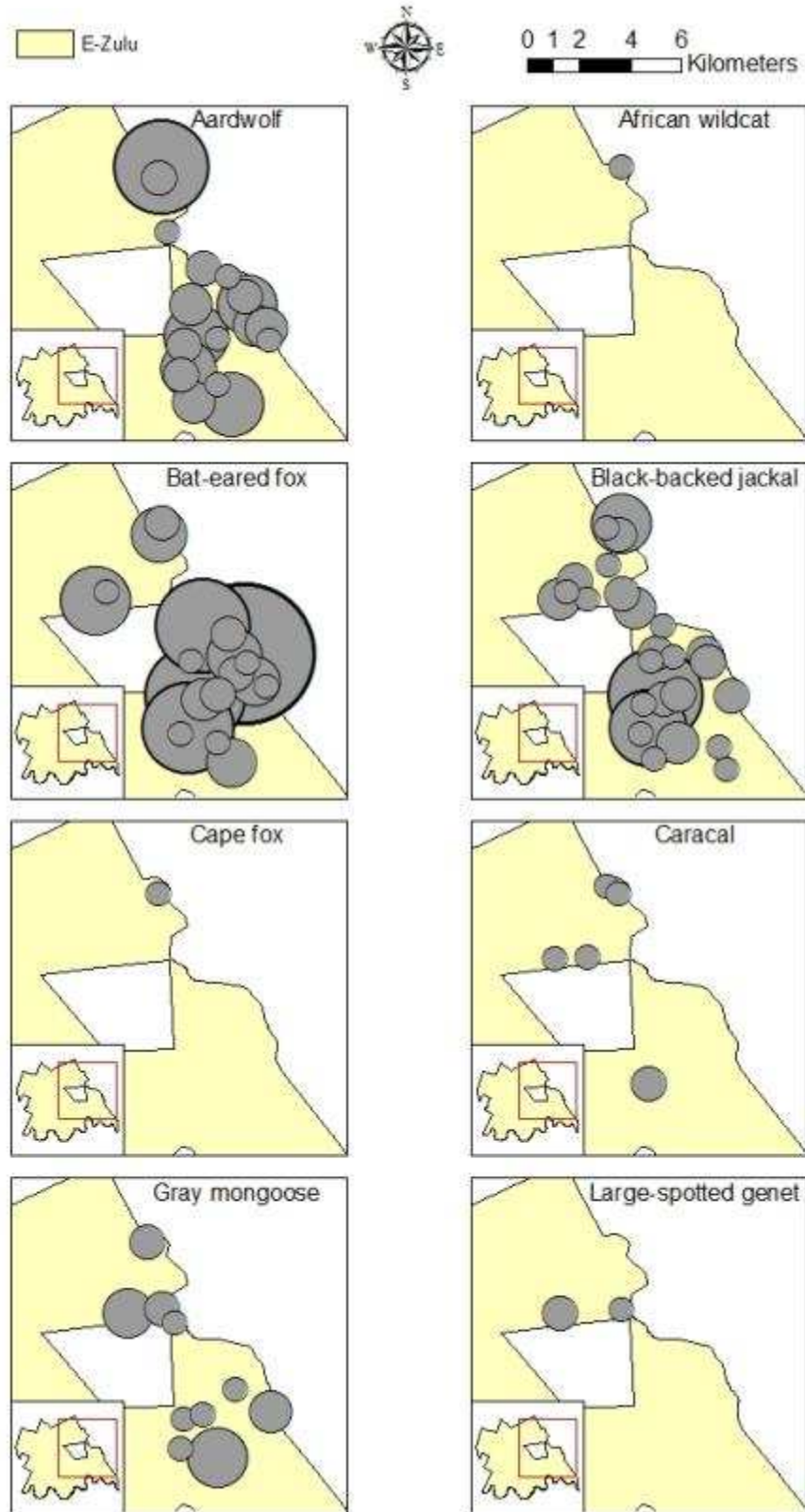


Figure 4.3.2. The camera stations at which each of the carnivore were photographed at E-Zulu. Circle size indicates proportion of total events for each species. Continues on next page.

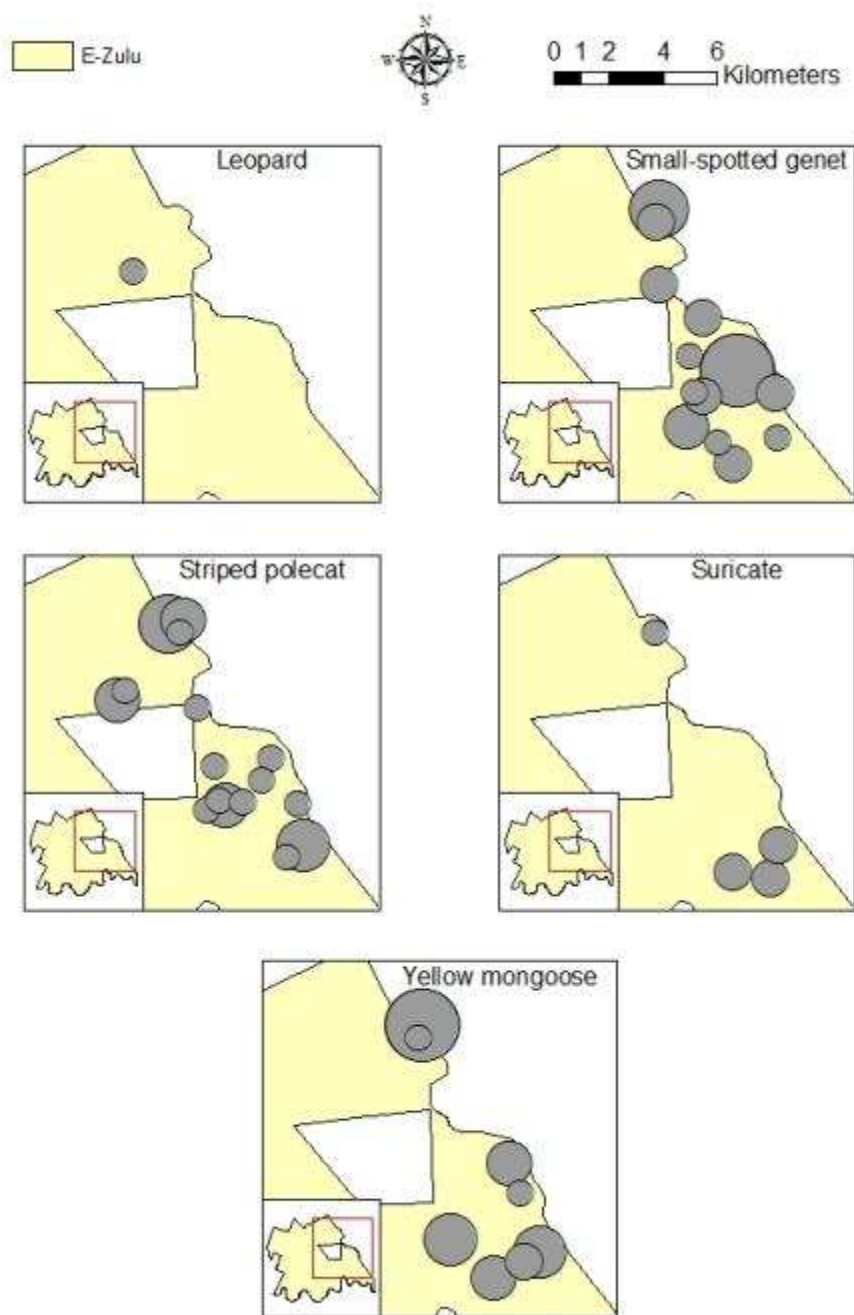


Figure 4.3.2. Continued

Activity patterns

Aardwolf and bat-eared fox activity was mainly nocturnal, though there was also some crepuscular activity (Figure 4.3.3). For both species, activity patterns were similar at both Kwandwe and E-Zulu (Figure 4.3.3). Small-spotted genet and striped polecat activity was also nocturnal, also with small amounts of crepuscular activity. However, peaks in activity occurred at different times at Kwandwe compared to E-Zulu (Figure 4.3.3). Striped polecats at Kwandwe showed a peak in activity between 03:00-04:00 and there was a slight dip in striped polecat activity at E-Zulu during this time (Figure 4.3.3). Small-spotted genet activity was highest between 01:00 and 02:00 at E-Zulu, whereas at Kwandwe, small-spotted genet activity peaked between 23:00 and 00:00 (Figure 4.3.3). Gray mongoose activity was crepuscular and diurnal and very similar at both sites, with the exception of a large peak in activity between 10:00 and 11:00 at E-Zulu (Figure 4.3.3). Black-backed jackal activity was cathemeral (i.e. no strong nocturnal, diurnal or crepuscular patterns), however activity was generally lowest during the middle of the day (Figure 4.3.3).

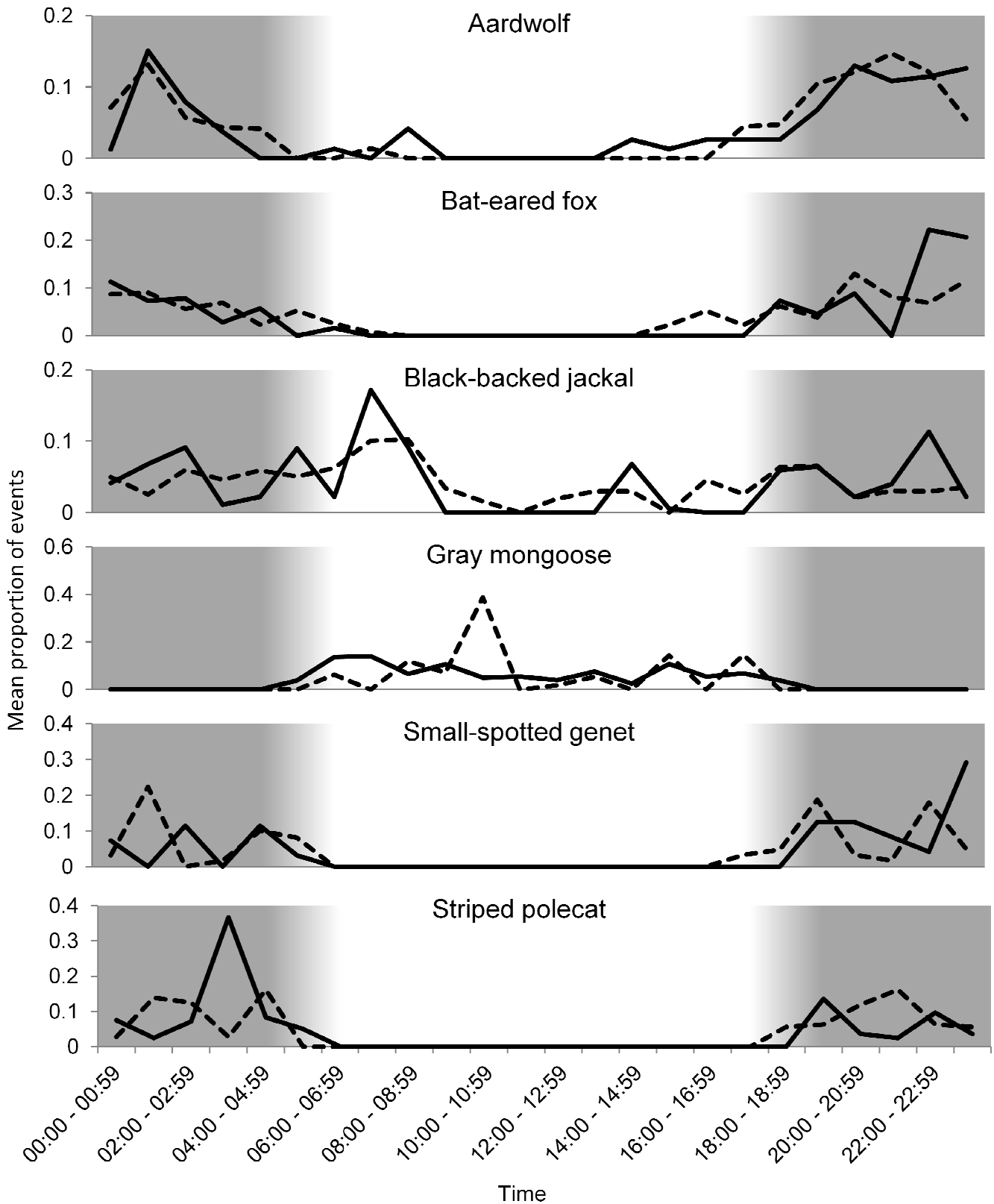


Figure 4.3.3. Mean proportion of total events per hour of the day, per rotation, for the six carnivore species with 10 or more independent events at Kwandwe (solid line) and E-Zulu (dashed line). Shaded areas indicate hours of darkness, daylight hours between 03/07/2012 and 19/08/2013 were calculated using Sun Times v7.1.

4.4 Discussion

Relative abundances and site use models

My results show that Kwandwe had a significantly higher relative abundance of leopards and brown hyaenas compared to E-Zulu. Furthermore, the populations of eleven lions and six cheetahs (*Acinonyx jubatus*) present at Kwandwe remained unchanged during my study period. With the exception of a single leopard photograph, no apex carnivores were recorded at E-Zulu. Black-backed jackals and bat-eared foxes had significantly higher relative abundances at E-Zulu compared to Kwandwe. These results are consistent with the MRH and suggest that black-backed jackals and bat-eared foxes may be 'released' from top-down forcing in the absence of apex predators (Prugh *et al.* 2009).

Several reasons exist which may explain the lower relative abundance of black-backed jackals at Kwandwe compared to E-Zulu, including competition for food and other resources (Caro & Stoner 2003). Dietary studies of lions (Hayward & Kerley 2005), cheetahs (Hayward *et al.* 2006b), and leopards (Nowell & Jackson 1996; Hayward *et al.* 2006a) have shown them to be obligate carnivores. This too is the case for brown hyaenas, with occasional supplementation of insects and eggs when vertebrate prey are scarce (Mills & Mills 1978). Black-backed jackals are a generalist predator that will readily consume many ungulate species and invertebrates (Bussiahn 1997; Sillero-Zubiri, Hoffmann & Macdonald 2004; Brassine 2011; Brassine & Parker 2011). This dietary overlap may put black-backed jackals in direct competition with any or all of the apex predators at Kwandwe. Therefore, the lower relative abundance of black-backed jackals at Kwandwe may be a result of competitive exclusion and/or interspecific killing, a phenomenon that is common among competing carnivores (Palomares & Caro 1999; Tannerfeldt, Elmhagen & Angerbjörn 2002; Mitchell & Banks 2005; Donadio & Buskirk 2006).

Quantifying levels of competitive exclusion and interspecific killing between black-backed jackals and apex carnivores is impossible from my data. However, previous studies have shown that interactions between black-backed jackals and lions, leopards or brown hyaenas can manifest in different ways. For example, brown hyaenas are primarily scavengers and have poor hunting skills (Mills 1978). Therefore, while black-backed jackal remains have been recorded in brown hyaena faeces (Mills & Mills 1978), it is likely they were scavenged after natural death, or when killed by other predators. Nevertheless, brown hyaenas have been shown to effectively exclude black-backed jackals at carcasses (van der Merwe *et al.* 2009). Conversely, leopards have often been reported to kill black-backed jackals (Kruuk & Turner 1967; Eloff 1984). One particular leopard killed 11 jackals (black-backed and golden

(*Canis aureus*) in a three week period in the Ngorongoro Crater of Tanzania (Estes 1967). To a lesser extent, lions have also been known to kill black-backed jackals, yet rarely consume them (Stander 1992).

Competition for food between apex predators and bat-eared foxes is unlikely. Bat-eared foxes are primarily insectivores, particularly of harvester termites (Family: Hodotermitidae), with infrequent consumption of small mammals and seasonal fruits (Lamprecht 1979; Koop & Velimirov 1982; Kuntzsch & Nel 1992; Sillero-Zubiri, Hoffmann & Macdonald 2004; Skinner & Chimimba 2005). The small degree of dietary overlap between bat-eared foxes and the apex predators at Kwandwe likely leads to little competition. Instead, the indication of lower relative abundance of bat-eared foxes at Kwandwe compared to E-Zulu may be a false artefact of habitat selection and/or food availability (see below).

The relative abundances of black-backed jackals and bat-eared foxes recorded during my study lends support for the MRH. However, these data should be interpreted with caution. Relative abundance indices are only accurate when detection probability remains constant across species, time and space (O'Brien 2011; Sollmann *et al.* 2013). Furthermore, large bodied species are more likely to trigger camera traps than small species (Tobler *et al.* 2008), and faster moving species are likely to encounter camera traps more often than slower species (Rowcliffe & Carbone 2008). Moreover, camera trap placement, e.g. proximity to roads and paths, may affect the detection probabilities of certain species more than others (Srbek-Araujo & Chiarello 2013; Mann, O'Riain & Parker 2014). For instance, one of my camera stations at Kwandwe was in a prominent drainage line and recorded two lion events, nine leopard events, 26 brown hyaena events and only two black-backed jackal events. Less than 2km away, another camera positioned on a road recorded only a single leopard event, three brown hyaena events and 46 black-backed jackal events. Clearly, such differences may have significant influences on relative abundance estimates, and may lead to false inferences regarding mesopredator release.

Interestingly, the more robust approach of occupancy modelling may strengthen the inference from relative abundances obtained during my study. The site variable (i.e. Kwandwe or E-Zulu) proved a significant predictor for site usage (ψ) in two of the top four performing models for bat-eared foxes. This suggests that when detection probabilities are taken into account, there is still a significant difference in bat-eared fox abundance at E-Zulu compared to Kwandwe, as was suggested by the relative abundance indices. However, the occupancy models for bat-eared foxes also showed that percentage cover was an important covariate for site use and detection, possibly indicating a strong habitat selection effect. For black-backed jackals, the site covariate appeared only in detection (p) models. Detection

probability can be a function of many variables such as body mass (Tobler *et al.* 2008) and movement speed (Rowcliffe & Carbone 2008), but can also be affected by overall abundance (Royle & Nichols 2003; Royle 2006). If life history traits such as body mass and movement speeds remain relatively unchanged between sites, then it may be that differences in black-backed jackal absolute abundance between Kwandwe and E-Zulu explain the occurrence of the site covariate in detection models.

Caracal events recorded during my study were too sparse to allow for occupancy modelling. Insufficient data may also be the reason why no significant difference in the relative abundance of caracals was found between study sites. Alternatively, it may be that caracals are not suppressed by apex predators and are instead regulated by other means. Caracals have a more specialist diet than black-backed jackals and consume mainly rodents (Melville, Bothma & Mills 2004; Mukherjee *et al.* 2004; Braczkowski *et al.* 2012). Their more specialist diet means they are less likely to exploit food sources such as reptiles, fruits and insects that black-backed jackals might. Studies of other specialist predators, such as horned lizards (*Phrynosoma* spp.) have shown that their populations are limited by food availability (Whitford & Bryant 1979; Suarez & Case 2002). Therefore, it might be that caracals are also regulated by bottom-up forces due to their narrower prey base. In addition, caracals rarely take carrion (Skinner 1979). The reluctance of caracals to scavenge from kills made by other species may reduce encounter rates between caracals and apex predators, therefore reducing the opportunity for interspecific killing.

My data showed no significant difference in micropredator relative abundances between sites. Interestingly, however, gray mongoose events were almost three times higher, and large-spotted genet events almost five times higher at Kwandwe compared to E-Zulu. For gray mongooses, this difference was also apparent during occupancy analysis, where the site covariate featured in many of the detection models. It may be that a higher abundance of gray mongooses at Kwandwe, compared to E-Zulu, influenced detection probability (Royle & Nichols 2003; Royle 2006). If so, these results suggest that the higher abundance of black-backed jackals and bat-eared foxes at E-Zulu may suppress the abundance of gray mongooses. Conversely, at Kwandwe, gray mongooses may be released from competition with black-backed jackals and bat eared foxes, allowing their population to increase. Other micropredator events, particularly those of small-spotted genets, were higher at E-Zulu compared to Kwandwe. Again, this was reflected in detection models of small-spotted genets, possibly suggesting higher abundance at E-Zulu compared to Kwandwe.

It should be noted that mongoose home ranges vary between 0.2 – 0.6 Km² (Cavallini & Nel 1990) and genet home ranges vary between 0.7 – 1.1 Km² (Camps Munuera & Llimona

Llobet 2004). With home ranges of these sizes, it is possible that mongoose and genet home ranges were not adequately surveyed by my camera trap array. Hence, some animals may have had very low or even zero probability of detection, ultimately underestimating relative abundances or reducing the accuracy of occupancy models for these species.

Spatial distribution

At both study sites, bat-eared fox distribution was significantly different from random. This suggests that the presence of apex predators at Kwandwe, or conversely, the absence of apex predators at E-Zulu has no noticeable effect on bat-eared fox distribution. Instead, the areas that recorded most bat eared fox photographs were relatively flat, open and had many termite mounds (pers. obs.). Therefore, it may be that bat-eared fox distribution is correlated with habitat suitability or food availability, rather than predator avoidance, as has been suggested for other species (Litvaitis & Villafuerte 1996). This result is consistent with previous studies which have shown bat-eared foxes preferentially select open grassland type habitats (Malcolm 1986; Mackie & Nel 1989). This habitat preference may also be the reason for the difference in bat-eared fox relative abundance described earlier. If bat-eared foxes at Kwandwe were selecting habitats outside of the effective trapping area, relative abundance estimates obtained during my study will not be representative of the whole reserve.

Interestingly, black-backed jackals at E-Zulu showed a random distribution, whereas, at Kwandwe, black-backed jackals were photographed significantly more in open, grassland type areas in the south of the camera grid. This result is in accordance with the findings of Loveridge & Macdonald (2003), who showed that black-backed jackals defended territories in grassland habitats. However, other studies have shown that black-backed jackals are negatively associated with grassland and utilize these areas less than expected (Kaunda 2001; Durant *et al.* 2010), or possibly prefer closed woodland (Fuller *et al.* 1989). It may be that black-backed jackals at Kwandwe are selecting flat, open areas in the south, rather than the steep, densely vegetated valley slopes in the north to avoid competition with, or predation by, leopards and brown hyaenas (Estes 1967; van der Merwe *et al.* 2009). Indeed, these apex predators utilized the northern areas of the camera grid more frequently and may have forced black-backed jackals to select 'safer' areas in the south of the camera grid. However, in the absence of apex predators at E-Zulu, black-backed jackals showed no such preference and utilized steep, densely vegetated valleys in roughly equal proportion to flatter, more open areas.

At Kwandwe, large-spotted genet photographs were significantly concentrated in the north eastern section of the camera grid, and their distribution showed zero overlap with bat-eared

foxes, black-backed jackals or small-spotted genets. This result may be a consequence of dense habitat selection by large-spotted genets, and may explain the occurrence of percentage vegetation cover in large-spotted genet occupancy models. Other studies have shown large-spotted genets to be positively associated with bush cover (Ramesh & Downs 2014). However, Ramesh & Downs (2014) also found that detection probability of large-spotted genets was negatively correlated with increased black-backed jackal abundance. Therefore, the non-overlap in terms of where large-spotted genets and black-backed jackals were photographed may be an indication of spatial avoidance of black-backed jackals by large-spotted genets (Ramesh & Downs 2014). At E-Zulu, large-spotted genets were also photographed in densely vegetated areas, supporting the habitat preference shown at Kwandwe. However, spatial avoidance of black-backed jackals would be less feasible at E-Zulu due to their ubiquitous distribution within my effective trapping area. Possibly then, at E-Zulu, spatial avoidance of black-backed jackals caused large-spotted genets to select habitats outside of my effective trapping area. This may also explain why the total number of large-spotted genet photographs was almost five times fewer at E-Zulu compared to Kwandwe.

Activity patterns

My results showed no significant differences in the activity patterns of any carnivore species between the two sites. This is hardly surprising as activity patterns and circadian rhythms are co-evolved with physical features such as large eyes, ears and olfactory systems that are best suited for activity at particular times of day (Kronfeld-Schor & Dayan 2003). However, the endogenous regulation of circadian rhythms can be overridden under high levels of environmental stress (e.g. predation, hunger or ambient temperature) (Monterroso, Alves & Ferreras 2013). For example, lowering ambient temperature and simulating food shortage led to changes in the circadian organization of mice (*Mus spp.*) (van der Vinne *et al.* 2014). In addition, European rabbits can suppress their tendency for nocturnality to avoid predation by mesopredators in south-western Europe (Monterroso, Alves & Ferreras 2013). My results suggest that environmental stress was not great enough to cause changes in daily activity patterns of any species. However, species behaviour may have changed in other ways undetectable by camera traps, e.g. diet, sociality or breeding behaviour (Sergio & Hiraldo 2008; Salo *et al.* 2008).

Predator activity patterns have also been linked to times of day when prey species are most active. For example, black-backed jackal activity periods closely match those of important prey species (Ferguson, Galpin & de Wet 1988), and Eurasian lynx activity closely matches that of their preferred prey, roe deer (*Capreolus capreolus*) (Heurich *et al.* 2014). As my data

suggest little difference in the activity patterns of the carnivore species between sites, it may be that activity periods of predators recorded during my study are linked to their prey, rather than temporal avoidance of larger predators.

Summary

Importantly, it must be noted that my study contained only one site with apex predators and one without. Therefore, any inferences from my results must be treated with caution. There may be study site specific factors affecting abundance, distribution and behaviour of animals that cannot be identified or quantified without the addition of more study sites. Predator manipulations may have reduced this uncertainty, however such manipulations provide serious logistical issues and often contradict land owner interests. Further, the effective trapping areas in my study covered only 14% of E-Zulu and only 19% of Kwandwe. Consequently, 'reserve-scale' conclusions should also be interpreted with caution.

However, my results indicate that within my effective trapping areas, the absence of apex carnivores caused black-backed jackal relative abundance to be significantly higher at E-Zulu compared to Kwandwe. This result gained support from occupancy analyses, where the site covariate was shown to be significant in black-backed jackal detection models, possibly due to higher abundance at E-Zulu. Furthermore, the spatial distribution of black-backed jackals at Kwandwe showed them to avoid steep, densely vegetated valleys which may be more suitable for leopards and brown hyaenas. However, at E-Zulu, black-backed jackals showed no such avoidance and readily used this habitat type. These results are consistent with multiple aspects of MRH and clearly merit additional investigation across the Eastern Cape, South Africa, and beyond.

Additionally, my results suggest an interaction between large-spotted genets and black-backed jackals. At Kwandwe, the areas that these two species were photographed showed zero overlap, possibly indicating spatial avoidance behaviour of black-backed jackals by large-spotted genets. At E-Zulu, spatial avoidance of black-backed jackals was less feasible due to their more uniform distribution when compared to Kwandwe. However, only three independent events of large-spotted genets were recorded at E-Zulu, compared to fourteen independent events at Kwandwe. This suggests that large-spotted genets may be selecting habitats outside of my effective trapping area where predation risk may be lower. Alternatively, the higher abundance of black-backed jackals at E-Zulu may increase interspecific killing of large-spotted genets, ultimately reducing their abundance. This suggests that mesopredator release of black-backed jackals may initiate trophic cascades affecting micropredator abundance and/or distribution. Further study is clearly needed to

fully understand how mesopredator release of black-backed jackals may affect smaller carnivores.

Chapter 5

Summary and Concluding Remarks

The broad aims of my study were to assess the effectiveness of camera traps and their use in monitoring predator populations. In general, the camera traps used in my study performed well and collected data for both predatory and non-predatory species. However, similar to previous studies, my results showed that different camera trap designs may influence the quality and quantity of the data collected (Swann *et al.* 2004; Kelly & Holub 2008; Hughson, Darby & Dungan 2010; Swan, Di Stefano & Christie 2014). This could be highly problematic in wildlife research, as it provides uncertainty over whether data accurately represents animal populations. For example, diversity and relative abundances of mammal species obtained by the two camera trap designs in my study exhibit little similarity. While the Cuddeback cameras recorded more species, there was no evidence to suggest which camera type produced the most accurate relative abundance estimates. In a broad sense, differences in data collected by different camera traps may ultimately lead to false inference and promote inadequate management policies.

Advances in camera trap technology are primarily driven by the hunting industry in North America (Meek & Pittet 2012; Rovero *et al.* 2013). Consequently, many camera traps are well suited towards photographing large game species such as deer (Cervidae), but may be less effective at detecting smaller species (Meek & Pittet 2012). Further, to prevent trap shyness at possible hunting locations, many newer camera trap models utilize infrared flashes. Therefore, when full colour nocturnal photographs are needed, the selection of white flash models may exclude cameras with otherwise desirable features. Moreover, several studies have found significant differences in performance when comparing camera traps of the same model, possibly due to manufacturing tolerances (Damm, Grand & Barnett 2010; Hughson, Darby & Dungan 2010). This issue may be of little consequence for recreational use, however camera traps should meet uniformly high standards if they are to be used for scientific studies.

Unfortunately, no 'ultimate camera trap' exists for scientific research. However, several authors have postulated the features such a camera trap should include (e.g. Meek & Pittet 2012; Rovero *et al.* 2013). Ideally, almost every feature would have settings that can be adjusted by the user. The list of features is extensive (see Meek & Pittet 2012), but possibly the most important programmable features, as highlighted by my data, would be detection area and trigger speed.

The effects of detection area and trigger speed are interactive (Figure 5.1). Wide detection areas with fast trigger speeds may photograph subjects before they are fully within the camera's field of view, whereas wide detection areas with slow trigger speeds may produce more photographs in which subject is centred in the camera's field of view (Figure 5.1). Conversely, narrow detection areas with fast trigger speeds would produce a high proportion of photographs with centred subjects, and slower trigger speeds would produce photographs in which the subject is leaving the camera's field of view (Figure 5.1). These effects may be less serious when subjects are further from the camera, as field of view increases with distance from the camera. However, in field situations, placement of camera traps at increased distances from target areas such as game trails is not always possible. Therefore, the ability to change detection area and/or trigger speed may allow the user to adjust the camera to their specific needs and maximise the quality of data obtained, particularly in confined areas.

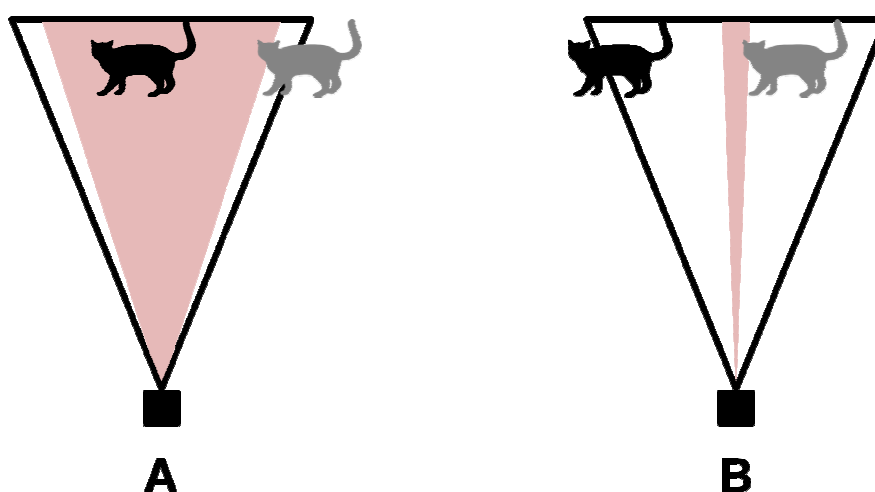


Figure 5.1. The relationship between detection area and trigger speed. Filled squares represent cameras, triangles represent the camera's field of view with superimposed detection zones (shaded areas). Subject colour refers to likely positioning in the field of view for cameras incorporating fast trigger speeds (grey) and slow trigger speeds (black). For wide detection areas (A), slow trigger speeds would produce more images with centred subjects. Conversely, for narrow detection areas (B), slow trigger speeds may fail to record animals before they leave the field of view.

Undoubtedly, variation within and/or between camera trap types affects the data that are collected. Therefore, even when studies focus on the same species and use similar methodologies, comparison between results may be difficult. For example, through the exclusion of detection probabilities, relative abundance indices are inherently questionable (O'Brien 2011; Sollmann *et al.* 2013). Differences in the detection efficiency of various camera designs only serve to increase this uncertainty, weakening comparison between results. Therefore, future studies should employ robust sampling designs that allow for rigorous statistical analyses of data using methods such as occupancy modelling (MacKenzie *et al.* 2002; Cove *et al.* 2013; Schuette *et al.* 2013) and random encounter models (Rowcliffe *et al.* 2008; Carbajal-borges, Godínez-gómez & Mendoza 2014).

During my study, camera traps with narrow detection zones and fast trigger speeds collected sufficient data to perform occupancy modelling for several species. Occupancy models provided some support for the relative abundance indices, which suggested that black-backed jackal abundance was higher in the absence of apex predators, as predicted by the mesopredator release hypothesis (MRH). Further, spatial avoidance of apex predators by black-backed jackals was apparent at Kwandwe. In the absence of apex predators at E-Zulu, black-backed jackals exhibited a more uniform distribution throughout the camera grid. Unfortunately, because my study contained only one site with apex predators, and one site without apex predators, caution should be exercised in the interpretation of these results. However, to the best of my knowledge, no other studies have demonstrated increased mesopredator abundance and/or distribution in the Eastern Cape, South Africa. Therefore, my data highlights the need for further studies of MRH, hopefully leading to a fuller understanding of the complex interactions between predator species.

If further studies were to corroborate the release of black-backed jackals suggested by my data, the consequences may be extensive and severe. For example, Estes (1967) noted that black-backed jackals were the biggest threat to Grant's gazelle (*Nanger granti*) fawns in the Ngorongoro crater of Tanzania. Therefore, a release of black-backed jackals may reduce neonate survival of similar sized antelope such as bushbuck (*Tragelaphus scriptus*) and impala (*Aepyceros melampus*) in South Africa. Regrettably, herbivore populations are heavily managed at both of my study sites, either for prey supplementation or commercial trophy hunting. Consequently, my data provide little information on how mesopredator release of black-backed jackals may affect herbivore populations in the Eastern Cape. Therefore, long term studies are needed to accurately assess how mesopredator release may influence herbivore population trends within enclosed reserves.

Black-backed jackals consume a wide range of prey items including small mammals, reptiles, invertebrates and birds (Bussiahn 1997; Brassine & Parker 2011), many of which can be important seed dispersers (Corlett 1998). Consequently, release of black-backed jackals may suppress populations of these prey items, and indirectly affect seed dispersal. Further, black-backed jackal diets can contain frugivorous elements (Brassine 2011). Therefore, similarly to other carnivores that consume fruits and seeds, black-backed jackals may themselves be important seed dispersal agents (Herrera 1989; Corlett 1998; Otani 2002; Koike *et al.* 2008). Ultimately, black-backed jackal release may directly and/or indirectly affect seed dispersal patterns, leading to altered distribution and/or species composition of plant communities (Roemer, Gompper & van Valkenburgh 2009). In turn, altered vegetation levels may affect soil erosion rates, influencing factors such as water retention, levels of soil organic matter and nutrient availability (Pimentel & Kounang 1998).

Additionally, mesopredators can be important hosts for disease (Loveridge & Macdonald 2001; Roemer, Gompper & van Valkenburgh 2009; Hollings *et al.* 2013). For instance, mesopredator release of feral cats (*Felis catus*), the definitive hosts of *Toxoplasma gondii*, has led to increased prevalence of the parasite in native intermediate hosts such as the Tasmanian pademelon (*Thylogale billardierii*) (Hollings *et al.* 2013). Further, high mesopredator densities are associated with cross species transmission of diseases caused by pathogens such as rabies and distemper viruses (Roemer, Gompper & van Valkenburgh 2009). Following this, the release of black-backed jackals may drastically increase transmission rates of pathogens that cause chronic disease in a wide range of mammalian species.

Evidently, apex predator removal can cause cascading effects that may permeate entire ecosystems. Ripple & Beschta (2006) demonstrated catastrophic regime shifts associated with declines in cougar (*Puma concolor*) populations in the Zion National Park, Utah, U.S.A. Reduced cougar densities allowed mule deer (*Odocoileus hemionus*) populations to increase, resulting in reduced cottonwood (*Populus fremontii*) recruitment and increased stream bank erosion. Further, Ripple & Beschta (2006) found relative abundances and diversity of wildflowers, amphibians, lizards and butterflies to be higher in areas where cougars were present, compared to areas where cougars were absent. Unfortunately, it is impossible to say if these results were due to mesopredator release, as abundances of mesopredators such as coyotes (*Canis latrans*) were not recorded. However, the results of Ripple & Beschta (2006) are consistent with ecological theory, which states that large predators promote biodiversity (Paine 1966; Estes, Crooks & Holt 2001).

Similarly, my results showed higher diversity of mammals, birds and reptiles in the presence of apex carnivores at Kwandwe where apex predators were present. However, as previously mentioned, large game species are possibly better suited to camera trapping and are somewhat managed at both sites. Further, camera traps are possibly less effective at recording small mammals, birds, reptiles and invertebrates than methods such as mist netting, pitfall trapping, audio recording of birds and bats and live trapping of small mammals (Stamm, Davis & Robbins 1960; Bury & Corn 1987; Waters & Walsh 1994; Kwan *et al.* 2006; Fagerlund 2007; Kok, Parker & Barker 2013). Therefore, although small mammals, birds, and reptiles were recorded during my study, they were far from exhaustively surveyed and no strong inference can be made regarding their diversity from my data. Clearly, alternative sampling techniques need to be employed alongside future camera trapping studies to provide additional insight regarding ecosystem processes such as mesopredator release and trophic cascading.

Suppression of mesopredators and increased biodiversity are strong arguments to support large predator re-introductions. However, such re-introductions may be logistically challenging and costly. Firstly, 2.4m electrified game fences must be installed or upgraded, and consent from surrounding land owners must be acquired before dangerous game can be introduced (Knight & Cowling 2011). Secondly, following re-introductions, large amounts of time and money may be expended to maintain fences. Thirdly, dangerous game increases the risks when walking, and staff may require higher level qualifications such as trails guiding and advanced rifle handling. Finally, game losses to predation by large carnivores are inevitable, and may be particularly costly if high value species such as disease-free buffalo (*Syncerus caffer*), sable (*Hippotragus niger*) and roan (*H. equinus*) are taken.

Nevertheless, these economic costs may be offset in several ways. For instance, target audiences may be expanded as large predators, particularly lions (*Panthera leo*) and leopards (*P. pardus*), often score highly among game viewing preferences of tourists (Lindsey *et al.* 2007; Di Minin *et al.* 2013). Further, as suggested by my results, apex predators appear to suppress mesopredators more effectively than anthropogenic control. Therefore, apex predators may decrease conflict between land owners and mesopredators. Moreover, population models by Berger & Conner (2008) have shown that neonate survival rates of pronghorn (*Antilocapra americana*) increase in the presence of wolves (*Canis lupus*) due to coyote suppression. Improved neonate survival of game species may allow for increased harvest rates and sales of excess game animals. Additionally, apex predator harvest may further offset losses caused by predation. However, apex predator harvest must be strictly regulated, and occur at a controlled and sustainable rate (Lindsey, Roulet & Románach 2007; Packer *et al.* 2011).

Importantly, re-introductions of large predators require extensive monitoring. It is possible that high populations of apex predators could severely reduce or extirpate mesopredator species, and initiate a plethora of cascading effects. Indeed, this may have been the case during my study, as opposed to black-backed jackals being released in the absence of larger predators. Clearly, further studies of carnivore interactions and predator-prey interactions are needed in order to develop appropriate management strategies. Camera trapping is an effective tool for monitoring large mammals, but should be used alongside additional sampling techniques to gain a fuller understanding of how predator manipulations affect whole ecosystems.

Chapter 6

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Appendix A

Table A1. Complete list of all bird, mammal, and reptile species photographed, with total number of photographs recorded by each camera type at E-Zulu when comparing camera trap designs in chapter 3.

Family	Genus	Species	Common name	Wildview	Cuddeback
-	-	-	Unidentified bird	-	17
Accipitridae	<i>Melierax</i>	<i>canorus</i>	Southern pale chanting goshawk	-	5
	<i>Polyboroides</i>	<i>typus</i>	African harrier-hawk	1	-
Numididae	<i>Numida</i>	<i>meleagris</i>	Helmeted guineafowl	-	1
Otididae	<i>Ardeotis</i>	<i>kori</i>	Kori bustard	5	4
Struthionidae	<i>Struthio</i>	<i>camelus</i>	Ostrich	7	3
Sturnidae	<i>Lamprotornis</i>	<i>nitens</i>	Cape glossy starling	-	1
	<i>Spreo</i>	<i>bicolor</i>	Pied starling	-	3
Threskiornithidae	<i>Bostrychia</i>	<i>hagedash</i>	Hadedda ibis	-	5
Upupidae	<i>Upupa</i>	<i>africana</i>	African hoopoe	-	1
Bovidae	<i>Aepyceros</i>	<i>melampus</i>	Impala	79	17
	<i>Connochaetes</i>	<i>taurinus</i>	Blue wildebeest	28	8
	<i>Damaliscus</i>	<i>dorcas</i>	Bontebok	42	2
	<i>Hippotragus</i>	<i>niger</i>	Sable	10	2
	<i>Kobus</i>	<i>ellipsiprymnus</i>	Waterbuck	170	91
	<i>Oryx</i>	<i>gazella</i>	Gemsbok	24	11
	<i>Raphicerus</i>	<i>campestris</i>	Steenbok	37	22
	<i>Silvicapra</i>	<i>grimmia</i>	Common duiker	160	186
	<i>Syncerus</i>	<i>caffer</i>	Cape buffalo	25	4
	<i>Tragelaphus</i>	<i>angasii</i>	Nyala	2	13
		<i>oryx</i>	Eland	16	26
<i>scriptus</i>		Bushbuck	9	8	
	<i>strepsiceros</i>	Greater kudu	802	435	
Canidae	<i>Canis</i>	<i>mesomelas</i>	Black-backed jackal	2	13
	<i>Otocyon</i>	<i>megalotis</i>	Bat-eared fox	6	13
Cercopithecidae	<i>Chlorocebus</i>	<i>pygerythrus</i>	Vervet monkey	7	25
	<i>Papio</i>	<i>ursinus</i>	Chacma baboon	132	86
Felidae	<i>Panthera</i>	<i>pardus</i>	Leopard	-	1
Giraffidae	<i>Giraffa</i>	<i>camelopardalis</i>	Giraffe	6	-

Table A1. Continued.

Family	Genus	Species	Common name	Wildview	Cuddeback
Herpestidae	<i>Cynictis</i>	<i>penicillata</i>	Yellow mongoose	2	4
	<i>Galerella</i>	<i>pulverulenta</i>	Cape gray mongoose	-	2
	<i>Suricata</i>	<i>suricatta</i>	Suricate	-	3
Hyaenidae	<i>Proteles</i>	<i>cristatus</i>	Aardwolf	-	18
Hystriidae	<i>Hystrix</i>	<i>africaeausstralis</i>	Cape porcupine	12	9
Leporidae	<i>Lepus</i>	<i>saxatilis</i>	Scrub hare	7	8
Mustelidae	<i>Ictonyx</i>	<i>striatus</i>	Striped polecat	-	6
Orycteropodidae	<i>Orycteropus</i>	<i>afer</i>	Aardvark	9	2
Pedetidae	<i>Pedetes</i>	<i>capensis</i>	Spring hare	1	1
Suidae	<i>Phacochoerus</i>	<i>africanus</i>	Warthog	696	499
	<i>Potamochoerus</i>	<i>larvatus</i>	Bushpig	10	6
Viverridae	<i>Genetta</i>	<i>genetta</i>	Small-spotted genet	-	4
Varanidae	<i>Varanus</i>	<i>albigularis</i>	Rock monitor	-	4

Table A2. Complete list of all bird and mammal species photographed, with total number of photographs recorded by each camera type at Kwandwe when comparing camera trap designs in chapter 3.

Family	Genus	Species	Common name	Wildview	Cuddeback
-	-	-	Unidentified bird	1	3
Burhinidae	<i>Burhinus</i>	<i>capensis</i>	Spotted thick-knee	2	-
Columbidae	<i>Streptopelia</i>	<i>capicola</i>	Ring-necked dove	-	9
Malaconotidae	<i>Laniarius</i>	<i>ferrugineus</i>	Southern boubou	-	3
Muscicapidae	<i>Cercotrichas</i>	<i>leucophrys</i>	White-browed scrub robin	-	3
	<i>Sigelus</i>	<i>silens</i>	Fiscal flycatcher	-	6
Phasianidae	<i>Pternistes</i>	<i>afer</i>	Red-necked spurfowl	-	1
Sturnidae	<i>Lamprotornis</i>	<i>nitens</i>	Cape glossy starling	1	11
Bovidae	<i>Aepyceros</i>	<i>melampus</i>	Impala	14	9
	<i>Alcelaphus</i>	<i>buselaphus</i>	Red hartebeest	-	1
	<i>Kobus</i>	<i>ellipsiprymnus</i>	Waterbuck	13	1
	<i>Oryx</i>	<i>gazella</i>	Gemsbok	13	2
	<i>Raphicerus</i>	<i>campestris</i>	Steenbok	14	10
	<i>Redunca</i>	<i>fulvorufula</i>	Mountain reedbuck	2	-
	<i>Silvicapra</i>	<i>grimmia</i>	Common duiker	50	49
	<i>Syncerus</i>	<i>caffer</i>	Cape buffalo	20	3
	<i>Tragelaphus</i>	<i>oryx</i>	Eland	4	2
		<i>scriptus</i>	Bushbuck	101	44
		<i>strepsiceros</i>	Greater kudu	381	107
Canidae	<i>Canis</i>	<i>mesomelas</i>	Black-backed jackal	14	54
	<i>Otocyon</i>	<i>megalotis</i>	Bat-eared fox	1	4
Cercopithecidae	<i>Papio</i>	<i>ursinus</i>	Chacma baboon	83	65
Elephantidae	<i>Loxodonta</i>	<i>africana</i>	African elephant	17	39
Equidae	<i>Equus</i>	<i>quagga</i>	Plains zebra	36	10
Felidae	<i>Panthera</i>	<i>pardus</i>	Leopard	16	3
Giraffidae	<i>Giraffa</i>	<i>camelopardalis</i>	Giraffe	13	1
Herpestidae	<i>Galerella</i>	<i>pulverulenta</i>	Cape gray mongoose	3	7
Hyaenidae	<i>Hyaena</i>	<i>brunnea</i>	Brown hyaena	36	6
	<i>Proteles</i>	<i>cristatus</i>	Aardwolf	45	20
Hystricidae	<i>Hystrix</i>	<i>africaeaustralis</i>	Cape porcupine	18	19
Leporidae	<i>Lepus</i>	<i>saxatilis</i>	Scrub hare	24	23

Table A2. Continued.

Family	Genus	Species	Common name	Wildview	Cuddeback
Leporidae	<i>Pronolagus</i>	<i>rupestris</i>	Red rock rabbit	5	10
Mustelidae	<i>Ictonyx</i>	<i>striatus</i>	Striped polecat	1	3
Nesomyidae	<i>Saccostomus</i>	<i>campestris</i>	Pouched mouse	-	1
Orycteropodidae	<i>Orycteropus</i>	<i>afer</i>	Aardvark	1	1
Rhinocerotidae	<i>Ceratotherium</i>	<i>simum</i>	White rhinoceros	23	19
	<i>Diceros</i>	<i>bicornis</i>	Black rhinoceros	1	1
Suidae	<i>Phacochoerus</i>	<i>africanus</i>	Warthog	261	290
	<i>Potamochoerus</i>	<i>larvatus</i>	Bushpig	6	8
Viverridae	<i>Genetta</i>	<i>genetta</i>	Small-spotted genet	-	3
		<i>tigrina</i>	Large-spotted genet	-	5

Appendix B

Table B1. Exact GPS locations of camera stations at Kwandwe and E-Zulu. Co-ordinates are in decimal degrees. Co-ordinates highlighted in grey were the camera stations used to compare camera trap models in chapter 3.

Rotation	Camera	Kwandwe		E-Zulu	
		Latitude	Longitude	Latitude	Longitude
1	1	-33.07623000	26.50143000	-32.96079000	26.14352000
	2	-33.07326000	26.52497000	-32.98780000	26.11587000
	3	-33.06655000	26.54174000	-32.98720000	26.12962000
	4	-33.08687000	26.50653000	-33.00713000	26.16489000
	5	-33.09291000	26.52345000	-33.00625000	26.17796000
	6	-33.08376000	26.53181000	-33.02125000	26.18845000
	7	-33.10626000	26.49101000	-33.03875000	26.18378000
	8	-33.10447000	26.50842000	-33.03713000	26.16698000
	9	-33.10221000	26.54831000	-33.02369000	26.15259000
2	1	-33.07268000	26.50321000	-32.97548000	26.13771000
	2	-33.06650000	26.52419000	-32.98076000	26.12409000
	3	-33.06391000	26.54182000	-32.99009000	26.14914000
	4	-33.08951000	26.50364000	-33.00636000	26.15778000
	5	-33.09658000	26.51409000	-33.00915000	26.17891000
	6	-33.09705000	26.53784000	-33.01603000	26.18220000
	7	-33.10261000	26.50489000	-33.04406000	26.17216000
	8	-33.11406000	26.52589000	-33.03396000	26.15137000
	9	-33.09962000	26.53844000	-33.02222000	26.16040000
3	1	-33.07103000	26.49741000	-32.96236900	26.13756700
	2	-33.07415000	26.51316000	-32.98730400	26.11803400
	3	-33.06882000	26.53763000	-32.98570200	26.14324900
	4	-33.09163000	26.49917000	-32.99644800	26.16083900
	5	-33.08114000	26.52747000	-32.99930600	26.17085800
	6	-33.08551000	26.53685000	-33.01742900	26.18690300
	7	-33.10474000	26.49710000	-33.04621800	26.18721300
	8	-33.10710000	26.52738000	-33.04294200	26.15721800
	9	-33.10043000	26.54848000	-33.02036600	26.15788100

Table B1. Continued.

Rotation	Camera	Kwandwe		E-Zulu	
		Latitude	Longitude	Latitude	Longitude
4	1	-33.06393700	26.49868100	-32.96510600	26.14225100
	2	-33.07263000	26.51583200	-32.98451500	26.12092900
	3	-33.07528600	26.53680500	-32.98370600	26.14618400
	4	-33.08430400	26.50261700	-33.00888700	26.15606200
	5	-33.08509400	26.51969000	-33.00742900	26.17362700
	6	-33.09181800	26.53729800	-33.01345200	26.17428700
	7	-33.10540600	26.48952800	-33.03553500	26.19012700
	8	-33.10453500	26.51650600	-33.03174100	26.15469200
	9	-33.09995300	26.53133900	-33.02077300	26.16667900

Appendix C

Table C1. Complete list of all bird, mammal and reptile species photographed, with total number of photographs recorded at Kwandwe and E-Zulu when testing the mesopredator release hypothesis in chapter 4.

Family	Genus	Species	Common name	Kwandwe	E-Zulu
-	-	-	Unknown bird	9	23
Accipitridae	<i>Melierax</i>	<i>canorus</i>	Southern pale chanting goshawk	-	5
	<i>Polyboroides</i>	<i>typus</i>	African harrier hawk	-	1
Burhinidae	<i>Burhinus</i>	<i>capensis</i>	Spotted thick-knee	-	1
Charadriidae	<i>Vanellus</i>	<i>coronatus</i>	Crowned plover	-	3
Columbidae	<i>Streptopelia</i>	<i>capicola</i>	Ring-necked dove	17	4
	<i>Turtur</i>	<i>chalcospilos</i>	Emerald-spotted dove	2	-
Malaconotidae	<i>Laniarius</i>	<i>ferrugineus</i>	Southern boubou	10	1
	<i>Telophorus</i>	<i>zeylonus</i>	Bokmakerie	1	1
Muscicapidae	<i>Cercotrichas</i>	<i>leucophrys</i>	White-browed scrub robin	5	1
	<i>Sigelus</i>	<i>silens</i>	Fiscal flycatcher	6	4
Numididae	<i>Numida</i>	<i>meleagris</i>	Helmeted guineafowl	13	16
Otididae	<i>Ardeotis</i>	<i>kori</i>	Kori bustard	-	4
Phasianidae	<i>Pternistes</i>	<i>afer</i>	Red-necked spurfowl	14	-
Sagittariidae	<i>Sagittarius</i>	<i>serpentarius</i>	Secretary bird	-	1
Struthionidae	<i>Struthio</i>	<i>camelus</i>	Ostrich	-	17
Sturnidae	<i>Lamprotornis</i>	<i>nitens</i>	Cape glossy starling	16	9
	<i>Spreo</i>	<i>bicolor</i>	Pied starling	2	3
Threskiornithidae	<i>Bostrychia</i>	<i>hagedash</i>	Hadedda ibis	-	6
Upupidae	<i>Upupa</i>	<i>africana</i>	African hoopoe	-	1
-	-	-	Unknown bat	7	-
Bovidae	<i>Aepyceros</i>	<i>melampus</i>	Impala	13	103
	<i>Alcelaphus</i>	<i>buselaphus</i>	Red hartebeest	16	46
	<i>Antidorcas</i>	<i>marsupialis</i>	Springbok	-	4
	<i>Connochaetes</i>	<i>gnou</i>	Black wildebeest	1	-
		<i>taurinus</i>	Blue wildebeest	-	76
	<i>Damaliscus</i>	<i>dorcas</i>	Bontebok	-	137
	<i>Hippotragus</i>	<i>niger</i>	Sable	-	7
	<i>Kobus</i>	<i>ellipsiprymnus</i>	Waterbuck	56	245
<i>Oryx</i>	<i>gazella</i>	Gemsbok	7	72	

Table C1. Continued.

Family	Genus	Species	Common name	Kwandwe	E-Zulu	
Bovidae	<i>Raphicerus</i>	<i>campestris</i>	Steenbok	28	98	
	<i>Redunca</i>	<i>fulvorufula</i>	Mountain reedbuck	1	2	
	<i>Silvicapra</i>	<i>grimmia</i>	Common duiker	213	488	
	<i>Syncerus</i>	<i>caffer</i>	Cape buffalo	51	74	
	<i>Tragelaphus</i>		<i>angasii</i>	Nyala	-	69
			<i>oryx</i>	Eland	6	63
			<i>scriptus</i>	Bushbuck	177	16
			<i>strepsiceros</i>	Greater kudu	574	1520
Canidae	<i>Canis</i>	<i>mesomelas</i>	Black-backed jackal	81	74	
	<i>Otocyon</i>	<i>megalotis</i>	Bat-eared fox	52	133	
	<i>Vulpes</i>	<i>chama</i>	Cape fox	-	1	
Cercopithecidae	<i>Chlorocebus</i>	<i>pygerythrus</i>	Vervet monkey	46	167	
	<i>Papio</i>	<i>ursinus</i>	Chacma baboon	569	352	
Elephantidae	<i>Loxodonta</i>	<i>africana</i>	African elephant	92	-	
Equidae	<i>Equus</i>	<i>quagga</i>	Plains zebra	124	-	
Felidae	<i>Caracal</i>	<i>caracal</i>	Caracal	5	6	
	<i>Felis</i>	<i>silvestris</i>	African wildcat	-	1	
	<i>Panthera</i>	<i>leo</i>	Lion	4	-	
		<i>pardus</i>	Leopard	26	1	
Giraffidae	<i>Giraffa</i>	<i>camelopardalis</i>	Giraffe	14	4	
Herpestidae	<i>Atilax</i>	<i>paludinosus</i>	Water mongoose	3	-	
	<i>Cynictis</i>	<i>penicillata</i>	Yellow mongoose	-	29	
	<i>Galerella</i>	<i>pulverulenta</i>	Cape gray mongoose	61	21	
	<i>Suricata</i>	<i>suricata</i>	Suricate	-	11	
Hyaenidae	<i>Hyaena</i>	<i>brunnea</i>	Brown hyaena	76	-	
	<i>Proteles</i>	<i>cristatus</i>	Aardwolf	48	69	
Hystriidae	<i>Hystrix</i>	<i>africaeausstralis</i>	Cape porcupine	90	53	
Leporidae	<i>Lepus</i>	<i>saxatilis</i>	Scrub hare	191	129	
	<i>Pronolagus</i>	<i>rupestris</i>	Red rock rabbit	28	21	
Macroscelididae	<i>Elephantulus</i>	<i>edwardii</i>	Cape elephant shrew	1	-	
Mustelidae	<i>Ictonyx</i>	<i>striatus</i>	Striped polecat	21	32	
Orycteropodidae	<i>Orycteropus</i>	<i>afer</i>	Aardvark	12	18	
Pedetidae	<i>Pedetes</i>	<i>capensis</i>	Spring hare	6	14	
Rhinocerotidae	<i>Ceratotherium</i>	<i>simum</i>	White rhinoceros	33	-	

Table C1. Continued.

Family	Genus	Species	Common name	Kwandwe	E-Zulu
Rhinocerotidae	<i>Diceros</i>	<i>bicornis</i>	Black rhinoceros	1	-
Nesomyidae	<i>Saccostomus</i>	<i>campestris</i>	Pouched mouse	1	-
Suidae	<i>Phacochoerus</i>	<i>africanus</i>	Warthog	610	1588
	<i>Potamochoerus</i>	<i>larvatus</i>	Bushpig	30	15
Viverridae	<i>Genetta</i>	<i>genetta</i>	Small-spotted genet	19	33
		<i>tigrina</i>	Large-spotted genet	14	3
Testudinidae	<i>Stigmochelys</i>	<i>pardalis</i>	Leopard tortoise	4	-
Varanidae	<i>Varanus</i>	<i>albigularis</i>	Rock monitor	-	4