

Optimising camera trap density and position to determine medium and large mammal species richness and occupancy on the Cape Peninsula, South Africa.

by

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ABSTRACT

Largely due to anthropogenic causes, biodiversity and particularly species diversity is changing at an extraordinary rate, with declines in species abundance, community composition and extinction risk being of crucial concern. Monitoring of state variables of biodiversity such as species richness and occupancy are of significant importance in determining the severity of threats placed on species, populations and communities. As a non-invasive monitoring method camera traps are noted as being an effective, accurate and rapid means of compiling species richness estimates of medium to large terrestrial mammals. However, crucial elements of camera trap survey design are rarely empirically addressed, which has questioned the need for a standardised camera trapping protocol.

Table Mountain National Park (TMNP) is a protected area that is under serious anthropogenic pressure through urban and peri-urban development. Although it is the last refuge for a number of large mammal species on the Cape Peninsula, current mammalian species richness knowledge within the TMNP are limited. Accurate and current species richness estimates are therefore needed within TMNP and more specifically the Cape of Good Hope (CoGH), which exclusively hosts a number of medium and large mammal species. The aims of this study were to optimise a camera survey protocol for the Peninsula region, with a focus on camera density, placement and survey duration that will enable accurate estimations of medium to large mammal species richness and occupancy.

The results from the implemented pilot survey indicated that both camera trap density and placement have a significant effect on species richness estimates. Results yielded greater measures of species richness, capture frequencies and independent animal sightings by relaxing the maximum offset from the specified grid points when placing cameras. Furthermore, positioning cameras near areas of good quality animal sign greatly improved the overall measures of species richness and capture frequency as well. Significantly, attaining the required survey effort in terms of camera days was the most important factor in providing accurate species richness estimates.

My study clearly indicates that camera traps are an efficient and rapid means of compiling accurate species richness estimates within a shrubland habitat. In the full survey of the CoGH over 55 days, we were able to record 84% of the species thought to occur and 94% of the species known to occur within the area. Remarkably, the pilot study which only covered 5.3% of the CoGH corroborated that localised intensive sampling combined with statistical methods of accounting for undetected species, is an effective method of compiling rapid and accurate species richness estimates across broader study areas. My analyses suggest that both

extrapolation of species accumulation curves and non-parametric species richness estimators required an actual survey effort of approximately $1\ 000 - 1\ 200$ camera days to produce accurate estimations of actual species richness. Therefore, by optimising survey design, both the efficacy and cost of monitoring initiatives can be maximised, allowing for a greater contribution to the fulfilment of wildlife monitoring objectives.

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DEDICATION

To my wife Rachel, our children, Joel and Lilia, as well as my parents Basil and Diana. It is a privilege and honour to have you in my life.

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GLOSSARY

AIC	Akaike's Information Criterion
CBD	Convention on Biological Diversity
CFR	Cape Floristic Region
CoGH	Cape of Good Hope
DEM	Digital Elevation Model
GPS	Global Positioning System
MPA	Marine Protected Area
SANParks	South African National Parks
TMNP	Table Mountain National Park

CHAPTER 1: GENERAL INTRODUCTION

1.1. Biodiversity monitoring and indicators

The impact of biodiversity loss is not only restricted to specific ecosystems, but has been noted to adversely impact human health as well (Hooper *et al.* 2012). In light of this, world leaders at the 2002 Convention on Biological Diversity (CBD) set targets to significantly reduce the rate of biodiversity loss by 2010. However, this target was not met with indicators of biodiversity status all showing declines and threats and pressures on biodiversity all showing increases (Butchart 2010). Subsequently, biodiversity and particularly species diversity is changing at an extraordinary rate, with declines in species abundance, community composition and extinction risk being of crucial concern (Butchart 2010).

The role of biological monitoring is noted as fundamental in sustaining ecosystems, understanding and mitigating impacts on species diversity and supporting human well-being through ecosystem services (Yoccoz *et al.* 2001, Scholes *et al.* 2008, Lidenmeyer *et al.* 2012). Biological monitoring is often defined as collecting data on state variables of biodiversity across a specified temporal period in order to ascertain trends or changes (Yoccoz *et al.* 2001). In this context, monitoring takes place within an ecosystem and can be focused within finer scale features such as communities or populations (Yoccoz *et al.* 2001). Similarly, biological indicators can be defined as metrics used to represent one or more state variables of biodiversity include species richness, species diversity, occupancy, biomass and population size (Yoccoz *et al.* 2001, O'Connell & Bailey 2011).

Species richness and diversity as state variables are regularly utilised to evaluate the anthropogenic impact, whether intervention or disturbance, on biodiversity (Yoccoz *et al.* 2001). Similarly, distributional data and species inventories are often relied upon when evaluating biodiversity loss (Tobler *et al.* 2008, Ahumada *et al.* 2011). The past decade has seen a surge in the use of occupancy as a state variable of biodiversity. Advantages of occupancy modelling include the ability to model occupancy probability over large geographic scales (Nichols *et al.* 2011). Furthermore, occupancy models can assess the relationship between the level of site occupancy and underlying landscape and environmental variables (Nichols *et al.* 2011). If these surveys are replicated over time, rate parameters of occupancy dynamics such as the probabilities of local extinction and colonisation can be investigated as well (Nichols *et al.* 2011).

Thorough and robust biological monitoring programmes are therefore needed in order to identify relevant biological indicators, changes in population trends and associated extinction risks (Lindenmeyer *et al.* 2012). However, often conservation management activities do not include thorough biological monitoring programmes due to management oversight or lack of funding (Lindenmeyer *et al.* 2012). Subsequently, in the absence of a monitoring programme, the success of conservation management activities, initiatives and interventions cannot be determined (Lindenmeyer *et al.* 2012). Accurate assessments of species presence, distributions and population densities are thus essential for directing conservation strategies and management practices in a given region (Silveira *et al.* 2003, Tobler *et al.* 2008, Roberts 2011).

To establish whether protected, conservation and stewardship areas are being impacted on or reducing the rate of biodiversity loss, thorough monitoring programmes focused on keystone species or species suites are needed (Simberloff 1998, Yoccoz et al. 2001, O'Brien et al. 2010, Espartosa et al. 2011). Terrestrial mammal species, particularly medium to large species, have often been noted as keystone species that could act as indicators of ecosystem health (Wright et al. 1994, Simberloff 1998). Numerous ecological roles are maintained by a variety of mammalian species or species suites, which in turn contribute to ecological diversity, functioning and sustainability (McShea & Rappole 1992, Mills et al. 1993, Wright et al. 1994, Simberloff 1998, Smith & Foggin 1998, Kotliar et al. 1999, Ahumada et al. 2011, Espartosa et al. 2011). In light of this, medium to large (>0.5 kg) terrestrial mammal species richness, diversity and population trends are currently being used as a measures of ecosystem health on both global (O'Brien et al. 2010) and regional (Ahumada et al. 2011, Ahumada et al. 2013) scales. On a local level within South Africa, Table Mountain National Park (TMNP) represents a protected area that hosts significant biodiversity, is under severe threat and therefore requires monitoring programmes to assess if it is being impacted on (Yoccoz et al. 2001, SANParks 2015).

1.2. Biodiversity and mammal monitoring in Table Mountain National Park

TMNP (ca. 24 000 ha) is situated at the south-western tip of Africa and occurs within of the Cape Floristic Region, an area of significant biological importance which is classified as one of the 34 global hotspots and a UNESCO World Heritage site (Mittermeier *et al.* 2004). However the national park is under extreme anthropogenic pressure as it is almost entirely surrounded by urban, peri-urban (e.g. small holdings) and agricultural developments (Pryke & Samways 2009, SANParks 2015). Although TMNP is prominently regarded for the significant botanical diversity hosted within it (Rebelo *et al.* 2006, SANParks 2015), it is also the last refuge for a number of large mammal species on the Cape Peninsula (SANParks 2015, SANParks 2016). An area of particular significance in terms of exclusively hosting a number

of large antelope species within the TMNP and broader Cape Peninsula, is the Cape of Good Hope (CoGH) (SANParks 2015, SANParks 2016). Furthermore, the CoGH is unique as it represents one of the largest, most contiguous and undisturbed natural areas within the TMNP (SANParks 2015, SANParks 2016). However, currently mammalian species richness knowledge within the TMNP and CoGH is more or less restricted to local, general or historical species lists. The problematic issue with local, general or pooled species lists is that they only represent a potential estimate of richness for a site over the entire duration of accumulated knowledge, as opposed to a current estimate of species richness (O'Brien 2008). In order to effectively direct conservation management practices within TMNP, accurate and current estimations of mammalian species richness are needed.

Various methodologies have been used to assess terrestrial mammalian species richness, resulting in indicator or keystone species based on either primary, secondary or summary data (Yoccoz *et al.* 2001, Ahumada *et al.* 2013). Indicator species based on primary data are noted as being more precise and less biased than secondary or summary data (Yoccoz *et al.* 2001). Sources of primary data include a wide variety of systematic field assessment methods, of which some are difficult to replicate and standardise (Ahumada *et al.* 2013). Furthermore, different methods utilised for surveying terrestrial mammals generally always result in varied levels of accuracy, precision, resource requirements and cost effectiveness (Gaidet-Drapier *et al.* 2006).

1.3. Methods for assessing terrestrial mammalian presence

Both direct and indirect survey methodologies have been utilised to assess the presence and status of terrestrial mammal species (Lyra-Jorge *et al.* 2008). Indirect methods such as track surveys, scat surveys and snow-tracking are often used for rare and elusive species such as carnivore communities (Gompper *et al.* 2006) where the probability of direct sightings is scarce (Lyra-Jorge *et al.* 2008). Track surveys involve the use of track plates, which need to be placed along open areas, particularly trails (Gompper *et al.* 2006). One limitation is that they need to be checked regularly, often as frequently as every 2 days (Gompper *et al.* 2006), whilst also often requiring bait (Gompper *et al.* 2006, Espartosa *et al.* 2011). Of further consideration is the need for experienced field workers able to identify either scat or tracks, which is further perplexed in multispecies studies and could result in potential bias (Gompper *et al.* 2006, Lyra-Jorge *et al.* 2008, Espartosa *et al.* 2011).

Direct methods utilized to assess terrestrial mammal inventories include line transects, point observations and camera trapping (Silveira *et al.* 2003, Gompper *et al.* 2006, Tobler *et al.* 2008, Roberts 2011). Line transect and point counts are methods that have conventionally been applied to survey large terrestrial mammals (Lyra-Jorge *et al.* 2008, Espartosa *et al.*

2011). A significant limitation of this method is however the bias associated with visibility in dense structured vegetation types and at night with nocturnal or crepuscular species (Espartosa et al. 2011). Additionally, low sighting rates are often recorded, particularly with regard to elusive species (Trolle *et al.* 2008). Subsequently, standardisation of this method to accommodate the above mentioned limitations and bias often results in the need for long transects, which are impractical in fragmented or highly heterogeneous landscapes (Espartosa et al. 2011). Camera trapping is noted as an accurate, efficient, easily replicable and nonintrusive surveying method for medium-to-large terrestrial mammals that enables users to survey over a wide range of environmental and temporal scales (Cutler & Swan 1999, Carbone et al. 2001, Silveira et al. 2003, Gompper et al. 2006 & Ahumada et al. 2011). Studies have noted comparable results between camera trapping and track surveys (Lyra-Jorge et al. 2008, Espartosa et al. 2011), camera trapping has been noted as to allow more precise species identification, estimation of population density, assessment of activity patterns and efficiently record low density, solitary or wide ranging species (Carbone et al. 2001, Espartosa et al. 2011). Indirect methods are also often noted as being less accurate than direct methods (Smallwood & Fitzhugh 1995).

As a surveying method, camera trapping is suited to standardisation as human error and influence is limited to the survey design and identification of photographs (Ahumada *et al.* 2011). Selecting the most efficient survey design and trapping equipment for the respective application is often problematic and a process of trial and error (Cutler & Swan 1999).

1.4. The development and history of camera trapping

George Shiraz is recognised as the pioneer of developing remote photography as a tool for monitoring wildlife (Kucera & Barrett 2011). He devised a preliminary camera trap device throughout the late 1890's, which included a film based camera, trip wire and magnesium flash gun that would be triggered by and photograph animals with minimal human intervention (Kucera & Barrett 2011). Shiraz was able to record numerous mammalian species through remote photography such as minks (*Mustela* spp.), raccoons (*Procyon lotor*), white-tailed deer (*Odocoileus virginianus*) and American beavers (*Castor canadensis*) (Kucera & Barrett 2011). The first likely attempt to intentionally compile an inventory of species present within an area using camera traps was conducted by the curator of Ornithology at the American Museum of Natural History in New York, namely Frank M. Chapman (Kucera & Barrett 2011). He utilized trip wire cameras and bait to record at least five species on Barro Colorando Island in Panama in 1927 (Chapman 1927).

One of the biggest drivers for the development and use of camera traps in wildlife management during the early 1990s was the need for a non-invasive, non-lethal, reliable and accurate

method of determining the presence and conservation status of animal species in wilderness and/or protected areas, particularly those species within carnivore guilds (O'Connell *et al.* 2011). Equally, another driver contributing to the growth in the camera trap industry during this respective period was the demand created by the hunting fraternity regarding the use of camera traps to locate trophy antelope and other desired species (O'Connell *et al.* 2011). By 1991 cameras with infrared trigger systems were incorporated into animal studies, whereby the infrared sensor pulsed a beam of infrared light that when broken by an object moving through it triggered the camera (Swann *et al.* 2011). Additionally, automatic exposure controls, a dedicated flash and an automatic time and date recorder were added to camera systems (Carthew & Slater 1991). In 2006, George Steinmetz established a reliable and more userfriendly approach to camera trapping wildlife when he became the first photographer to use digital camera traps (Kucera & Barrett 2011).

Camera trapping has been used as an ecological monitoring tool since the early 20th century, but its use has increased substantially in the past decade due to increased affordability and the improvement in camera technology and accessibility (Chapman 1927, Rowcliffe & Carbone 2008, Tobler et al. 2008, Noss et al. 2012). Initially, camera use in wildlife ecology was largely focused on nest ecology and assessing activity patterns of large vertebrates (Cutler & Swan 1999, Maffei & Noss 2008, Silveira et al. 2003, Dillon & Kelly 2007), but application thereof has greatly expanded since then including the study of rare species (Surridge et al. 1999, Delgado et al. 2004), rare events (Hirakawa & Sayama 2005), compilation of species inventories (Cutler & Swan 1999 and Silveira et al. 2003), the description of habitat use (Cutler & Swan 1999, Maffei & Noss 2008, Silveira et al. 2003, Dillon & Kelly 2007) and estimating population dynamics such as relative abundance, density, occupancy, survivorship and recruitment (Cutler & Swan 1999, Karanth et al. 2004, Trolle & Kelly 2005, Maffei & Noss 2008, Rowcliffe & Carbone 2008). The application of camera trap studies has however been largely focused on, but not restricted to, mammal species inhabiting dense, closed forest habitats (Carbone et al. 2001, Karanth et al. 2003, Gompper et al. 2006, Tobler et al. 2008, Ahumada et al. 2011). However, camera trap studies in more open habitat types have been conducted and proved efficient in compiling species inventories (Silveira et al. 2003, Roberts 2011).

1.5. Camera Trap Survey Design

When considering survey design, trap spacing, placement and trapping period are three crucial aspects that need to be defined (Foster & Harmsen 2012).

1.5.1. Trap Spacing

Trap spacing can directly influence the capture probability of the target species or species suite (Dillon & Kelly 2007). When trap spacing is defined too widely it could result in survey gaps,

thereby possibly failing to capture individuals or species that inhabit home ranges between traps (Foster & Harmsen 2012). Likewise, spacing them too closely essentially duplicates effort and wastes resources (O'Brien 2008). By enhancing trap spacing, the coverage of the survey area can be efficiently maximised (Foster & Harmsen 2012). Within multispecies surveys, trap spacing is noted as a fundamental consideration when assessing site occupancy, as opposed to it being relatively unimportant when using jackknife estimators to assess species richness (O'Brien 2008). A study by Tobler *et al.* (2008) in forest habitats utilising two different camera spacing (1 km and 2 km) and grid size (ca. 15 and 50 km²) designs of equal survey effort (camera nights), yielded almost identical results and did not influence survey success. This result was however established in forest habitats and whether it can be applied to other habitat types is yet to be determined. When sampling includes rare or elusive species, survey design and placement should consider sampling both intensively and extensively (O'Brien 2008).

1.5.2. Trap placement

Capture probability for a given species is also influenced through trap placement (Foster & Harmsen 2012). Placing traps on trails or in specific microhabitats could bias results towards species or individuals within a species that are more likely to utilise the respective landscape or habitat feature (O'Brien 2008, Harmsen *et al.* 2010). The capture rate of a species known to utilise roads or trails is further influenced by the time since trail/road establishment, the trail/road width and the substrate it dissects (Foster & Harmsen 2012). In multispecies surveys, selecting optimal trap placement for increased capture probability of specific species may result in non-random and biased placement for the detection of other species (Harmsen *et al.* 2010, Foster & Harmsen 2012). When considering abundance estimation, utilising a single survey method for a multispecies survey may result in biased and imprecise density estimations as the optimal trap placement, spacing and survey area required could differ between the respective species (Foster & Harmsen 2012). When the goal of the study is to assess species richness, a stratified or systematic trap placement design may be most appropriate (O'Brien 2008).

Camera traps are known to have a fairly wide detection rate on a horizontal plane, but not necessarily on a vertical plane (Kelly 2008). Studies have shown that capture probability is also influenced by species body size (Kelly 2008, Swan *et al.* 2004 and Tobler *et al.* 2008). In a study utilising DeercamTM traps, the maximum horizontal detection distance for smaller and larger mammals was 6 m and 20 m respectively (Li *et al.* 2010). Therefore camera trap survey results might be biased towards larger species due to their higher capture probability. Roberts (2011) recorded a weighted mean horizontal camera detection arc and distance of 70° and 5 m respectively. The subject of camera height has not yet been fully addressed in studies (Gompper *et al.* 2006, Kelly 2008). Kelly (2008) suggests that lowering camera height to 20 –

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30 cm may increase the detection rate of smaller species, whilst not compromising the detection rate of larger species.

1.5.3. Trap period

Tobler *et al.* (2008) noted that survey effort equating to 400 - 500 camera days should be sufficient to detect and record the most common species in the respective forest habitat. Common species recorded in the particular study yielded capture frequencies (captures per 1000 camera days) of four or more. When camera frequencies for certain elusive and rare species dropped to below 3, the survey effort required ranged between 1 500 and 3 000 camera nights respectively to achieve a 95% capture probability. The capture frequency for all species ranged between 0.4 and 66 (Tobler *et al.* 2008). Trolle & Kery (2005) recorded 23 species with a survey effort of 504 camera days in predominantly forest and woodland habitat types. Whilst in a study conducted within a grassland habitat, 17 of the 28 species (64%) were recorded with a survey effort of 1 035 camera days (Silveira *et al.* 2003). Capture frequency for each species in a region is influenced by species-specific behavioural characteristics, body size, home range size and stochastic variation (Tobler *et al.* 2008).

There is currently a lack of standardisation across camera trap studies focusing on the same species or species suites and has subsequently raised debate on whether standardised camera trapping protocols are needed (Dillon & Kelly 2007, Kelly 2008). Furthermore, studies assessing survey design have largely take place in dense habitat types (Carbone et al. 2001, Karanth et al. 2004, Gompper et al. 2006, Tobler et al. 2008, Ahumada et al. 2011), which validates a need to assess survey design in other habitats. When considering survey design, the question regarding the most efficient trap density, placement and arrangement has rarely been empirically addressed (Gompper et al. 2006). Therefore, although there are many benefits regarding the use of camera traps in vertebrate studies, there are also limitations with regard to survey design that need further investigation. In this study, I addressed three aspects of survey design, namely trap density, placement and spacing in a fynbos shrubland environment. I then use the results to do a much needed estimation of current mammalian species richness and occupancy within the CoGH. This assessment of survey design could improve the efficiency of further surveys within this habitat type (Gompper et al. 2006), while the survey of the CoGH would greatly contribute to the understanding and conservation of target mammalian species.

1.6. Objectives

The main objectives of the study were:

- 1. To optimise camera survey protocol for the Peninsula region, with a focus on camera density, placement and survey duration that will enable accurate estimations of medium to large mammal species richness and occupancy.
- To use the optimised survey protocol to determine the status and occupancy of medium (1
 - 10 kg) and large (> 10 kg) mammals across the Cape of Good Hope (CoGH) section of
 the TMNP.
- 3. To compare detection probabilities of species and/or species guilds in relation to different landscape and environmental parameters.

1.7. Structure of the thesis

This thesis consists of five chapters of which chapters 3 and 4 have been compiled to serve as individual manuscripts to facilitate publication in peer-reviewed journals.

Chapter 2 provides contextual background to the ecology, topography and vegetation within the broader TMNP and locally within the CoGH.

Chapter 3 aims to determine the most accurate and efficient camera trap survey design to estimate medium to large terrestrial mammal species richness. Three elements of survey design were addressed and tested, namely trap spacing, placement and density.

Chapter 4 implements the most efficient survey design identified in chapter 3 to provide a baseline of two state variables of biodiversity across the CoGH, namely species richness and occupancy.

Chapter 5 acts as a synthesis chapter where the implications of study objectives on survey design are explored and recommendations are provided to enhance survey efficiency for future surveys.

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CHAPTER 2: STUDY AREA

2.1. Introduction

The study was conducted in the 8 000 ha Cape of Good Hope (CoGH) section of the Table Mountain National Park (TMNP) on the Cape Peninsula in the Western Cape. The Cape Peninsula is located in the south-western tip of Africa and falls within the Fynbos Biome (Mucina & Rutherford 2006) (Figure 2.1). The area also forms part of the Cape Floristic Region (CFR), which encompasses an area of approximately 87 892 km² (Mucina & Rutherford 2006). The CFR is recognised as one of 34 global biodiversity hotspots (Mittermeier *et al.* 2004), one of six floral kingdoms (Goldblatt 1997), listed as a UNESCO World Heritage Site (UNESCO 2004) and an area of significant biological importance (Goldblatt 1997, Pryke & Samways 2008). More than 30% of the CFR has already been transformed through largely agricultural and urban developments (Cowling *et al.* 2003).



Figure 2.1: The Cape Peninsula is located at the south-western tip of South Africa and falls within the Fynbos Biome (Mucina & Rutherford 2006). The Cape of Good Hope is the southernmost section of Table Mountain National Park (TMNP), which is comprised of both a terrestrial and Marine Protected Area (MPA).

The CFR is known as a centre of diversity and endemism of mammals (Brooks *et al.* 2001) and invertebrate classes (Picker & Samways 1996, Branch 1998). It is also classified as an

Endemic Bird Area (Stattersfield *et al.* 1998), a global 200 Ecoregion (Olson & Dinerstein 1998) and a Centre of Plant Diversity (Davis *et al.* 1994).

TMNP is a protected area of approximately 24 000 ha that is under serious anthropogenic pressure through urban and peri-urban development (SANParks 2015). The TMNP was originally proclaimed in 1998 as the Cape Peninsula National Park, but later changed to Table Mountain National Park in 2004 (SANParks 2015). The protected area was further expanded in 2004 to include adjacent marine and coastal environments, which was proclaimed as the Table Mountain Marine Protected Area (Figure 1). The terrestrial protected area incorporates Signal Hill, Lion's Head, Table Mountain, Devil's Peak, the Twelve Apostles, Orange Kloof, Silvermine, Boulders Beach, sections of Red Hill and the Cape of Good Hope (SANParks 2015). The study site (CoGH) comprises approximately 80 km² of the TMNP and is comprised of a fenced protected area surrounded by coastline on 60% of its boundary (ArcGIS 2015).

2.2. Climate

The Cape Peninsula has a temperate Mediterranean climate, with distinct seasonal variation in both rainfall and temperature. Seasons are characterised by cold (averaging 7 - 20°C), wet winters and warm (averaging 15 - 27°C), dry and windy summers (Cowling *et al.* 1996, Mucina & Rutherford 2006). The Mean Annual Precipitation (MAP) for the Cape Peninsula is approximately 470 mm (South African Weather Service 2014). However, the rainfall gradient across the peninsula is highly varied and steep, influenced primarily by altitude and topographical features across the respective landscape (SANParks 2015). Recorded rainfall across the peninsula displays significant variation, averaging between 400 – 2 270 mm per year (SANParks 2015).

The broader study site receives a MAP of 780 mm, which peaks between May and August (Rebelo *et al.* 2006). Mean Annual Temperature is 15.2°C, with mean maximum and minimum temperatures of 25.0°C and 7.2°C respectively (Rebelo *et al.* 2006). The Mediterranean climate experienced within the CoGH is expressed in relatively high indices of Mean Annual Potential Evaporation (1 747 mm) and Mean Annual Soil Moisture Stress (59%). Furthermore, the climatic regime results in very few annual frost days in winter (*ca.* 3) (Rebelo *et al.* 2006).

The CoGH is noted as the windiest area in South Africa (South African Weather Service 2014), often experiencing wind speeds in excess of 100 km/h. Summers are generally characterised by strong south-easterly winds and winters by north-westerly winds (South African Weather Service 2014). The site is comprised of a narrow finger of landscape surrounded by coastline on the southern, eastern and western peripheries. The southern, eastern and western peripheries incorporate 2.5 km, 12.5 km and 21 km of shoreline respectively. The maximum

and minimum land surface between the eastern and western peripheries within the CoGH is approximately 7.7 km and 1.2 km respectively. The locality and associated topography thereby exposes the CoGH to significant maritime climatic influences (Rebelo *et al.* 2006).

2.3. Topography

As part of the Southwest Fynbos Bioregion (Mucina & Rutherford 2006), the Cape Peninsula is noted as a Bioregion with relatively low altitude and highly restricted area (ca. 2 500 km²). The CoGH is comprised of mountainous terrain with undulating valleys (Figure 2.2). Elevation within the CoGH varies between 0 and 324 meters above sea level (m.a.s.l), with associated slopes varying from flat valley bottoms (0°) to steep sided mountain slopes (> 50°).

Three distinct areas with higher altitude and more rugged terrain are noted within the CoGH, located along the northern, eastern and southern boundaries (Figure 2.2). The most rugged area within the CoGH is located along the eastern periphery where the mountainous terrain stretches along the coast for approximately 8 km² (10%). Three elevation zones were identified within the study site using the spatial analyst toolbox in ArcGIS, namely low, mid and high altitude areas. Low altitude areas (< 80 m.a.s.l) form the majority of the site covering approximately 48 km² (60%), followed by mid-altitude areas (80 – 120 m.a.s.l) covering approximately 20 km² (25%) and high altitude areas (> 120 m.a.s.l) covering 12 km² (15%) (Figure 2.2).



Figure 2.2: A terrain roughness map (left) compiled for the Cape of Good Hope, comprised of hillshade, slope and elevation layers. The scale of terrain ruggedness is shaded from green (low) to red (high). A Digital Elevation Model (DEM) (right) created for the Cape of Good Hope with altitude shading from white (low) to black (high).

2.4. Geology and soils

The geology of the Fynbos Biome is largely typified by that of the Cape Fold Belt (Rebelo *et al.* 2006), which is largely comprised of sandstone and shales of the Cape Super group (Forsyth & van Wilgen 2008, Mucina & Rutherford 2006). Prevalent groups within the Cape Super group include the Table Mountain, Bokkeveld, Kango and Witteberg Groups (Rebelo *et al.* 2006).

The Fynbos Biome is characterised by a large variation in soil types and soil associations, a result of a number of environmental factors. Soils within the CoGH originate from three sources, namely Ordovician sandstones, leached acid tertiary sand from coastal dunes and stabilised old calcareous or neutral dunes outside of the influence of salt spray (Rebelo *et al.* 2006). This results in Lamotte soil formations being prominent across the study site, but could also include Houwhoek forms and grey regic sands (Rebelo *et al.* 2006). Due to soil composition on the Cape Peninsula generally being from shales and sandstones, results in leached and nutrient poor soils (Forsyth & van Wilgen 2008).

2.5. Vegetation

The Fynbos Biome is comprised of three major vegetation complexes, namely fynbos, renosterveld and strandveld (Rebelo *et al.* 2006). The majority of the vegetation within the study site is comprised of fynbos, with small extents of the strandveld type occurring along the coastline (Rebelo *et al.* 2006). Vegetation characteristics that typify fynbos and therefore the CoGH as well, include restios, ericoid shrubs, proteoid shrubs, leaf spinescence, high sedge cover and low grass cover (Rebelo *et al.* 2006). Structurally, fynbos can be classified according to dominant vegetation cover present, resulting in asteraceous, restioid, graminoid, proteoid, waboomveld, ericoid and wet restioid fynbos types (Rebelo *et al.* 2006) (Table 2.1). The niche separation between these types are largely driven by water availability and soil depth (Rebelo *et al.* 2006).

Table 2.1: A general description of structural fynbos classes as provided by Mucina and Rutherford 2006.

Fynbos	Description
Туре	Description
	High cover of generally tall dominant proteoids, with ferns, geophytes
Proteoid	and wide-leaved sedges being characteristic as well. Having deep root
	systems they can exploit deep water systems generally unavailable to
	other fynbos types. Generally confined to deeper and more fertile soils
	along the foot of mountains.
	Dominated by a high cover of ericoids and restioids, whilst a high cover
Ericaceous	of segdes can also be characteristic. Generally occur in permanently
	wet and cool areas, as well as at higher altitudes than proteoid fynbos.
Restioid	Dominated by a high cover of restios and low cover of shrubs. Can
	occur on warmer north facing slopes and are more tolerant of drought
	prone habitats like dunes and sandy plateaus.
Asteraceous	Has a relatively lower total vegetation cover, often with high graminoid
	and elytropappoid cover. Generally occurs on hot, lower and north-
	facing slopes.
Waboomveld	Characterised by the presence of Protea nitida (Waboom), which
	generally forms a tall 2 - 5 m tree over storey. Generally confined to
	lower slopes with deeper soils.
Grassy/	Characterised by high grass cover and non-proteoid species.
Graminoid	Generally confined to areas of finer textured and richer soils, as well
Fynbos	as areas that are less drought prone relative to other fynbos types.

The CoGH is comprised of four fynbos vegetation types, including Cape Flats Dune Strandveld, Cape Seashore Vegetation, Hangklip Sand Fynbos and Peninsula Sandstone Fynbos (Rebelo *et al.* 2006). Of the vegetation types present, all except Cape Seashore Vegetation are listed as threatened ecosystems and are classified as Endangered (Mucina & Rutherford 2006). The majority of vegetation present is comprised of Peninsula Sandstone Fynbos (70%), followed by Hangklip Sand Fynbos (15%), Cape Flats Dune Strandveld (12%), Cape Lowland Freshwater Wetlands (1%), Peninsula Granite Fynbos (1%) and Cape Seashore Vegetation (1%) (Figure 2.3).



Figure 2.3: Vegetation types present within the Cape of Good Hope (Mucina & Rutherford 2006).

The dominant features characterising each of the vegetation types found within the study site can be described as follows (Mucina & Rutherford 2006):

Peninsula Sandstone Fynbos

Sandstone Fynbos is the most extensive vegetation group in the Fynbos Biome and as such Peninsula Sandstone Fynbos is also the dominant vegetation type within the CoGH (Figure 2.4). As a vegetation type it is restricted to the Western Cape, occurring from the CoGH through to Table Mountain and Lion's Head (Rebelo *et al.* 2006). It generally occurs on gentle to steep slopes, but within the CoGH is also found along valley bottoms. Vegetation structure is generally comprised of relatively tall proteoid, ericaceous, restioid and asteraceous fynbos types (Rebelo *et al.* 2006) (Figure 2.4 & 2.5).



Figure 2.4: A section of Peninsula Sandstone Fynbos within the CoGH, displaying a largely restioid dominant fynbos type (Colyn 2014).



Figure 2.5: A section of Peninsula Sandstone Fynbos within in the CoGH, displaying asteraceous and proteoid fynbos components (Colyn 2014).

Hangklip Sand Fynbos

Sand fynbos is the second largest vegetation group both within the Fynbos Biome and the CoGH. The specific sand fynbos type within the CoGH, namely Hangklip Sand Fynbos, is comprised of ericaceous, proteoid, restioid and some asteraceceous fynbos types. Vegetation structure is driven by soil depth and can vary from tall dense shrubland, generally proteoid or ericoid, through to relatively low restioid fynbos (Rebelo *et al.* 2006). It generally occurs on sand dunes and sandy valleys near coastlines. A characteristic feature of all sand fynbos types are a lower occurrence of fires, which is a result of the reduced vegetative cover along dune structures (Rebelo *et al.* 2006).

Cape Flats Dune Strandveld

This vegetation type is restricted to flat and undulating dune field within the CoGH and is comprised of tall and evergreen shrubland (Figure 2.6). A high cover of grasses and herbs are characteristic of this vegetation type (Rebelo *et al.* 2006). Within the study site it is restricted to the coastline periphery, with a maximum altitude range of 0 to 60 m.



Figure 2.6: An example of Cape Flats Dune Strandveld within the CoGH, displaying a relatively tall and dense evergreen shrubland (Colyn 2014).

Cape Lowland Freshwater Wetlands

As a vegetation type this unit is described as temporarily or permanently flooded restiolands, sedgelands and rush-beds (Mucina *et al.* 2006 a) (Figure 2.7). Within the CoGH, this vegetation type is largely comprised of seasonally flooded restiolands and sedgelands, which occur along very localised and restricted areas (1%). The vegetation structure is generally comprised of a low dense shrubland (Mucina *et al.* 2006).


Figure 2.7: A seasonal wetland within the CoGH, surrounded by adjacent restioland and sedgeland (Colyn 2014).

Peninsula Granite Fynbos

This is a highly localised and restricted vegetation type, occurring across only 2% of the Fynbos Biome and 1 % of the study site, generally found along steep sandstone slopes and undulating hills. Vegetation structure is varied, but is often comprised of tall dense shrubland, that can give way to open to dense tall trees. Subsequently, structural types found within this vegetation type are varied and can include proteoid, restioid, ericaceous and asteraceous types. Waboomveld is also a common occurrence, which can give way to afrotemperate forest if fire is excluded (Rebelo *et al.* 2006).

Cape Seashore Vegetation

Landscape features are largely comprised of beaches, coastal dunes, coastal slacks and cliff lines (Mucina *et al.* 2006). Vegetation generally includes graminoid and dwarf shrub components, which are characterised by pioneer species. Within the CoGH this vegetation type is restricted to a small area of coastal dunes and sandy beaches (Mucina & Rutherford 2006).

2.6. Fire management

Ecologically, fynbos is a fire prone and fire-maintained ecosystem. Fires should be recurrent on a 5 - 50 year rotation, but generally more prominent on a 10 - 30 year rotation (Rebelo *et al.* 2006). Fire frequency can impact on community composition, with overly frequent fires removing serotinous species and favouring resprouting species, whilst longer fire intervals favour obligate reseeding species (Rebelo *et al.* 2006). Natural sources of ignition include rock falls and lighting, however the majority of fire ignition sources in recent times are anthropogenic in nature (Rebelo *et al.* 2006). Furthermore, specific elements of fire occurrence could drive varied changes within the same vegetation community, particularly fire frequency, intensity, season and past fire history (Rebelo *et al.* 2006).

Within the TMNP, conservation management undertake routine controlled burns to obtain a desired fire return period and resultant veld age (Forsyth & van Wilgen 2008). Fire interval directly determines veld age, which has been noted to impact on mammalian herbivore use as certain species favour specific vegetation height, cover or structure thresholds (Boshoff & Kerley 2001). The current veld age within the CoGH varies from 1 to 38 years old (Figure 2.8). The majority (38%) of veld is at an age of between 4 - 8 years, followed by > 24 years (31%), 14 - 23 years (19%), 9 - 13 years (10%) and < 1 year (2%).



Figure 2.8: The recorded veld age during the study period, scaled from oldest (dark green) to youngest (red) vegetation patches (SANParks 2013).

2.7. Fauna

Interactions by large herbivore species, particularly foraging and physical disturbance, are known to change and alter ecosystem properties, particularly vegetation species composition, biomass, production and structure (Rebelo *et al.* 2006) (Figure 2.9). Historically, 42 medium-to-large (> 2 kg) mammalian species were known to occur in the CFR, of which one is now extinct, namely the endemic blue antelope *Hippotragus leucophaeus* (Boshoff & Kerley 2001). Of the remaining 41 species, three are noted as being endemic or near-endemic to the CFR, namely bontebok *Damaliscus dorcas dorcas*, Cape grysbok *Raphicerus melanotis* and Cape mountain zebra *Equus zebra* (Boshoff & Kerley 2001).

Historic records indicate that 23 medium and large mammals potentially occurred on the peninsula, whilst currently it is believed that there are 19 species left within the CoGH (Table 2.2). However, the current status and presence of some species are uncertain as they are known from old records or pooled species lists. Two species with particular uncertainty regarding the current presence within the CoGH include steenbok *Raphicerus campestris* and common duiker *Sylvicapra grimmia*. Furthermore, there is concern on the current status of klipspringer *Oreotragus oreotragus* within the CoGH and reintroduction programmes are currently underway (SANParks 2016).



Figure 2.9: A graminoid dominant grazing lawn established within a restioid fynbos type through consistent grazing pressure by bontebok (Colyn 2016).

No mammal distribution maps exist for the CoGH but the majority of species are thought to occur throughout the area, particularly the medium-to-large antelope and carnivore species (SANParks 2016). However, based on habitat specific preferences, a number of species are

expected to be restricted to local habitat types, marsh mongoose *Atilax paludinosus* and cape clawless otter *Aonyx capensis* are expected to occur along freshwater bodies, rivers and coastlines (Arden-Clarke 1986, Boshoff & Kerley 2001), klipspringer and rock hyrax are expected to occur along rocky outcrops and rugged terrain (Norton 1980, Davies 1994, Boshoff & Kerley 2001), whilst common duiker could be expected in densely vegetation areas within the CoGH (Pienaar 1974, Boshoff & Kerley 2001). However, fine scale distribution and area of occupancy for numerous species are largely unquantified.

Common Name	Scientific Name	Foraging	Regional	
		Group	Status	
Bontebok	Damaliscus pygargus	Herbivore	Vulnerable	
Cape clawless otter	Aonyx capensis	Carnivore	Least Concern	
Cape fox	Vulpes chama	Carnivore	Least Concern	
Cape grysbok	Raphicerus melanotis	Herbivore	Least Concern	
Cape mountain zebra	Equus zebra zebra	Herbivore	Vulnerable	
Caracal	Caracal caracal	Carnivore	Least Concern	
Chacma baboon	Papio ursinus	Omnivore	Least Concern	
Common duiker	Sylvicapra grimmia	Herbivore	Least Concern	
Eland	Tragelapus oryx	Herbivore	Least Concern	
Grey rhebok	Pelea capreolus	Herbivore	Least Concern	
Klipspringer	Oreotragus oreotragus	Herbivore	Least Concern	
Large-spotted genet	Genetta tigrina	Carnivore	Least Concern	
Porcupine	Hystrix africaeaustralis	Herbivore	Least Concern	
Red hartebeest	Alcelaphus buselaphus	Herbivore	Least Concern	
Rock hyrax	Procavia capensis	Herbivore	Least Concern	
Small grey mongoose	Galerella pulverulenta	Carnivore	Least Concern	
Steenbok	Raphicerus campestris	Herbivore	Least Concern	
Striped polecat	lctonyx striatus	Carnivore	Least Concern	
Marsh mongoose	Atilax paludinosus	Carnivore	Least Concern	

Table 2.2: Medium to large terrestrial mammal species still known or thought to occur within the CoGH (SANParks 2016).

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CHAPTER 3:

OPTIMISING CAMERA TRAP SURVEY DESIGN TO ASSESS MEDIUM AND LARGE MAMMAL SPECIES RICHNESS AND DISTRIBUTION IN A FYNBOS ENVIRONMENT

3.1. Introduction

Thorough and accurate estimates of species richness, diversity and distribution of wildlife are essential to effectively guide conservation management strategies, policies and practices (O'Brien 2008, Tobler *et al.* 2008, Roberts 2011). Invasive monitoring techniques (e.g. GPS collars) which involve the capturing and handling of target species are seldom possible for multiple species at large spatial scales, are expensive to purchase and deploy and may also compromise the welfare of the target species (Midlane *et al.* 2014). Non-invasive monitoring techniques are thus considered to be more appropriate for the assessment of multiple species over large geographic ranges (Tobler *et al.* 2008). These include, line transects (Trolle *et al.* 2008, Thomas *et al.* 2009), track and scat surveys (Sadlier *et al.* 2004, Gompper *et al.* 2006, Midlane *et al.* 2014), track plate surveys (Gompper *et al.* 2006), scent post surveys (Gompper *et al.* 2008). Tobler *et al.* 2008). Tobler *et al.* 2008).

Camera traps are considered to be a non-invasive, accurate, efficient, cost effective and easily replicable monitoring technique for estimating species richness and compiling species inventories of medium-to-large terrestrial and semi-terrestrial mammals (Silveira *et al.* 2003, Gompper *et al.* 2006, Ahumada *et al.* 2011, O'Connell *et al.* 2011). Camera trapping or remote photography was pioneered in the early 1880's by George Shiraz on a number of woodland mammal species. The methodology and respective use was further developed throughout the 1900's and applied to numerous studies, habitats and species (Cutler & Swan 1999, O'Connell *et al.* 2011). A significant surge in the use of camera traps in animal ecology followed the development of the infrared flash in the early 1990's, as well as improved construction quality and technology of camera units (Cutler & Swan 1999). This subsequently resulted in camera traps becoming more reliable, compact, portable and generally easier to use in remote areas (Cutler & Swan 1999, Rowcliffe & Carbone 2008, Tobler *et al.* 2008, O'Connell *et al.* 2011).

The application of camera traps in wildlife monitoring and ecology includes the compilation of species inventories (Cutler & Swan 1999, Silveira *et al.* 2003, Srbek-Araujo & Chiarello 2005, Kelly 2008, Srbek-Araujo & Chiarello 2013), assessing activity and habitat patterns (Cutler & Swan 1999, Maffei *et al.* 2002, Silveira *et al.* 2003, Dillon & Kelly 2007, Bridges & Noss 2011), determining species presence and distribution (Cutler & Swan 1999, Ahumada *et al.* 2011, Ahumada *et al.* 2013), population density and dynamics (Cutler & Swan 1999, Karanth *et al.* 2004, Trolle & Kelly 2005, Kelly 2008, Maffei & Noss 2008, Rowcliffe & Carbone 2008), feeding

and foraging dynamics (Cutler & Swan 1999, Harmsen *et al.* 2010, O'Connell *et al.* 2011), as well as aspects of avian nest ecology (Cutler & Swan 1999, O'Connell *et al.* 2011).

Three key elements of camera trap survey design that need to be carefully established prior to surveying are trap placement, trap spacing and trapping period (O'Connell *et al.* 2011, Foster & Harmsen 2012). However, when considering survey design, the question regarding the most efficient trap density, placement and arrangement has rarely been empirically addressed (Gompper *et al.* 2006). A study conducted by Hamel *et al.* (2013) evaluated survey design with regard to camera type utilised, problem-free camera days required and appropriate time intervals needed. The study was however highly specific to habitat type and target species sampled, as it was conducted on arctic scavenger guilds, whereby camera traps were placed at baited survey points during specific seasonal periods.

Trap spacing directly determines the survey gap between cameras and can therefore influence the capture probability of a species and/or specific individuals within a species (O'Brien 2011). The relationship between camera spacing and resultant camera density ultimately determines the survey design dynamics (O'Brien 2011). By allocating trap spacing appropriately, the coverage of the survey area can be efficiently maximised (Foster & Harmsen 2012). Trap spacing has been given specific consideration in the context of studies addressing abundance estimation of a target species, whereby spacing is tailored specifically to the target species and the type of habitat it utilises (Karanth & Nichols 1998, Karanth et al. 2002, Dillon & Kelly 2007, O'Brien et al. 2010). However, trap spacing is also noted as a fundamental consideration for multispecies studies and/or studies utilising occupancy modelling estimators (O'Brien 2008). Additionally, trap placement is known to influence the capture probability of species, whereby targeted placement could bias results towards specific species (O'Brien 2008, Harmsen et al. 2010). When considering multispecies surveys, selecting optimal trap placement for increased capture probability of specific species may result in non-random and biased placement for the detection of other species (Harmsen et al. 2010, Foster & Harmsen 2012).

Studies assessing terrestrial mammalian species richness vary considerably in trap spacing, including < 1 km (Trolle & Kelly 2005, Di Bitetti *et al.* 2014), 1.5 km (Silveira *et al.* 2003), 2 km (Tobler *et al.* 2008) and a varied trap spacing between 1.75 km and > 5 km within the same study (Srbek-Araujo & Chiarello 2013). Similarly, camera trap height varied between 0.3 m and 0.5 m above ground in different studies (Gompper *et al.* 2006, Dillion & Kelly 2007). Camera trap arrays may be linear or grid-based and placement may be stratified, random or optimal for a particular target species (Silveira *et al.* 2003, Tobler *et al.* 2008, Harmsen *et al.* 2010, Ahumada *et al.* 2011, Espartosa *et al.* 2011, Foster & Harmsen 2012). Survey effort in terms

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of camera days also varies greatly (109 to 8 725 days) between studies (Silveira *et al.* 2003, Trolle & Kelly 2005, Tobler *et al.* 2008, Rovero & Marshall 2009, Ahumada *et al.* 2013, Srbek-Araujo & Chiarello 2013, Di Bitetti *et al.* 2014). Clearly there is a lack of standardisation in the use of camera traps across different studies which may in large part be explained by focusing on the different species and/or suites of species and habitat types. This variation has however stimulated debate on the need for a more consistent camera trapping protocol (Cutler & Swan 1999, Dillion & Kelly 2007, Kelly 2008) that will encourage comparisons across study areas for the same species and for diversity estimates in different habitats.

Due to the current lack of standardisation pertaining to camera trapping protocols (spacing and placement), the main aim of this study was to determine the most accurate and efficient camera trap survey design to estimate medium-to-large mammal species (> 0.5 kg) richness and distribution within mesic fynbos shrublands.

More specifically my objectives assessed whether species richness estimates are influenced by:

- a) the spacing of camera's on a grid array at 0.5 X 0.5 km, 1 X 1 km and 2 X 2 km, which equates to camera densities of 25, 9 and 4 per 4km² respectively.
- b) the number of camera days necessary to obtain reliable and representative species richness estimates.
- c) optimising camera placement by positioning cameras in areas with animal sign (within 20 m or 120 m from a particular site on a pre-determined grid array).
- d) the presence and condition of a trail at the camera site.

3.2. Methods

3.2.1. Study Site

This pilot study was conducted within a 4 km² area within the COGH, Table Mountain National Park (Chapter 2). The site fell within the Peninsula Sandstone Fynbos vegetation type, with height above sea level for individual camera points ranging from 70 m to 110 m. To reduce detection probability bias associated with habitat type I attempted to limit habitat heterogeneity, therefore resulting in all cameras excluding one occurring within a single fine scale vegetation community, namely wet restioid fynbos. The remaining camera point was marginally represented within proteoid fynbos, as it was located 70 m from the border of wet restioid fynbos (Figure 3.1).



Figure 3.1: The stratified camera trap grids for both restricted placement (blue dots) and expansive placement (red dots) in predominantly wet restioid fynbos. The dotted circle indicates one camera point that was nullified due to camera loss.

3.2.2. Survey design

3.2.2.1.Camera spacing/density

To enable direct and unbiased comparisons between different grid spacings, a sampling area of 2 x 2 km was populated with 25 Bushnell HD camera traps which were evenly spaced with an oblique distance of 500 m between them. From this grid I could selectively eliminate cameras in a stratified manner to provide richness estimates that cover the same area, over the same time period, but at camera spacingsof 2 x 2 km, 1 x 1 km and 0.5 x 0.5 km apart (Figure 3.2).



Figure 3.2: A schematic representation of the camera trap grid that was established within a 4 km² patch of Peninsula Sandstone Fynbos. The full grid incorporating 25 cameras spaced 500 m apart is shown in A. In B the density of camera traps was reduced to nine (small dots represent grid sites with no camera) by omitting data from 16 cameras and in C the density was further reduced to four cameras by omitting data from 20 cameras.

3.2.2.2.Camera Placement

Two camera positions were used to assess the influence of camera placement, relative to each grid point, on species accumulation curves and estimates of species richness. The first camera placement was restricted to a maximum distance of 20 m from each grid point. The second, which I refer to as expansive, allowed placement to a maximum of 120 m from each designated grid point. Final camera placement positions varied between 10 m and 115 m from respective original GPS grid points.

Camera grid waypoints within the stratified grid were digitised using ArcMAP and located in the field utilising a handheld GPS device with uploaded waypoints. Upon arrival at each grid point, I searched firstly within 20 m and subsequently within 120 m for any sign of animal presence including game trails, grazing lawns, scat and spoor. In order to reduce the bias of placing camera traps for the increased capture probability of specific species, a placement protocol was devised. For the restricted placement protocol, the surveyor walked in a clockwise spiral from the digitised camera waypoint position until the 20 m buffer mark was reached. The camera would be placed at the first area of animal activity that incorporated field signs of more than one species, including tracks, scat, and/or foraging signs (Table 3.1). If no areas were located with activity signs of more than one species, the placement would default to the first area found with signs of at least one species. If no signs of animal activity were found at all within the 20 m buffer, the camera would be placed in an area that provided the least obscured detection arc in terms of vegetation, as well as elements of potential animal interest (rivers, streams, trail, opening/funnel in dense vegetation, etc.). For the more expansive placement protocol, the same criteria were utilised, but a clockwise spiral was walked until the 120 m buffer was reached. The more expansive approach hypothetically increases the chance of

discovering a placement with multiple mammal signs. I categorised signs of animal presence according to four levels (Table 3.1) and always attempted to position the camera at a level 4 site for both 20 m and 120 m buffer zones. For each camera trap site, I further categorised the trail type (Table 3.2) and recorded the strength of animal sign and proximity to point/s of interest observed (stream, rocky outcrop, drainage line, none).

Table 3.1: The four different categories of animal sign that were recorded within the surveygrid where 1 = no sign and 4 = clear sign of mammal presence.

Level	Criteria
1	Trail and/or animal sign not present - no scat and spoor present.
2	Trail and/or animal sign established, but not well utilised - old or minimal scat and
	spoor present.
3	Well established trail and/or animal sign with fresh scat and/or spoor present.
4	Well established trail and/or animal signs with fresh scat and/or spoor of 2 or more
	species.

Feature	Approximate	Definition		
	width			
Management	2 – 3 m	An anthropogenic trail established to accommodate		
Track		vehicle access through vegetation, either in use or		
		disused.		
Hiking Trail	0.3 – 1.0 m	An anthropogenic trail established for recreational use by		
		hikers, generally accommodating single file hiking.		
Game Trail	0.1 – 1.0 m	A trail establish through continual animal use, varying in		
		size relative to the associated species and densities		
		utilising the trail.		
None	N/A	N/A		

Table 3.2: The classifications of features used to define the area of animal activity.

Camera traps were secured to wooden stakes at a height of 0.3 m from the ground surface (Figure 3.3) to improve the detection of smaller species (e.g. mongoose). Vegetation obscuring the camera detection arc was cropped in a 2 m arc in front of each camera to reduce false trigger rates associated with wind driven vegetation movement (Swan *et al.* 2004, Kelly 2008, Tobler *et al.* 2008). Camera placement did not include any form of baiting. Camera settings included a 30 second delay or interval between trigger events, three photographs per trigger event and both the sensor and flash sensitivity set to high. Infrared flash was used to provide minimal disturbance to animals, whilst additionally reducing the risk of human theft. High speed Lexar SD cards (class 10) were used to store images. Cameras were left to survey for 69

consecutive days within one season, namely winter. Winter was chosen as it was the first available season to conduct the surveys in, whilst also potentially providing less excessively windy days (South African Weather Service 2015) and therefore potentially lower false trigger rates. Surveys commenced on the 13 of May 2013 and were completed by 21 July 2013.



Figure 3.3: Robin Colyn fixing a camera trap to a wooden stake at a height of 0.3 m in wet restioid fynbos (Colyn 2013).

3.2.3. Data analysis

SD cards were downloaded twice during the study (after 30 days and at the end of the study) and processed using the software CameraBase (Tobler 2003). Consecutive photographs of the same species at a given camera station were deemed independent if photographs were taken > 1 hour apart (Bowkett *et al.* 2007, Tobler *et al.* 2008). The final dataset was filtered to only include terrestrial mammal species with an average adult weight (Skinner & Chimimba 2006) of more than 0.5 kg. Thus all small mammal and rodent species, except porcupine *Hystrix africaeaustralis*, were excluded from analyses. Each species was also classified according to foraging group and weight class using Skinner and Chimimba (2006). Weight classes delineated small (< 5 kg), medium (< 20 kg) and large (> 20 kg) species across herbivore, carnivore and omnivore foraging groups (Skinner and Chimimba 2006). Capture frequency, defined as the number of sightings of a given species per 1 000 camera days, was determined for each species.

Species accumulation curves were compiled for both restricted and expansive camera placement protocols at each of the three camera densities (25, 9 and 4 per 4 km²). The curve reached an asymptote when all focal species were recorded (Tobler *et al.* 2008). EstimateS

was used to compile sample-based rarefaction curves, with 1 000 randomisation runs (Colwell *et al.* 2004, Tobler *et al.* 2008). Species richness data for survey efforts of four and nine cameras per four km² yielded a Chao's estimated CV of incidence distribution that were greater than 0.5 (0.85 and 0.56 respectively). This necessitated the use of Chao's classic estimator as opposed to the bias corrected option. Survey effort of 25 cameras per four km² yielded a Chao's estimated CV of incidence substantiating the use of the bias corrected option of less than 0.5, therefore substantiating the use of the bias corrected option in data analysis (Colwell 2006).

Three approaches can be utilised to account for undetected species, namely the use of parametric species abundance distribution estimators, nonparametric species richness estimators and the extrapolation of compiled species accumulation curves (O'Connel *et al.* 2011). The survey was conducted within one season and consequently I used non-parametric species richness estimators under the assumption that community composition remained the same, i.e. closed-community, and that variation in detection probability was minimal (Chao 2004). I used non-parametric incidence-based estimators including Incidence-based Coverage Estimator (ICE), Chao 2, first-order Jackknife (Jack 1) and second-order Jackknife (Jack 2) to estimate species richness. The relationship between trail condition at each site and species richness was assessed using Spearman's rank correlation.

3.3. Results

3.3.1. Species richness and capture frequency

The camera trap survey yielded a total of 29 847 photos over the 69 day survey period. The survey was expected to yield a total survey effort of 3 450 camera days, but one camera station on the restricted placement grid was not retrieved due to removal by either a chacma baboon (*Papio ursinus*) or a human (Figure 3.1). In order to prevent bias in the comparative data analysis between grids (expansive and restrictive), the associated expansive camera positioning data at the respective grid point was removed to equalize survey effort per grid type. Subsequently, the resultant survey effort for the study was 3 312 camera days, or 1 656 camera days per grid type (i.e. expansive and restrictive grids). Of the total photos captured, 1 146 (3.84%) were of animals, whilst 28 701 (96.16%) were false trigger events. Of the animal triggered events, 897 (78.27%) were of target species (medium and large mammals), whilst 249 (21.73%) were of non-target species (Table 3.3 and Appendix 1).

Camera trap survey	Positioning type		
	Expansive	Restricted	
Total number of photos captured	7 338	22 509	
Total number of trigger events	2 446	7 503	
Number of false trigger photos	6 591	22 110	
Number of false trigger events	2 197	7 370	
Number of animal triggered photos	747	399	
Number of target species trigger events	187	112	
Number of non-target species trigger events	62	21	

Table 3.3: A summary of the trigger events and photographs taken across the entire camera trap survey for both the restricted and expansive camera placement protocols.

A total of 299 independent large mammalian sightings were recorded, comprising 13 mammalian species in seven different families (Table 3.4). The most frequently recorded species' were bontebok (*Damaliscus pygargus pygargus*) (n = 115), red hartebeest (*Alcelaphus buselaphus*) (n = 42) and chacma baboon (n = 34). The least frequently recorded species were eland (*Tragelapus oryx*) (n = 2), porcupine (*Hystrix africaeaustralis*) (n = 1) and large-spotted genet (*Genetta tigrina*) (n = 1). Two recorded mammalian species were excluded from analysis as they were both small rodent species (< 0.5 kg), namely vlei rat (*Otomys irroratus*) and four-striped field mouse (*Rhabdomys pumilio*). Additionally, 10 avian species and one reptile species were recorded during the survey period (Appendix 1).

Table 3.4: The number of sightings and capture frequency (sightings/1 000 camera days) for each mammal species (> 0.5 kg) that were recorded in the restricted and expansive camera placement protocol survey. R = restricted, E = expansive.

	Species		No of		Capture	
		Common Name	Sightings		Frequency	
Order & Family			Placement		Placement	
			Туре		Туре	
			R	Е	R	E
<u>Carnivora</u>						
Felidae	Caracal caracal	Caracal	1	9	0,6	5,4
Canidae	Vulpes chama	Cape fox	8	12	4,8	7,2
Viverridae	Genetta tigrina	Large-spotted genet	0	1	0	0,6
	Galerella	Small grey	4	0	24	5 /
	pulverulenta	mongoose	4	9	2,4	5,4
	Atilax paludinosus	Marsh mongoose	0	5	0	3,0
<u>Artiodactyla</u>						
Povidoo	Raphicerus	O an a survey back	2	4	1 0	2.4
Bovidae	melanotis	Cape grysbok	Z	4	۲,۷	∠,4
	Palea capreolus	Grey rhebok	6	20	3,6	12,1
	Damaliscus	Bontobok	45	70	27.2	123
	pygargus pygargus	DOMEDOK	40	10	21,2	42,5
	Alcelaphus	Red bartebeest	18	24	10.9	14 5
	buselaphus	Red Hartebeest	10	27	10,0	14,0
	Tragelapus oryx	Eland	1	1	0,6	0,6
Perissodactyla						
Equidae	Equus zebra	Cape mountain zebra	10	14	6,0	8,5
Primates						
Cercopithecidae	Papio ursinus	Chacma baboon	17	17	10,3	10,3
Rodentia						
Hystricidae	Hystrix africaeaustralis	Porcupine	0	1	0	0,6

3.3.2. Camera placement – Restricted vs. expansive grids

Species richness estimates were higher for the expansive camera placement method (n = 13) compared to the restrictive placement (n = 10). Average capture frequencies (8.7 vs. 5.2) and the total number of sightings (187 vs. 112) were also higher for expansive versus restricted placements (Table 3.3, Table 3.4 and Figure 3.4). Three species, namely marsh mongoose, porcupine and large-spotted genet, were only detected on the expansive grid.

These patterns remained consistent with variation in camera trap density and the mean number of species recorded per camera station was significantly higher (T = -2.36, p = 0.023, n = 24) for expansive (mean = 2.92 ± 1.5) versus restricted (mean = 1.96 ± 1.3) placement. Furthermore, of the total 9 567 false trigger events, 7 370 (77%) were recorded on the restricted grid, whilst only 2 197 (23%) were recorded on the expansive grid.



Figure 3.4: A comparison of the total number of species detected with time using the expansive (solid line) and restricted (dashed line) camera trap placements (EstimateS).

3.3.3. The effects of animal sign

More placement sites with prominent animal signs could be located using the expansive (mean = 2, max = 4) versus restricted (mean = 1, max = 3) camera trap placement protocol (Figure 3.5). Similarly, the average number of species recorded per camera trap was higher for the expansive placement (avg. = 3, max = 6) when compared to the restricted placement (avg. = 2, max = 4) (Figure 3.5). The number of species recorded was strongly correlated to the quality of animal sign present for both the expansive (R = 0.82, p < 0.0001, df = 19) and restricted (R = 0.85, p < 0.0001, df = 19) grids. Similarly, both grey rhebuck (R = 0.66; p = 0.01, df = 12) and Cape mountain zebra (R = 0.62, p = 0.05, df = 8) yielded strong positive correlations with sign quality. Species that yielded lower linear correlations included bontebok, red hartebeest

and small grey mongoose, whilst the remaining species either did not yield any linear correlations or had insufficient data to run correlation tests.



Figure 3.5: The relationship exhibited between camera placement types (restricted and expansive), species richness and strength of animal sign.

3.3.4. Camera density and survey effort

The overall shape of the rarefaction curves varied greatly with camera trap density (Figure 3.6). Only at the highest camera density (cameras spaced 0.5 km apart) did the species rarefaction curve show signs of reaching an asymptote (ca. 1 000 camera days or 40 survey days). The 95% confidence interval for this grid varied between ± 0.95 to ± 2.72 species, but averaged at approximately ± 2.54 species in the latter half of the survey (Figure 3.6 a).

When survey effort was reduced to include a 1 km camera spacing, i.e. nine cameras per 4 km², the rarefaction curve seemed to commence smoothing-off towards the end of the survey period at approximately 585 camera days or 65 survey days, but no asymptote was reached (Figure 3.6 b). The respective confidence coefficient varied between ± 0.45 and ± 1.93 species during the survey period. Conversely, the 2 km grid spacing, i.e. four cameras per 4 km², yielded no asymptote or appropriate curve due to insufficient survey effort and resultant camera days (Figure 3.6 c). This is further supported by the respective confidence coefficient, which increased consistently throughout the survey period.

However, when different camera spacings were expressed over the same survey effort (camera days), similar trends and species richness estimates were obtained (Figure 3.6 d). At 250 camera days, all three grids produced between 7.31 and 8.07 species, whilst at 600 camera days the 1 km and 0.5 km grids produced 9.9 and 10.7 species respectively.



Figure 3.6: Rarefaction graphs with 95% confidence intervals for expansively placed cameras at a) 0.5 km spacing, b) 1 km spacing and c) 2 km spacing. d) Rarefaction graphs of all three camera spacings(a, b and c) expressed over the same survey effort (camera days).

First order and Second order Jackknife estimators reached an asymptote after 500 camera days at the highest camera trap density (0.5 km spacing), whilst Chao 2 and ICE estimators yielded almost identical results at higher survey efforts, viz., 900 camera days (Figure 3.7 a). Additionally, Chao 2 and ICE estimates were similar to the observed species accumulation trend and provided closer estimates of species richness (13.5 and 14 species respectively) than either Jack 1 or 2 (14.97 and 15.96 species respectively). Although Jack 1 and Jack 2 resulted in higher estimates of species richness than the observed, a similar overall species accumulation trend was produced.

At a survey effort of nine cameras per 4 km² (1 km spacing) all estimators were higher than the actual observed species richness trend for the first 400 - 500 camera days (Figure 3.7 b). Jack 2 and Chao 2 yielded comparable results with species richness estimates similar to the observed values following 600 camera days. ICE and Jack 1 provided similar results with final species richness estimates of 11.95 and 11.97 species respectively.



Figure 3.7: The observed (actual) and predicted (non-parametric estimators) relationship between species richness and varied camera spacing, including a) 0.5 km spacing, b) 1 km spacing and c) 2 km spacing.

When capture frequency was grouped according to weight class and foraging group, results indicated that the largest weight classes across all respective foraging groups yielded the highest measures of capture frequency (Figure 3.8). This noted relationship was most apparent within the herbivore foraging group, with small herbivores yielding a 90.4% lower capture frequency than that of large herbivores. Although carnivores adhered to this noted relationship as well, the difference was less substantial than that of herbivores, with small carnivores yielding a 25% lower capture frequency that medium carnivores.





3.4. Discussion

3.4.1. Species richness and capture frequency

The results from this study clearly indicate that both camera trap density and placement have a significant effect on species richness estimates. Only cameras spaced at 0.5 km provided rarefaction curves that approached an asymptote within the time frame of the study. Positioning camera traps near good quality animal sign by relaxing the maximum offset from the specified grid points also improved species richness estimates within the survey period. The nonparametric species richness estimators used in this study to account for undetected species, yielded species richness estimates of between 13.5 and 16 species, comprising between 79 - 94% of the total 17 expected species occurring within the CoGH (Figure 3.7). Jack 1 and Jack 2 estimators yielded the closest species richness estimates to that of the expected total species occurring within the study site, whilst additionally performing better than ICE and Chao 2 estimators under lower survey efforts (< 900 camera days). The performance of lower order Jackknife estimators (Jack 1 and Jack 2) in this study concur with findings from a study conducted in tropical forest, whereby Jack 1 and Jack 2 estimators performed the best

out of five estimators assessed at survey efforts exceeding 1 400 camera days (Tobler *et al.* 2008).

Passive infrared camera traps, such as used in this study, are noted to produce less false triggers when compared to active triggered traps (Swan *et al.* 2011). However, this study yielded a significant quantity of false triggers, predominantly attributed to moving vegetation. Although cameras were checked and serviced after 30 days, this was not sufficient to prevent false triggers related to vegetation regrowth within the 2 m detection arc associated with camera points near rivers, streams or seasonal wetlands. A shorter service time interval (Kelly & Holub 2008, Tobler *et al.* 2008) can be applied to curb vegetation regrowth, but would in all likelihood not be practical in light of the required field time and human resource requirements for long term studies (O'Brien *et al.* 2010, Ahumada *et al.* 2011, Rovero *et al.* 2014). Furthermore, the majority of false triggers were associated with vegetation movement beyond the 2 m cleared arc, particularly restiod and graminoid vegetation. The use of time triggered cameras at 10 minute intervals as assessed by Hamel *et al.* (2013) would nullify the number of false triggers. However, due to time triggered cameras being non-selective to animal presence, baiting might be required to produce sufficient captures of target species and it would therefore not be applicable to broad multi species studies (Hamel *et al.* 2013).

3.4.2. Camera placement – Restricted vs. expansive grids

Studies throughout predominantly dense forest habitat have noted that camera placement along areas of animal activity such as trails yield higher rates of capture success of multiple or specific species (Trolle & Kelly 2005, Trolle *et al.* 2008, Harmsen *et al.* 2010, Srbek-Araujo & Chiarello 2013). Similarly, my results yielded greater measures of species richness, capture frequencies and independent animal sightings by relaxing the maximum offset from the specified grid points for all species except eland and chacma baboon which yielded equal capture frequencies irrespective of placement criterion (Table 3.4).

Another factor greatly influencing recorded measures of species richness and capture rates was the presence of a trail and associated quality of animal sign as per the established criterion (Table 3.1 and 3.2). More established trails with a greater quality of animal signs yielded higher measures of both species richness and respective capture rates (Figure 3.5). The relationship exhibited between camera placement, trail presence and increased associated species richness measures have been assessed in other studies and my results corroborate these findings (Silveira *et al.* 2003, Trolle & Kelly 2005, Gompper *et al.* 2006, Harmsen *et al.* 2010, Srbek-Araujo & Chiarello 2013). However, both trail preference and avoidance are documented within some studies (Trolle & Kelly 2005, Tobler *et al.* 2008), particularly where certain prey species (e.g. herbivores) avoid trails and/or roads where large carnivores are

present. One such example indicated trail avoidance by tapir (*Tapirus terrestris*) and trail preference by numerous carnivore species including puma (*Puma concolor*) (Trolle & Kelly 2008). Results from my study do not support any significant trail avoidance, but two species, namely small grey mongoose and red hartebeest, appeared to be relatively impartial to trail presence. The absence of large carnivore species (> 40 kg) within the CoGH is however a notable factor that was true for the above mentioned noted examples of trail avoidance and preference (Trolle & Kelly 2008).

Camera placement also influenced false trigger rates, which were significantly higher for restricted placements. Together, these findings suggest that both species richness estimates and false trigger events can be improved by optimising camera trap placement with respect to signs of animal presence and selecting trails. Furthermore, the cropping of vegetation is widely utilised across studies to reduce false trigger rates (Tobler *et al.* 2008, Trolle & Kelly 2008, Swan *et al.* 2011). Additionally, time-lapse settings have been utilised as a further method to control for false triggers (Trolle & Kelly 2008, Hamel *et al.* 2013).

3.4.3. Camera density and survey effort

Observed species richness estimates at different camera trap densities, but comparable survey efforts, were similar at 275 and 620 camera days (Figure 3.6 d). This suggests that it is not camera density or spacing that is essential to compiling species richness estimates, but rather survey effort in terms of the total survey period and the resultant number of camera days. These findings are in accordance with those from two studies conducted in tropical forest ecosystems with South American mammal assemblages (Tobler *et al.* 2008, Srbek-Araujo & Chiarello 2005). Both studies reported almost identical final species richness estimates across different camera spacings, but similar survey efforts (camera days).

Determining the asymptote in species richness assessments provides an indication of the survey effort required to inventory the majority of species within a given study area (Silveira *et al.* 2003, Rovero *et al.* 2008, Tobler *et al.* 2008, Ahumada *et al.* 2011, Roberts 2011). Studies within forest habitat types in South America have often reached asymptotes between 500 and 1 000 camera days (Tobler *et al.* 2008). Similarly, studies within woodland and grassland habitats reached asymptotes at approximately 400 and 870 camera days respectively (Silveira *et al.* 2003, Roberts 2011). The total species richness results for my study indicated that the majority (> 90%) of recorded species could be detected with a survey effort of approximately 1 000 camera days, which corresponds to a study conducted within south-central Tanzania (Rovero *et al.* 2014). Exceptions were eland, porcupine and large-spotted genet that yielded capture frequencies below one within the study site and therefore required more than 1 000 camera days to be detected. Survey effort required to capture more elusive, wide ranging

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and/or marginally distributed species can increase significantly, as shown in a study conducted by Tobler *et al.* (2008), whereby resultant survey effort could increase by three to six times of that required for more common species.

The noted relationship between body weight/size and detection probability, whereby larger animals exhibit higher detection rates relative to that of smaller animals, was maintained for both the carnivore and herbivore foraging groups recorded in my study. Accordingly, medium carnivore and large herbivore foraging groups yielded higher rates of capture frequency than small carnivores and small herbivores respectively (Figure 3.8). The groups with the highest capture frequencies were large herbivores (> 20 kg) and primates (> 10 kg), which is not only a function of the relative body size of individual animals within each species, but also the respective social organisation exhibited in most species within these groups generally being that of a gregarious nature (Boshoff *et al.* 2001, Tobler *et al.* 2008, Harmsen *et al.* 2010, O'Connel *et al.* 2011). Although body weight/size is a crucial contributor to respective detection probability, there are exceptions as in Silveira *et al.* (2003) whereby certain species yielded capture frequencies contrary to their weight class. Two exceptions within my study that corresponded with these findings were eland and porcupine, which yielded the lowest recorded capture frequencies (Table 3.4).

3.5. Conclusion

Empirical evaluation of the survey design, including camera placement and survey effort, are important for accurate and reliable species richness estimates when commencing large scale surveys. My data confirms that camera trapping is an effective and rapid means of inventorying medium-to-large terrestrial mammals (> 0.5 kg) in a shrubland ecosystem, but that camera placement and survey effort are critical elements of a successful survey design. Appropriate camera placement in terms of placement buffer and targeting areas of animal activity, contributes to more complete species richness estimates as well as significantly reducing the rate of false trigger events. False trigger rates were reduced by 54% by appropriately placing cameras, which would contribute to greatly reduced time spent on data processing and collation.

Attaining the required survey effort in terms of camera days was the most important factor in providing accurate species richness estimates. A minimum of 1 000 camera days was required to record the majority of species present on site, whilst three species could require up to 1 600 camera days to be detected. For the detection of more elusive species, between 1 600 and 3 000 camera days could be required (Tobler *et al.* 2008, Srbek-Araujo & Chiarello 2013). An alternate strategy for capturing very rare species could be to sample at a moderate intensity

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across multiple study sites, compared to sampling intensively at fewer study sites for more common species (MacKenzie & Royle 2005).

Survey design must however be tailored and focused to meet the research objectives. If species inventories are the objective, survey effort should take precedence over camera spacing and number of camera points. Conversely, if occupancy studies are the objective, then the number of camera points, i.e. spatial coverage, can be as important as the resultant survey effort per sample area (MacKenzie et al. 2002). Two assumptions impacting resultant camera spacing that need to be considered during occupancy studies include independence and population closure (O'Connell & Bailey 2011). My results suggest that cameras spaced at 1 km intervals for 55 consecutive days will yield an appropriate measure of survey effort (ca. 4 300) to record both common and rare species, thereby obtaining a reliable estimate of species richness. Furthermore, this 1 km stratified spacing would provide the spatial representation required to determine site occupancy of species present, whilst maintaining independence as well (O'Connell & Bailey 2011). Conducting extensive surveys at a stratified grid spacing of 0.5 km would not only negate independence, but become excessively labour (time) and cost (number of cameras) intensive.

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CHAPTER 4:

SPECIES RICHNESS, DISTRIBUTION AND SITE OCCUPANCY OF MEDIUM AND LARGE TERRESTRIAL MAMMALS IN THE CAPE OF GOOD HOPE, SOUTH AFRICA

4.1. Introduction

Biological monitoring can be defined as the process of gathering data on one or more state variables that influence a given ecosystem, population or community (Yoccoz *et al.* 2001). State variables of biodiversity such as species richness, species diversity, biomass and population size are regularly utilised to evaluate anthropogenic impacts on biodiversity (Yoccoz *et al.* 2001). Similarly, species distributional data, species inventories and habitat associations are three primary aspects relied upon when estimating the biodiversity status within an area (Tobler *et al.* 2008, Ahumada *et al.* 2011). Despite the importance of biological monitoring, particularly for elusive, wide ranging and rare mammal species, there is a lack of data collected at the appropriate scale for determining either the current status or temporal trends for most mammalian communities (Gompper *et al.* 2006, Ahumada *et al.* 2011).

Invasive monitoring techniques employed over large spatial scales, particularly related to wide ranging carnivore species, are usually impractical in terms of associated financial and human resource requirements (Gompper *et al.* 2006). Camera traps allow for a rapid, accurate, non-invasive, easily replicable and cost effective means of data collection, particularly in monitoring medium to large terrestrial mammals (Gompper *et al.* 2006, Tobler *et al.* 2008, Rovero & Marshall 2009, O'Brien *et al.* 2010, Ahumada *et al.* 2011, O'Connell *et al.* 2011). As a survey technique, camera traps are increasingly being utilised to assess the spatial and temporal dynamics of animal populations (Nichols *et al.* 2011). Incorporating occupancy modelling into studies can enable camera traps to assess species occupancy across large spatial scales (Nichols *et al.* 2011). Additionally, occupancy modelling can shed light on numerous other facets of animal ecology, including the assessment of animal distributions, metapopulation dynamics, habitat relationships/responses, resource selection and species interactions (Kery 2011). Additionally, for some species, occupancy can provide a measure of relative abundance and therefore act as a surrogate for abundance estimates (MacKenzie & Nichols 2004).

With replication through long term studies, species richness and occupancy modelling studies can provide crucial insight into the change in conservation status of species, species guilds and community structure (O'Brien *et al.* 2010, Ahumada *et al.* 2013). My study aims to provide a baseline with regard to two state variables, namely species richness and occupancy, within the Cape of Good Hope (CoGH) section of Table Mountain National Park (TMNP), South Africa. The objectives of this chapter were as follows:

- 1. Derive species richness estimates for medium to large mammals in the CoGH through the use of camera traps.
- 2. Conduct occupancy modelling and derive site occupancy estimates for the mammal species recorded within the COGH.
- 3. Compare the capture frequencies and detection probabilities of species and/or species guilds in relation to landscape and environmental variables.

4.2. Methods

4.2.1. Study site

The study site encompassed the entire Cape of Good Hope (CoGH), which is comprised of the southern tip of Table Mountain National Park (TMNP) (Chapter 2).

4.2.2. Survey Design

The survey design with regard to camera spacing in this study was directly informed by the findings presented in Chapter 3. I deployed 82 Bushnell HD Trophy Cam camera traps spaced 1 km apart within a stratified grid across the study site (Figure 4.1). Stratified camera grid waypoints were digitised in ArcMAP 10.3 using the Fishnet tool, which overlaid 1 km² polygons across the study site. The centroid of each polygon was extracted and uploaded onto a handheld GPS so that the site could be located in the field. Data collection took place for 55 days in summer between 16 December 2013 and 16 February 2014.

Cameras were secured to wooden stakes at a height of 0.3 m above the ground to improve the probability of detecting smaller mammals (Kelly 2008). Vegetation was cropped in a 2 m arc in front of each camera in order to reduce false triggers associated with wind driven movement of plants (Swan *et al.* 2004, Kelly 2008, Tobler *et al.* 2008). Camera orientation was adjusted to minimise the period spent facing directly into a sunrise or sunset, as direct light minimises the ability to identify animals photographed due to overexposure.



Figure 4.1: The location of the study site (Cape of Good Hope) including fine scale vegetation types (SANParks 2012) and the sites (black dots) for the 79 camera traps deployed on a 1x1km grid.

Camera sites were not baited and were selected according to the expansive placement protocol devised in Chapter 3. Thus upon arrival at a grid waypoint, I searched for a suitable site by walking in a spiral, outwards from the waypoint as far as a radial distance of 120 m from the waypoint. Cameras were placed at the first area of animal activity encountered that incorporated field signs (spoor, scat or foraging signs) of more than one species (Table 4.1). If no areas were identified with established trails and/or signs of more than one animal species (level 4 criteria), placement would default to the next best respective placement criteria available within the 120 m placement radius.
Table 4.1: The four different categories of animal sign that were recorded within the survey grid where 1 = no sign and 4 = clear sign of mammal presence.

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I	Criteria
1	Trail and/or animal sign not present - no scat and spoor present.
2	Trail and/or animal sign established, but not well utilised - old or minimal scat and
	spoor present.
3	Well established trail and/or animal sign with fresh scat and/or spoor present.
4	Well established trail and/or animal signs with fresh scat and/or spoor of 2 or more
	species.

4.2.3. Data Analysis

Data were downloaded twice during the survey period, namely on day 25 and 55 of the survey. Photographs were collated using the software package Camerabase (Tobler 2003), with consecutive sightings of a given species deemed independent when separated by a one hour time interval (Bowkett *et al.* 2007, Tobler *et al.* 2008). The full dataset was then filtered to include only target species, namely medium to large (> 0.5 kg) terrestrial mammals. Additionally, the capture frequency, defined as the number of independent sightings per 1 000 camera days, was evaluated per species. Each species was also classified according to foraging group and weight class using Skinner and Chimimba (2006). Weight classes delineated small (< 5 kg), medium (< 20 kg) and large (> 20 kg) species across herbivore, carnivore and omnivore foraging groups (Skinner and Chimimba 2006).

Two state variables of biodiversity were assessed, namely species richness and occupancy (Yoccoz *et al.* 2001, MacKenzie *et al.* 2002, O'Brien *et al.* 2010).

4.2.3.1. Species Richness

Species richness estimates, accumulation trends and undetected species were assessed using the software package EstimateS (Pryke & Samways 2009, Tobler *et al.* 2008). Analyses included the compilation of sample-based rarefaction species accumulation curves, as well as the use of non-parametric species richness estimators. Due to the survey taking place within a single season, non-parametric species richness estimators were utilised under the assumption that the community was closed and composition remained the same (no immigration or emigration) (Chao 2004). Non-parametric estimators utilised included Incidence-based Coverage Estimator (ICE), Chao 1, Chao 2, first-order Jackknife (Jack 1) and second-order Jackknife (Jack 2) (Tobler *et al.* 2008). Additionally, Spearman's Rank Correlations were utilised to assess the relationship between capture frequency, average body weight and camera days required to detected a given species.

4.2.3.2.Occupancy

Occupancy, defined as the probability that a given site is occupied by a particular species (O'Connell *et al.* 2011), was assessed using the software package PRESENCE (Kery 2011). PRESENCE utilises presence/absence data, site covariate data such as environmental variables and sample covariate data such as season to model potential species presence across a given geographical range (Kery 2011, O'Connell & Bailey 2011). Species richness data were condensed into the appropriate presence/absence matrices for use within the software package PRESENCE. As the timeframe of our study fell within a single season and assumed community closure, I used the single-season analysis tool to run occupancy analyses. Additionally, the custom model tool was used to accommodate the inclusion of covariates into the analyses.

For this study, only site-specific (sampling point) covariates were included in the analyses and comprised both continuous and categorical data types. Categorical covariates were translated into multiple series' of binary indicator variables depicted as 0 or 1 (MacKenzie 2012). The ideal range for continuous covariate data inputted into PRESENCE is between -5 and +5, therefore all continuous covariate data were standardised according to the z-transformation equation (MacKenzie 2012), depicted as:

$$x_i^* = \frac{x_i - a}{b}$$

Where Xi is the covariate value, a is the mean of the respective covariate dataset and b is the standard deviation of the covariate dataset (MacKenzie 2012). A total of 11 covariates were identified, collated and utilised in occupancy modelling analyses (Table 4.2). Covariates were identified as those primary landscape environmental variables impacting on animal distribution for which data were available (Bailey *et al.* 2004, O'Connell *et al.* 2006, Ahumada *et al.* 2011, Ahumada *et al.* 2013, Rovero *et al.* 2014). Covariates measured in the field at each respective sampling point included vegetation height and trail width. Vegetation height was calculated by taking eight measurements, at one and two meter distances from the camera trap location in a North, South, East and West orientation (Figure 4.2). The vegetation height measurements were recorded in the field using a marked rope (1 m and 2 m distances), a measuring stick (0-150 cm) and a wooden stake for securing the rope at the origin and distal points of sampling (Figure 4.3). Trail width was estimated by measuring the maximum distance across a trail (if present) within the camera trap focal area at respective positions. Trail types measured

included any trail with or without associated animal sign (Table 4.1) and included game trails, footpaths and management tracks.



Figure 4.2: A schematic representation of the protocol used to measure vegetation heights around the respective camera trap points (grey circle). A measurement was taken at one and two meter distances across four different orientations.

All covariates, excluding vegetation height and trail width, were calculated on a landscape level using ArcGIS 10.3 algorithms and analyst tools. These covariates included elevation, slope, vegetation age, distance to permanent fresh water source, distance to coast, distance to human track, broad vegetation type (Mucina & Rutherford 2012), fine scale vegetation type (SANParks 2013) and land cover type (Geoterraimage 2015). Elevation was calculated by creating a Digital Elevation Model (DEM) for the CoGH using the spatial analyst tool within ArcGIS (Appendix 2). Similarly, slope was calculated by creating a digital slope model from the respective DEM using the spatial analyst tool within ArcGIS (Appendix 3).

Covariate Type	Data type	Description			
Vegetation types of Southern	Categorical	Broad vegetation types described by			
Africa	Categorical	Mucina & Rutherford 2012.			
	Categorical	Fine vegetation units within the CoGH			
Fine Scale vegetation units		described by Taylor 1984 and further			
		refined by SANParks.			
Land Cover	Categorical	2013-2014 South African National Land			
	Calegonical	Cover Dataset (GeoTerralmage 2015).			
	Continuous	Vegetation age in relation to fire history,			
Vegetation Age	Continuous	as mapped out by SANParks			
	(years)	Management 2013.			
Vagatation Haight	Continuous	Measured in field (see methods).			
	(cm)				
	Continuous	Digital Elevation Model (DEM) depicting			
Elevation		elevation (m) per pixel/cell of raster			
	(111.a.s.1)	layer.			
Slope	Continuous	Digital slope model depicting slope (°)			
Slope	(degress)	per pixel/cell of raster layer.			
	Continuous	Direct distance from each camera trap			
Distance to Water	(m)	to a freshwater source (River, stream or			
	(11)	dam).			
	Continuous	Direct distance from each camera trap			
Distance to Track		to a mapped anthropogenic track			
		(footpaths and vehicle tracks).			
Distance to Coast	Continuous	Direct distance from each camera trap			
	(m)	to the coastline.			
	Continuous	The width of a trail (anthropogenic or			
Trail Width	(cm)	animal made) measured at each			
		camera trap if present.			

 Table 4.2: Covariates included in occupancy analyses using the software PRESENCE.



Figure 4.3: Vegetation height measurements were taken in the field at each camera point using a marked rope (1 m and 2 m), measuring stick and wooden stake (Colyn 2014).

Analyses were conducted on all species with capture frequencies greater than 2.5 (10 independent sightings over the survey period), as species with very limited data could produce imprecise occupancy estimates (MacKenzie *et al.* 2002). Furthermore, species yielding detection probabilities of less than 0.15 can be problematic in terms of producing accurate occupancy estimates and associated inferences (O'Connell *et al.* 2006). The best model fit per species was determined using the Akaike's Information Criterion (AIC) model selection criteria, which includes AIC, delta AIC, AIC weight and Model Likelihood values (Anderson and Burnham 2002). Occupancy maps per species were created from the finalised PRESENCE results within ArcMap using the Spatial Join and Polygon-Raster Conversion tools.

In the event that specific camera points were compromised through data loss, the 'phantom unit' approach was utilised within PRESENCE to predict occupancy in the absence of presence/absence data (Mackenzie 2012). This approach allows for camera points with compromised data to be inputted into the model with the 'data type' indicated as missing (Mackenzie 2012). The site covariate data for these respective points was still inputted into PRESENCE, thereby allowing for the model to predict occupancy at these respective points based on the relationships exhibited across camera points with presence/absence data (Mackenzie 2012).

Two crucial underlying assumptions to occupancy modelling are closure and independence. Some models accept that there is closure within years or seasons (Ahumada *et al.* 2013). Similarly, some studies accepted independence when cameras were spaced > 1 km apart (O'Connell *et al.* 2006). Because our study includes a camera spacing (1 km) that would be smaller than a number of the recorded species average home range (O'Connell & Bailey 2011), occupancy results were interpreted as the probability that a site was utilised as opposed to the probability that a site was occupied.

4.3. Results

Over the 55 day sampling period, the study accumulated 3 630 camera days of the expected 4510 camera days. Of the 82 camera trap sampling points, only 69 yielded full datasets, with the remaining 13 camera points being interfered with resulting in incomparable survey effort. At the first camera field service period, namely 25 survey days, 19 camera stations (24%) had been disturbed through animal interference. Disturbance included the change of camera orientation (13%), height (8%) and/or the complete removal of the camera trap (4%). The majority of interferences were associated with the chacma baboon (n = 15), but large antelope species also caused interference with red hartebeest (n = 1), bontebok (n = 1) and eland (n = 1)1) each disturbing camera operations. Data loss on the respective camera stations varied between 5 and 25 camera days, which resulted in them having to be resampled for the respective duration. Although selected and short term resampling was initiated to control for data loss associated with animal/human interference, 13 camera trap sampling points experienced extensive data loss and were therefore omitted from analyses. Furthermore, the respective omitted camera trap sampling points resulted in a total data loss of 713 camera days (16.5%) and associated camera trap loss of nine units. Figure 4.4 displays the final layout of cameras yielding full survey effort and reliable datasets.

A total of 6501 images of target animal species was recorded, of which 2 167 images were considered independent animal sightings of target species. A resultant mean sighting density of 32.8 (s.d. = 52.7) and a range of 0 - 358 sightings per camera trap was recorded. Of the 19 medium to large terrestrial mammal species thought to occur within the CoGH, 16 (84%) were recorded during the study (Table 4.3). The mean number of species recorded per camera trap was 4.15 (s.d. = 1.64), with an associated range of 0 - 8 species. Similarly, the number of sightings per species and associated capture frequency varied greatly, with sightings per species ranging from 1 - 730 and capture frequency ranging from 0.28 - 201.10 per 1 000 camera days (mean = 37.2, s.d. = 60.8). A total of 16 non-target species were also recorded, including predominantly avian species (n = 14) (Appendix 4).

Table 4.3: All medium to large mammal species recorded throughout the study, with associated numbers of sightings, capture frequencies and foraging groups. SC = small carnivore, MC = medium carnivore, SH = small herbivore, LH = large herbivore & Om = omnivore.

Order & Family	Species	Common Name	Number of Sightings	Capture Frequency	Forag- ing group
Carnivora					
Felidae	Caracal caracal	Caracal	43	11,85	MC
Canidae	Vulpes chama	Cape fox	10	2,75	SC
Viverridae	Genetta tigrina	Large-spotted genet	22	6,06	SC
	Galerella pulverulenta	Small grey mongoose	51	14,05	SC
	Atilax paludinosus	Marsh mongoose	1	0,28	SC
	Aonyx capensis	Cape clawless otter	1	0,28	МС
Artiodactyla					
Bovidae	Raphicerus melanotis	Cape grysbok	33	9,09	SH
	Sylvicapra grimmia	Common duiker	1	0,28	SH
	Oreotragus oreotragus	Klipspringer	12	3,31	SH
	Palea capreolus	Grey rhebok	43	11,85	LH
	Damaliscus pygargus	Bontebok	730	201,10	LH
	Alcelaphus buselaphus	Red hartebeest	227	62,53	LH
	Tragelapus oryx	Eland	540	148,76	LH
Perissodactyla					
Equidae	Equus zebra zebra	Cape mountain zebra	33	9,09	LH
Primates Cercopi- thecidae	Papio ursinus	Chacma baboon	369	101,65	Om
Rodentia					
Hystricidae	Hystrix africaeaustralis	Porcupine	48	13,22	SH



Figure 4.4: The final camera trap layout across the COGH, with lost data points indicated as white dots.

Rarefied species accumulation curves showed that an asymptote was reached at approximately 880 days with a resultant species richness total of 13 species, which incorporated 81% of the total species recorded (Figure 4.5). Species requiring a greater measure of survey effort included common duiker, marsh mongoose and Cape clawless otter. Of these species, common duiker required > 1 000 camera days, whilst both marsh mongoose and Cape clawless otter required more than > 3 000 camera days. All non-parametric species richness estimators, excluding Jack 2, produced almost identical accumulation trends and sample means (p = 0.33, f = 1.14, f crit = 2.64) after 385 camera days (Figure 4.6). Final species richness estimates for ICE, Chao 1, Chao 2, Jack 1 and Jack 2 was 19.41, 19.00, 18.95, 18.95 and 21.86 respectively. All estimators produced species richness estimations higher than the observed number of species, but were closer to the expected number of species (n = 19) than the observed value (n = 16). ICE, Chao 1, Chao 2 and Jack 1 performed the best under the specific survey effort, whilst Jack 2 produced a final estimate 26.8% higher than the observed value.



Figure 4.5: Rarefied species accumulation curve with 95% confidence intervals.



Figure 4.6: The actual and predicted relationship between four non-parametric species richness estimators calculated using EstimateS.

Estimated mean occupancy across species for the CoGH was 0.41 with a range of 0.10 - 0.72 (s.d. = 0.21), with estimates for five species (31%) falling below 0.3 (Table 4.4). The species yielding the highest occupancy estimate was chacmca baboon (psi = 0.72), whilst the species with the lowest estimate was klipspringer (psi = 0.10). Detection probability within the CoGH under the respective study design was high with a mean estimate of 0.78 (s.d. = 0.25) per species. Out of the total of 16 species recorded, three were omitted from occupancy analyses

due to very low capture frequencies and detection probabilities (O'Connell *et al.* 2006), namely Cape clawless otter, marsh mongoose and common duiker. Of the 13 species included in occupancy analyses, all responded well to occupancy models with covariates, producing AIC weights greater than 0.1 (Table 4.4, Figures 4.7, 4.8, 4.9, 4.10, 4.11 & 4.12).

Two species, namely bontebok (VegHeight β -1.80, Elev β -0.99) and eland (VegHeight β -1.98, Elev β -0.64), responded most strongly to elevation and vegetation height, with occupancies decreasing significantly with an increase in both vegetation height and elevation. Cape fox occupancy increased with distance from the coast (Coast β 1.74), whilst as the only medium-sized carnivore, caracal occupancy increased with the presence of anthropogenic tracks (Track β -0.59), and trail diameter (Trail β 1.30). Two antelope species, namely Cape grysbok and red hartebeest, showed sensitivity to broad and fine scale vegetation types respectively, whilst Cape grysbok occupancy decreased with distance from water source (Water β -0.98). Chacma baboon occupancy increased with specific land cover types (shrubland, thicket/dense bush and wetlands) and decreased with distance from anthropogenic tracks (Track β -0.57). Cape mountain zebra occupancy responded negatively to slope (Slope β -3.15) and positively to distance from coast (Coast β 1.28), but more strongly to slope than coast. Grey rhebuck occupancy responded negatively to veld age, with occupancy decreasing with veld age (Veld Age β -76.04). Klipspringer occupancy responded very strongly and positively to slope (Slope β 140.84) and elevation (Elev β 179.70), whilst porcupine responded negatively to distance from coast (Coast β -4.22) and positively to vegetation age (Veld Age β 1.67). Small-grey mongoose occupancy responded positively with slope (Slope β 2.00) and negatively with distance from trail (Trail β -0.97). Lastly, large-spotted genet responded positively to both elevation (Elev β 2.41) and trail diameter (Trail β 1.17). Occupancy maps were created for all 13 species with modelled occupancy estimates (Figures 4.7, 4.8, 4.9, 4.10, 4.11 & 4.12).

Table 4.4: Summary of the occupancy model results per species analysed. Model Covariates: Elev = Elevation, VegHeight = Vegetation height, Coast = Distance from coast, Trail = Trail diameter, Track = Distance from track, Lcov = 2013/2014 SA Land Cover, Sanbi = 2012 SANBI Vegetation Types, Water = Distance from water source, Slope = Slope, VeldAge = Vegetation age and Finevegtype = Fine scale vegetation map for the CoGH.

							Mean
							Occu-
				Model	No.		pancy
			AIC	Likeli-	of	-2*Log	Estimate
Species	Model	AIC	weight	hood	Par.	Like	(Psi)
Bontebok	psi(Vegheight+Elev),p (.)	66,53	0,5586	1	4	58,53	0,66
Cape fox	psi(Coast),p(.)	36,46	0,3523	1	3	30,46	0,12
Caracal	psi(Trail-Track),p(.)	59,46	0,4187	1	3	51,46	0,21
Baboon	psi(Lcov+Track),p(.)	76,8	0,1184	1	7	62,8	0,72
Cape grysbok	psi(Sanbi+Water),p(.)	76,32	0,2748	1	7	62,32	0,29
Cape mountain	noi/Slang (Capat) n()	41.00	0.501	1		22.06	0.17
zebra		41,00	0,501	I	4	33,00	0,17
Eland	psi(Vegheight+Elev),p (.)	76,42	0,4561	1	4	68,42	0,60
Grey rhebuck	psi(VeldAge),p(.)	77,08	0,3505	1	3	71.08	0,81
Klipspringer	psi(Slope+Elev),p(.)	17,56	0,6964	1	4	9,56	0,10
Large-spotted genet	psi(Elev+Trail),p(.)	64,38	0,2783	1	4	56,38	0,47
Porcupine	psi(VeldAge+Coast),p (.)	56,8	0,5714	1	4	48,8	0,41
Red hartebeest	psi(Finevegtype),p(.)	87,19	0,2088	1	8	71,19	0,53
Small grey mongoose	psi(Slope+Track),p(.)	79,79	0,2086	1	4	71,79	0,60



Figure 4.7: Mapped occupancy results for all small herbivore species assessed, namely porcupine, cape grysbok and klipspringer.



Figure 4.8: Occupancy maps for all large bovidae herbivore species assessed, namely eland, grey rhebuck, bontebok and red hartebeest.



Figure 4.9: The occupancy map for the only large equidae herbivore species assessed, namely cape mountain zebra.



Figure 4.10: Mapped occupancy results for all small carnivore species assessed, namely cape fox, small grey mongoose and large-spotted genet.



Figure 4.11: Mapped occupancy results for the only medium carnivore species assessed, namely caracal.



Figure 4.12: Mapped occupancy results for the only omnivore species assessed, namely chacma baboon.

Capture frequency correlated positively (Spearman's r = 0.50, p = 0.49, df = 14) with predicted body weight (Figure 4.13) across all species. Within our study, the relationship between capture frequency and camera days required was significant (Spearman's r = -0.78, p < 0.001, df = 14) (Figure 4.14). Three of the four species with the highest rates of capture frequency (bontebok, eland and red hartebeest), were also the three species with the highest average body weights (Table 4.3). Chacma baboons were the third most captured species (c.f. = 101.65, mean = 37.2), despite having a relatively small body weight (12 - 45 kg). Species yielding capture frequencies below two required a survey effort of between 1 188 and 3 630 camera days.



Figure 4.13: The relationship displayed between body weight (kg) and capture frequency (sightings/1 000 camera days).



Figure 4.14: The noted relationship between capture frequency and resultant camera days required to obtain a sighting of a given species.

4.4. Discussion

Our results suggest that camera traps are an effective and rapid means of compiling species inventories and obtaining species richness estimates of medium to large terrestrial mammals in a shrubland habitat type. Numerous studies conducted across varied ecosystem types, including tropical forests (Srbek-Araujo & Chiarello 2005, Tobler *et al.* 2008, Ahumada *et al.* 2011, Espartosa *et al.* 2011, Ahumada *et al.* 2013), temperate forests (O'Connell *et al.* 2006, Kelly & Holub 2008), forest clearings (Gessner *et al.* 2013) and grasslands (Silveira *et al.* 2003) all support the efficiency of camera traps in compiling robust species inventories. Of the total species recorded within our dataset, 81% were recorded within 900 camera days, whilst the remaining three species (Cape clawless otter, marsh mongoose and common duiker) were rare with very low capture frequencies and are restricted to marginally sampled habitat types.

The Cape clawless otter and marsh mongoose, are both semi-aquatic carnivores known to favour well established perennial rivers with boulders and reed-beds, as well as coastal areas in the case of the Cape clawless otter (Whitfield & Blaber 1980, Arden-Clarke 1986, Somers & Nel 2004). Similarly, the common duiker, can inhabit a wide range of habitat types, but favours dense habitats including woodland, thicket and shrubland (Pienaar 1974), with the only sighting occurring adjacent to an isolated patch of forest habitat.

Our cameras successfully recorded 84% of the species thought to occur in the area. The exceptions were rock hyrax *Procavia capensis*, striped polecat *Ictonyx striatus* and steenbok *Raphicerus campestris*. Rock hyrax and striped polecat are both relatively small bodied animals (average < 3 kg), with rock hyrax inhabiting steep, rocky outcrops with adjacent low to medium structured vegetation (Kotler *et al.* 2002, Davies 1994). The current presence of steenbok within the CoGH is unconfirmed as the species has not been observed in numerous years (J. Buchman *pers comm.*). The study did however record a similar sized sympatric species, namely Cape grysbok. When considered in conjunction with the above noted absence of sightings, it could be presumed that steenbok is possibly absent from the study site.

Lower order Jackknife estimators, followed by the Chao 1, Chao 2 and ICE estimators, have been found to produce better results under larger survey efforts (> 1 000 camera days) (Tobler *et al.* 2008). Likewise, in the same study, high order Jackknife estimators performed poorly following 1 000 camera days. Our study confirms that ICE, Chao 1, Chao 2 and Jack 1 all performed well after 300 camera days and produced a final species richness estimate almost identical to the expected total based on species lists for the study site. The value of non-parametric species richness estimators is further evident in that Jack 1 and Jack 2 species richness results from the pilot survey (Chapter 3) conducted in 2013 were 14.97 and 15.96 respectively. Therefore, results from non-parametric species richness estimators from a 4 km²

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plot within the greater study site yielded between 93.5 and 99.8 % of the total species recorded in the full survey across the entire study site.

The species with the lowest mean occupancy estimate (psi = 0.10), klipspringer, is also the species that had the most restricted occupancy distribution across the CoGH (Figure 4.6). This is largely due to the preferred habitat of klipspringer, namely rocky mountainous terrain, which is confined to the northern and north-eastern periphery of the CoGH (Chapter 2) (Appendix 2 and 3) (Norton 1980). Of the four species responding positively to either the presence of a trail nearby or the associated diameter of the trail, three were carnivores (viz. caracal, large-spotted genet and small-grey mongoose, Table 4.4). The general preference of trails by carnivore species has been documented both locally for leopards (Balme *et al.* 2009) and globally for medium to large species such as jaguar *Panthera onca*, puma *Puma concolor*, ocelot, jaguarondi *Herpailurus yagouaroundi* and crab-eating fox *Cerdocyon thous* (Harmsen *et al.* 2010, Di Bitetti 2014).

Large herbivores, particularly grazers, are known to exhibit a preference for younger veld within fynbos habitats (Kraaij & Novellie 2010). My results supported this with Bontebok showing strong selection for veld less than two years old, red hartebeest a preference for two year old veld and Cape mountain zebra and grey rhebuck preferring veld up to four years old. The negative response to vegetation height by bontebok in my data further confirms the respective foraging preference of this species being that of shorter and younger veld (Kraaij & Novellie 2010). Through a negative occupancy response to veld age, grey rhebuck displayed a strong (β -76.04) preference for younger veld as well.

Detectability or also called detection probability (p) addresses a significant source of variation in occupancy studies (O'Connell & Bailey 2011). It can be defined as estimating the probability of detecting a species at survey points where it was not recorded, given it occurs at the respective site (MacKenzie *et al.* 2002, O'Connell & Bailey 2011). My study yielded a high mean measure of detection probability (p = 0.78, s.d. = 0.28), as well as a number of high individual species estimates of detection probability. A study conducted by Ahumada *et al.* (2011) in tropical forests yielded a much lower mean detection probability of 0.058, whilst a study conducted in temperate forests by O'Connell *et al.* (2006) also yielded a lower mean detection probability (O'Connel *et al.* 2011). My study was conducted extensively across the entire fenced CoGH, whilst also being conducted intensively at a 1 km stratified camera spacing. This respective survey effort could have resulted in higher measures of detection probability when compared to other studies cited above.

Two species yielding very high detection probabilities (p = 1), namely chacma baboon and red hartebeest, are both gregarious and well represented within the CoGH (Figures 4.6 and 4.11) and in the case of red hartebeest one of the largest mammals present (Table 4.3). Conversely, two species yielding high detection probabilities, namely Cape fox and klipspringer, were neither large bodied or gregarious. However, based on presence data recorded for these species across both the 2013 pilot study (Chapter 3) and this study, both species had spatially confined and clustered data points. It is therefore postulated that the localised habitat preference of these species resulted in higher occupancy estimates. Klipspringer was only recorded in steep, mountainous sections of the CoGH, whilst cape fox was largely recorded within wet restioid fynbos across the central valley of the CoGH.

An important factor influencing the detection of a species is spatial variation and coverage of camera traps within a given study site (O'Connell *et al.* 2011). My study, with the use of 1 km² camera spacing, surveyed the majority of the total area within the study site. The use of a survey design that sampled both extensively and intensively may explain the high levels of detection probabilities and occupancy estimates in my study (MacKenzie *et al.* 2002, MacKenzie & Royle 2005).

The positive correlation (Spearman's r = 0.53 p = 0.49, df = 14) between body mass and capture frequency recorded within my study is similar to previous studies (Wemmer *et al.* 1996, Carbone *et al.* 2001, Silveira *et al.* 2003, Tobler *et al.* 2008) across varied animal communities. A primary factor influencing capture frequency in relation to increased body weight is the sensitivity of the camera trap infrared sensors to large bodied mammals (Kucera & Barrett 2011). Larger bodied animals emit a greater heat signature which increases the probability of triggering the infrared sensor at further distances when compared to small bodied animals (Kucera & Barrett 2011). Capture frequency also increased with the number of camera days as predicted by Tobler *et al.* (2008). Studies that incorporate species that are wide ranging, elusive, niche specific and/or have smaller average body weights should structure the survey design to maximise potential capture probability and resultant detection probability.

Adaptations to survey design could include surveying more extensively (MacKenzie & Royle 2005, O'Brien 2011), surveying more intensively (Tobler *et al.* 2008, O'Brien 2011), targeting camera placement to specific environmental features (Harmsen *et al.* 2013, Di Bitetti *et al.* 2014), baiting camera traps for selected species (Hamel *et al.* 2013), adapting camera placement height (Trolle & Kery 2003, Dillion & Kelly 2007) and selecting specific camera trap models (Kely & Holub 2008, Meek & Pittet 2012). My study also highlighted the challenges of surveying in an area with a relatively large number of chacma baboon troops and other large mammal species. Animal interference with camera traps resulted in a 15.6% data loss across

12 camera locations. Modifying camera placement to include a deeper placement of wooden stakes, using cable ties and/or adhesive tape in conjunction with the standard camera trap strap and using camera trap protective boxes if feasible could reduce interference and associated data loss.

4.5. Conclusion

My data clearly indicates that camera traps are an efficient and rapid means of compiling accurate species richness estimates as we managed to record 16 species in 55 days, which accounts for 84% of the total species thought to occur within the study site. It is possible that both the striped pole cat *lctonyx striatus* and steenbok are now extinct within the reserve as there have been no other sightings of either species for many years. Rock hyrax are however known to occur within the broader TMNP, but their range is restricted to select rocky outcrops within small portions of the reserve which may have been missed by the camera array. Thus the most optimistic outcome of the survey is that 94% (16 out of 17 spp.) of species that are known to occur within the reserve were detected. However, it is important to note that all species richness estimators produced estimates that were higher than the observed number of species and closer to the expected number of species (n = 19) for the reserve. This suggests that some species are either exceptionally rare or unlikely to be detected within the parameters of this survey (1 x 1 km grid for 55 days).

Importantly the species richness estimate from chapter 3 was 13 or 81% of the species detected in the full array despite covering only 5.3% of the total area covered by the large array. Furthermore, two of the species that were missing (Cape clawless otter and marsh mongoose) are niche specialists (freshwater and intertidal) that could not have been detected in the site chosen for chapter 3 (homogenous, flat and inland). Thus rather remarkably the spatially restricted sampling protocol (Chapter 3) within the reserve detected 13 out of 14 (92%) possible species for that habitat type. Although camera traps are recognised as a rapid means of inventorying terrestrial mammals (Silveira *et al.* 2003, Tobler *et al.* 2008, Ahumada *et al.* 2011, Ahumada *et al.* 2013), my data confirms that the survey effort required to confirm species with capture frequencies dropping below three, increases drastically (Figure 4.13).The application of these methods is particularly relevant for studies with incomplete species inventories or highly elusive or rare species (Tobler *et al.* 2008). However, caution needs to be applied as autocorrelation can influence the results if a significant number of camera points are spaced too close together or are shared during data analyses (Kelly 2008).

When assessing survey design, it is imperative that the goals and objectives of the study are clearly defined (O'Connell *et al.* 2011). Species richness assessments allow for the varied use of either extensive or intensive sampling (MacKenzie & Royle 2005, O'Brien 2011). Spatial

representation within my study was found to be less crucial than overall survey effort in obtaining species richness estimates and hence could advocate the use of intensive sampling. However, spatial coverage, closure and independence are three elements that need to be carefully considered when occupancy modelling is a goal (O'Connell *et al.* 2011).

My study identified the responses of 13 species to specific covariates analysed, which in turn provided a greater understanding of the underlying drivers of species presence, distribution and occupancy (Ahumada *et al.* 2011, O'Connell *et al.* 2011, Ahumada *et al.* 2013). Through the replication of occupancy assessments in long term studies, occupancy estimates can act as an indicator and state variable of biodiversity status, change and/or loss (O'Brien *et al.* 2010, O'Connell *et al.* 2011, Ahumada *et al.* 2013). Subsequently, occupancy assessments could provide a tool to measure the trends in the distribution and abundance of species, increase the management effectiveness of protected areas and monitor the extinction risk of species over time (Ahumada *et al.* 2013).

4.6. References

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CHAPTER 5:

CONCLUSIONS REGARDING MEDIUM TO LARGE MAMMAL SURVEYS USING CAMERA TRAPS IN A FYNBOS ENVIRONMENT

Thorough and robust biological monitoring programmes are crucial to identify relevant biological indicators, changes in population trends and associated extinction risks (Lindenmeyer *et al.* 2012). A significant challenge facing biodiversity researchers and managers are the limited and often scarce conservation funds available to address an ever growing need for biological monitoring initiatives (Balmford *et al.* 2003, Gaidet-drapier *et al.* 2006, Nichols & Williams 2006). For a study to be both cost and outcome efficient, survey objectives and associated survey design needs to be thoroughly addressed (Gaidet-drapier *et al.* 2006, Nichols *et al.* 2011). However, fundamental aspects of survey design are rarely empirically assessed (Gompper *et al.* 2006). Furthermore, the majority of studies that have assessed one or more facets of survey design have largely occurred in densely forested habitat types (Trolle & Kelly 2005, Trolle *et al.* 2008, Harmsen *et al.* 2010, Srbek-Araujo & Chiarello 2013). The aim of my study was to optimize camera trap density and position to determine medium and large mammalian species richness and occupancy on the Cape Peninsula, South Africa.

The optimization of camera trap survey design was investigated within a relatively small 4 km² pilot site within the Cape of Good Hope (CoGH) (Chapter 3). Three crucial aspects of survey design were empirically evaluated, namely camera density, spacing and placement. Additionally, the influence of trail presence and condition on species richness at camera locations was investigated.

This study confirmed that both camera density as a measure of survey effort and camera placement had a significant influence on resultant species richness. My analyses indicate that at least 1 000 camera days were required to reach an asymptote through rarefied species accumulation curves, which accounted for 90% of the total recorded species. The required survey effort exhibited in this study was comparable to a study conducted in forest habitat (Tobler *et al.* 2008), but conversely was 250% and 58% greater than the survey effort required in studies conducted across European woodland (Roberts 2011) and South American grassland (Silveira *et al.* 2003) habitats respectively. Subsequently, the required survey effort in my study equated to 40 consecutive survey days with the full grid of cameras (25 cameras per 4 km²) spaced 0.5 km apart, or 111 consecutive surveys days if cameras were spaced at 1 km apart (9 cameras per 4 km²). My results furthermore highlighted that while 1 000 camera days accounted for most species, a larger survey effort was required to register low density,

wide ranging and rare species. This was particularly pertinent to species yielding capture frequencies below two, which also is aligned with results from studies in forested habitats (Tobler *et al.* 2008).

Interestingly, survey effort expressed as camera days was more important in obtaining accurate species richness estimates compared to camera density or camera spacing alone. When varied camera spacingsand resultant camera densities were expressed over the same survey effort (camera days), species accumulation trends and resultant species richness estimates were nearly identical. This suggests that it is more important to obtain the required minimum number of camera days within a given area than being overly concerned about whether cameras are spaced 0.5 km, 1 km or 2 km apart. However, camera points do need to represent varied habitat types present within the given area, thereby necessitating a minimum number of camera survey points needed in order for this result to hold true.

Camera positioning restrictions around pre-determined placement locations significantly impacted on recorded species richness estimates. More lenient positioning (i.e. further distances from pre-determined location allowed) resulted in greater measures of species richness, capture frequencies and independent animal sightings per camera trap. Furthermore, placing cameras near high quality animal signs such as game trails yielded an average of 33% more species than cameras placed near poor quality animal signs. A camera placement height of 0.3 m was effective at recording both the largest and smallest target species, corroborating the height recommendation made in a study conducted in forest habitats in South America (Kelly 2008).

The optimised camera trap survey design was implemented on a broad landscape level across the entire CoGH (Chapter 4) with the aim to assess the species richness, distribution and site occupancy of medium and large terrestrial mammals. My results confirm that camera traps are an effective and rapid means of compiling species inventories and obtaining species richness estimates of medium-to-large terrestrial mammals within a shrubland habitat type. These findings are consistent with studies conducted in tropical forests (Srbek-Araujo & Chiarello 2005, Tobler *et al.* 2008, Ahumada *et al.* 2011, Espartosa *et al.* 2011, Ahumada *et al.* 2013,), temperate forests (O'Connell *et al.* 2006, Kelly & Holub 2008), forest clearings (Gessner *et al.* 2013) and grasslands (Silveira *et al.* 2003). The survey effort required to register the majority of target species was 900 camera days, which supports the comparable results of the pilot study (1 000 camera days) conducted in a small pilot site within the CoGH (Chapter 3). By using the optimised survey design across the entire CoGH, 84% of the species thought to occur within the study site were recorded during the respective survey period of 3 740 camera days. Of these, 81% had sufficient presence points and capture frequencies to obtain

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occupancy estimates across the CoGH. Two of the three species not recorded, namely steenbok and striped polecat, are thought to have disappeared from the study site as species within the same foraging group and similar weight classes were recorded efficiently. Furthermore, no recent sightings of steenbok within the protected area have been recorded for a number of years.

My results highlighted a significant relationship between capture frequency and average body weight, with larger bodied animals yielding higher rates of capture frequency. This finding is supported by studies conducted in both forest and grassland habitats with associated mammal guilds (Wemmer *et al.* 1996, Carbone *et al.* 2001, Silveira *et al.* 2003, Tobler *et al.* 2008). Subsequently, the species with the highest mean occupancy estimates were predominantly large herbivores, including grey rhebuck, bontebok, eland and red hartebeest. However, exceptions were noted with chacma baboon and small grey mongoose, which yielded high mean occupancy estimates as well. Factors that appears to be driving occupancy rates were vegetation height (bontebok, eland), presence of a trail (caracal, baboon, large-spotted genet, small grey mongoose), elevation and slope (klipspringer), distance from coast (Cape fox), vegetation type (Cape grysbok, red hartebeest) and vegetation age (grey rhebuck, porcupine). This investigation therefore provided the CoGH protected area with an accurate current measure of species richness, as well as fine scale occupancy estimates and associated covariate factors explaining occupancy results for the majority of species recorded.

A significant challenge faced within both surveys (Chapter 3 & 4) was high false trigger rates. False trigger control measures provided in other studies were implemented in both of my surveys (Swan *et al.* 2004, Kelly 2008, Tobler *et al.* 2008), but failed to maintain low false trigger rates in the respective fynbos environment. The pilot study yielded a 96% false trigger rate, whilst the full CoGH survey yielded a 97% false trigger rate. The accumulative number of false triggers across the two surveys included 19 134 false trigger events incorporating 57 402 false trigger photos. Although false triggers do not influence the final species richness estimates or survey outcomes (O'Connell *et al.* 2011), it does provide an unnecessary waste of human resource with regard to time spent on data collation. I postulate that lowering camera trap sensitivity settings and/or extending the trigger interval would lower false trigger rates. However, it could impact on the detection of smaller bodied species (Tobler *et al.* 2008). Further studies could aim to ascertain a more efficient use of camera settings to reduce false trigger rates, whilst maintaining detection probability at an appropriate level. An additional recommendation could include the extension of cropped areas beyond 2 m in front of camera traps as used in this study.

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The need for accurate, effective and rapid species richness assessments can be crucial in informing and monitoring conservation management practices and strategies (O'Brien 2008, Tobler *et al.* 2008, Kery 2011, Roberts 2011). If the objective is to compile species richness estimates, two approaches can be applied, namely surveying intensively over a smaller area or extensively over a larger area (O'Brien *et al.* 2010). MacKenzie & Royle (2005) recommended that surveying over fewer sampling units more intensively is more effective for more common species (intensive sampling), whilst surveying over more sampling units less intensively is more effective for rare species (extensive sampling). However, my results, as well as studies conducted in tropical forest habitats, found that camera spacing and total area covered had little impact on resultant species richness estimates (Srbek-Araujo & Chiarello 2005, Tobler *et al.* 2008, Srbek-Araujo & Chiarello 2013). It was rather sufficient survey effort per sampling point that determined the detection of both rare and common species alike.

The full survey of the CoGH with a 1 km camera spacing grid provided the opportunity to further evaluate the impact of camera spacing as it enabled the creation of a 2 km spaced camera grid by simply removing the records of every second camera post-hoc. The extrapolation of rarefied species accumulation curves allowed for the direct comparison of the 1 km spaced actual grid and 2 km post-hoc grid. The subsequent results confirmed that the two variations of camera density, spacing and total area covered, yielded identical species richness estimates, which corroborated the findings from studies conducted in other habitat types (Srbek-Araujo & Chiarello 2005, Tobler *et al.* 2008, Srbek-Araujo & Chiarello 2013) (Figure 5.1). Additionally, the pilot study (Chapter 3) incorporated sampling intensively within a very limited section (5.3%) of the CoGH and yielded 81% of the total species recorded across an extensive full survey of the CoGH (Chapter 4). These results confirm that neither extensive sampling (Chapter 4) nor intensive sampling (Chapter 3) are the most crucial factors determining species richness estimates, rather meeting the required survey effort in terms of camera days was.



Figure 5.1: Rarefied curves (with extrapolation) for two survey efforts, namely 1 km spacing and 2 km spacing of camera stations.

Four methods commonly used to account for undetected species within species richness assessments includes: extrapolation of species accumulation curves (Gotelli & Colwell 2001), parametric species abundance distribution estimators (Pielou 1977), non-parametric species richness estimators (Tobler *et al.* 2008) and closed population Capture-Recapture models, where individuals are substituted for species (Burnham & Overton 1979). Extrapolation of species accumulation curves in both my full survey (Chapter 4) and pilot survey (Chapter 3) yielded accurate measures of final species richness. Furthermore, the use of Jacknife non-parametric species richness estimators within my 4 km² pilot study (Chapter 3) yielded 88 – 94 % of the total species accounted for in the full Cape of Good Hope (CoGH) study (Chapter 4) covering approximately 79 km².

These findings related to the use of non-parametric species richness estimators and extrapolation of species accumulation curves could substantially increase the cost effectiveness of future surveys in the respective ecosystem. My results suggest that rapid, intensive sampling over one or more relatively small sample sites could provide accurate and reliable measures of species richness. This offers monitoring initiatives focusing on species richness estimation a greater yield of survey cost efficacy related to human (field workers) and asset (camera traps) resources required. My analyses suggest that both extrapolation of species accumulation curves and non-parametric species richness estimators required an actual survey effort of approximately 1 000 – 1 200 camera days to maintain accuracy of projections. Furthermore, with this respective survey effort, extrapolations were projected with accuracy up to the full actual survey effort of 3 640 camera days. However, one limiting factor of this approach would be that although accurate final species richness estimates are obtainable rapidly, analyses of species composition could be limited in relation to the scale of extrapolation or projection.

My study highlights the influence of survey design on resultant species richness estimations. Although this study was restricted to a fynbos shrubland ecosystem, findings could be of relevance beyond the Fynbos Biome to areas yielding similar topographical, species and habitat characteristics. Furthermore, my study was restricted to one winter and summer season respectively. In light of the ongoing pressure placed on the CoGH as a protected area through various threats (SANParks 2001), it would be of importance to continue monitoring long term trends in species richness, distribution and occupancy. In light of my study identifying high survey effort in terms of camera days being the primary factor needed to obtain accurate species richness estimations, as opposed to camera spacing or density, I recommend the use of small intensive stratified grids. Grids could have the same survey design and structure as the 1 km grid utilised in the pilot study (Chapter 3), incorporating nine cameras in a 4 km² sample, as long as the required survey effort is reached (ca. 1 000 camera days, 111 consecutive survey days). The advantage of this grid size is that it only requires a moderate resource investment in terms of camera traps and time spent on camera placement. Alternatively, if a shorter consecutive survey period is desired (i.e. 40 days), the full 0.5 km grid incorporating 25 cameras can be used. In order to achieve spatial representation, it is recommended that the grid be sampled over multiple topographical types, namely coastal, flat/undulating valley bottom and mountainous terrain.

It is imperative that future studies clearly evaluate survey objectives and then construct the most effective survey design required to meet the objectives (Nichols *et al.* 2011). Monitoring efficiency should not only be gauged on survey outcomes, but also on the associated cost in time, money and effort incurred to achieve the respective outcome (Gaidet-drapier *et al.* 2006, Nichols & Williams 2006). By optimising survey design, both the efficacy and cost of the monitoring project can be maximised.
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APPENDICES

Appendix 1

Avian and reptile (non-target) species recorded in the pilot survey within the Cape of Good Hope.

Class	Species	Common Name	No of Sightings
Mammalia	Otomys irroratus	Vlei rat	1
		Four-striped grass	
	Rhabdomys pumilio	mouse	1
Aves	Buteo rutotuscus	Jackal buzzard	2
	Bubo africanus	Spotted eagle-owl	2
	Scleroptila	Grey-winged	
	levaillantoides	francolin	12
		Hottentot	
	Turnix hottentottus	buttonquail	2
	Burhinus capensis	Spotted thick-knee	5
	Struthio camelus	Common ostrich	73
	Ardea	Black-headed	
	melanocephala	heron	2
		White-necked	
	Corvus albicollis	raven	2
	Cercomela familiaris	Familiar chat	1
	Macronyx capensis	Cape longclaw	7
Reptilia	Chersina angulata	Angulate tortoise	1

Appendix 2

The Digital Elevation Model (DEM) created to extract elevation covariate data per respective camera position. The value field is measured in metres above sea level.



Appendix 3

The digital slope model created to extract slope covariate data per respective camera position. The value field is measured in degrees.



Appendix 4

All non-target species and associated number of sightings per species recorded during the full Cape of Good Hope survey.

Class	Species	Common Name	No of
			Sightings
Aves			
	Struthio camelus	Common Ostrich	252
	Burhinus capensis	Spotted Thick-knee	5
	Scleroptila	Grey-winged	
	levaillantoides	Francolin	4
	Bubo africanus	Spotted Eagle-Owl	3
	Pternistis capensis	Cape Spurfowl	3
	Ardea melanocephala	Black-headed Heron	3
	Motacilla capensis	Cape Wagtail	3
	Telophorus zeylonus	Bokmakierie	3
	Buteo rufofuscus	Jackal Buzzard	1
	Cercomela familiaris	Familiar Chat	1
	Columba guinea	Speckled Pigeon	1
	Pycnonotus capensis	Cape Bulbul	1
	Alopochen aegyptiaca	Egyptian Goose	1
	Cosypha capensis	Cape Robin-chat	1
Reptilia			
	Chersina angulata	Angulate tortoise	42
		Southern Rock	
	Agama atra atra	Agama	1