LIVESTOCK, LEOPARDS AND BROWN HYAENAS: CONFLICTS OF COHABITATION IN THE ROODEWALSHOEK CONSERVANCY, MPUMALANGA

By

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Dissertation submitted in fulfillment of the requirements

for the degree Magister Scientiae in the

Faculty of Natural and Agricultural Sciences

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January 2012

"There is an ancient African legend which claims that the spots of a leopard reflect the spoor of all the wild animals living around it. And because of this, the leopard is capable of changing into any one of these animals, making it the source of life."

Heather Dugmore, 2001

DECLARATION

I, Michelle van As, the undersigned, hereby declare that the work contained in this dissertation is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree. I furthermore cede copyright of the dissertation in favor of the University of the Free State.

Signature…………………………………………………………….

Date………………………………………………………………...

DEDICATION

This work is dedicated to Oom Gert Stoltz (04/02/1944 – 09/04/2012) for whom I hold the highest regard and without whom this study would not have been possible.

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ABSTRACT

Conflict between livestock farmers and large carnivores has prevailed since the domestication of animals were first attempted by man. Inadequate information on predator dynamics, especially in regions outside formal protected areas where they are perceived as problem animals, render control methods arduous. The aim of this study was to explore the relationships between leopard *Panthera pardus* (Linnaeus, 1758) and brown hyena *Parahyaena brunnea* (Thunberg, 1820), their potential prey populations and its relevance to cattle losses in the Roodewalshoek Conservancy, Mpumalanga. This study was the first of its kind in this specific conflicted area. Assessment of utilization of the area by these large predators was conducted with the aid of digital motion-sensor camera traps, combined with field observations of any physical signs of these animals. During this study, 16 potential prey species (>2 kg) were recorded and peaks in circadian, monthly and lunar rhythms were unique to each species. A total of seven predatory species were recorded, also with unique circadian, monthly and lunar rhythms to each species. Small and large predators seemed to exhibit spatial and temporal separation and individual predators exhibited unique behavioural responses to their shared environment. Both leopards and brown hyaenas proved equally responsible for livestock losses, which increased from January 2005 to October 2010. Inter-predator competition was observed between these two species. The majority of calves were caught during low moonlight intensity and in the wet season. Both predators displayed surplus-killing behaviour. Even though sufficient occurrences of natural prey could be found in the Roodewalshoek Conservancy, predation on livestock persists during the calving season.

Keywords: leopard; brown hyaena; livestock losses; lunar; surplus-killing

1

Introduction

CHAPTER 1
INTRODUCTION

1.1. Human-carnivore conflict

The enduring conflict between humans and carnivores has been and remains until this day a complex issue (Athreya & Belsare, 2007), with its most common source one of extensive economical loss in the form of livestock depredation (Skovlin, 1971; Denney, 1972; Freedman, 1989; Lawson, 1989; Mills, 1991; Newmark *et al.,* 1993; Oli *et al.,* 1994; Du Toit, 1995; Kreuter & Workman, 1996; Weber & Rabinowitz, 1996; Kharel, 1997; Mishra, 1997; Ciucci & Boitani, 1998; Conner *et al.,* 1998; Linnell *et al.*, 1999; Mizutani, 1999; Vitterso *et al.,* 1999; Smith *et al.*, 2000a; 2000b; Kangwana & Mako, 2001; Treves *et al.,* 2002; Linnell *et al.,* 2003; Marker *et al.,* 2003a; 2003b; Polisara *et al.,* 2003; Santiapillai & Jayewardene, 2004; Herfindal *et al.,* 2005; Ray *et al.*, 2005; Woodroffe *et al.,* 2005; Al-Johany, 2007; Van Bommel *et al.,* 2007). The expansion of agricultural land-use due to greater food demand has brought wildlife and people into increased contact and conflict with one another over diminishing shared resources (Butler, 2000; Treves & Karanth, 2003; Santiapillai & Jayewardene, 2004; Graham *et al.*, 2005; Holmern *et al.*, 2007). Therefore the depredation of livestock, as well as the feeding ecology of carnivores responsible for this predation, has been studied in various areas of conflict (Kruuk, 1980; Skinner *et al.*, 1980; Andelt, 1992; Hoogesteijn *et al.*, 1993; Andelt, 1999; Karanth *et al.,* 1999; Rasmussen, 1999; Hoogesteijn, 2000; Funston *et al.*, 2001; Conforti & Azevedo, 2003; Hemson, 2003; Hussain, 2003; Marker *et al.*, 2003; Ogada *et al.*, 2003; Bagchi & Mishra, 2006).

Livestock depredation more often than not results in the persecution of predators by farmers in the form of eradication of perceived problem animals (Mishra, 1982; Hussain, 2003; Rahalkar, 2008). This may be viewed as a contra-productive act, since the presence of a variety of predators in an area is indicative of a balanced system resulting from sensible land-use management (Hodkinson *et al.,* 2007). Livestock predation in South Africa varies widely from region to region and according to Ray *et al.* (2005), the most losses generally tend to occur where natural prey density is low. However, Polisara *et al.* (2003) contradictively showed that predators often kill livestock in areas that contain adequate numbers of natural prey. Therefore, any livestock farming practice needs to take the necessary precautions to protect livestock from predators (Hodkinson *et al.,* 2007). According to Georgiadis *et al.* (2007), predator-prey dynamics can be affected upon directly and indirectly by the presence of cattle in the landscape and livestock depredation rates can also be influenced by local environmental conditions such as abundance of natural prey (Mizutani, 1999; Polisara *et al.*, 2003) and rainfall (Patterson *et al.*, 2004; Woodroffe & Frank, 2005).

Investigations on the feeding ecology of large predators in an area has improved the understanding of the behavioural ecology of such animals (Mills, 1992). Up until about 20 years ago, both leopards *Panthera pardus* (Linnaeus, 1758) and brown hyaenas *Parahyaena brunnea* (Thunberg, 1820) were almost exclusively studied in protected areas where these animals could be observed directly (Eisenberg & Lockhart, 1972; Schaller, 1972; Muckenhirn & Eisenberg, 1973; Guggisberg 1975; Mills & Mills, 1977; Mills, 1978; Owens & Owens, 1978; Mills, 1981; 1982; Bothma and Le Riche, 1984; Le Roux, 1984; Norton & Lawson, 1985; Bothma & Le Riche, 1986; Norton & Henley, 1987; Le Roux & Skinner, 1989; Hes, 1991; Mills & Biggs, 1993; Bailey, 1993; Mills, 1994; Bothma, & Le Riche, 1995; Miththapala, *et al.,* 1996; Chauhan *et al.* 2000; Hancock, 2000; Henschel & Ray, 2003; Hunter *et al.,* 2003; Uphyrkina & O'Brien, 2003; Balme & Hunter, 2004; Santiapillai & Jayewardene, 2004; Bothma 2005; Hayward *et al.,* 2006; Bothma & Bothma, 2006; Maheshwari, 2006; Schwarz & Fischer, 2006; Balme *et al.,* 2009). Since the behaviour and population distribution of prey can have a major influence on the quality of a predator's habitat (Maheshwari, 2006), data on the ecology of available prey species is essential in gaining knowledge on the ecology of the predator. In turn, it is vitally important to understand the ecological requirements of a species in order to maintain successful conservation of that species (Balme *et al.*, 2007).

Over the last decade numerous complaints were made by farmers of the Roodewalshoek Conservancy, Mpumalanga Province, South Africa to nature conservation officials on predation of livestock. The depredation on livestock by brown hyaenas and leopards is usually restricted and highly localized to certain well-defined areas (Hodkinson *et al,.* 2007) and these two species are the only large predators occurring in the Roodewalshoek Conservancy, which render this an ideal study site to investigate the ongoing conflict between farmers and predators. The conservancy is situated in a valley characterized by a mountainous landscape and apart from secondary roads to household dwellings, is almost inaccessible by vehicle or on foot. The use of remote sensing techniques to collect data is therefore essential.

For nearly the entire 20th century, the camera trap has evolved as a scientific tool and the use of camera traps during recent years to study wild animals has improved understanding of ecological relationships and population dynamics (O'Connell *et al.*, 2011). Long *et al.* (2008) stated that the increasing interest in animal welfare has led to an increasing interest in non-invasive sampling techniques, such as remote-sensor camera traps. A camera trap allows the researcher to conduct undisturbed observations in various habitats on a wide variety of species, under various weather conditions, twenty-four hours a day. This non-invasive tool can be used to detect rare species, monitor behaviour, determine species distributions and assist in estimating population sizes (O'Connell *et al.*, 2011).

Chapman (1927) was the first person to make use of trip-wire triggered remote photography as an aid to documenting the species present in an area. He was also able to distinguish between individuals of the same species in the photos, based on the markings on the body. Gregory (1927) was also an early developer of the animal-triggered remote camera and he made use of lures such as catnip oil to maximize the possibility of taking a photograph of his target species. Later on, other researchers such as Gysel & Davids (1956), Pearson (1959, 1960), Dodge & Snyder (1960), Winkler & Adams (1968), Seydack (1984) and Hiby & Jeffery (1987) used various forms of remote-triggered cameras to obtain information on a wide variety of wildlife species in various parts of the globe.

Carthew & Slater (1991) developed the first automatic photographic system that employs a pulsed infrared beam as a trigger device and the use of automated camera traps became the preferred method of camera trapping ever since. Since the mid-nineties camera traps have been used for research on carnivores by several researchers, including focusing on aspects such as estimated population densities (O'Brien *et al.*, 2003; Kawanishi & Sunquist, 2004; Silver *et al.*, 2004; Henschel & Ray, 2003) and reproductive behaviour (Bridges *et al.,* 2004a). Remote photography has also proven valuable in documenting the presence of rare cryptic species (Surridge *et al.*, 1999; Moriarty *et al.*, 2009). Silveira *et al*. (2003) and Srbek-Araujo & Chiarello (2005) concluded that camera trapping is more efficient in conducting faunal assessments of mammals in remote areas than transect or observation methods. Thus, camera traps have allowed researchers previously unimaginable access into the daily activities of target species.

Camera traps for remote censussing are the newest tool for researchers assessing the behaviour and activity patterns of animals (Bridges & Noss, 2011). Before the development of radio-telemetry in the 1960's, direct visual observation was the predominant ethological technique utilized. This technique is still widely used today, despite the fact that, according to Bridges & Noss (2011), the presence of a human can lead to an alteration of natural activity patterns and behaviour of wildlife. Although the flash, camera housing and associated sounds may also potentially alter natural behaviour, Griffiths & van Schaik (1993), Alexy *et al.* (2003) and Bridges *et al.* (2004a) suggested that this disturbance is less than it would be if a researcher was physically present, observing the animals' behaviour directly. Bridges *et al.* (2004b) suggested that the entire faunal population at a sampling site is potentially exposed to being photographed. Fedriani *et al.* (2000), de Almeida Jacomo *et al.* (2004) and Wachner & Attum (2005) concluded that camera traps allow simultaneous study of activity patterns of multiple species and can thus be used to examine the partitioning of temporal activity of sympatric species and the associated implications for niche overlap.

Recently, several studies were carried out where the use of remote camera traps was used to assess the circadian rhythms of large felids (Azlan & Sharma, 2006; Di Bitetti *et al.*, 2006). Camera traps were placed along game trails and roads in densely wooded areas to assess the activity patterns of various species in Bolivia, Java and Sumatra (van Schaik & Griffiths, 1996; Wallace *et al.*, 2002; Noss *et al.*, 2003; Maffei *et al.*, 2004, 2005; 2007; Gómez *et al.,* 2005). According to Bridges & Noss (2011) data obtained via camera traps may also leave room for inter- and intraspecific avoidance behaviour as well as analyses of spatial and temporal separation.

During this study, the ecological and ethological traits of potential prey species as well as that of predators were examined. Numbers and trends of livestock losses were determined and the relationships between calf depredation, predator observations and potential prey rhythms were investigated. Since October 2010, all cattle have been removed from the Roodewalshoek Conservancy, and a preliminary assessment in December 2011 indicated that the behavioral patterns of both brown hyaenas and leopards have changed to these different circumstances. This trend needs more in-depth investigation over a prolonged period of time, which, in retrospect, will expectantly provide detailed information on the actual effect of the presence of livestock on the natural species residing in the Roodewalshoek Conservancy.

1.2. Objectives of the study

Consequently this study was undertaken to fulfill the following objectives:

- Investigate the ecological and ethological relationships between potential predator as well as prey species in the Roodewalshoek Conservancy
- Determine the current standing of calf losses in the Roodewalshoek Conservancy
- Investigate the influence of cyclical events such as seasonal, meteorological as well as lunar variations on predators, prey species and calf depredation rates
- Determine the most important predator of livestock in the Roodewalshoek Conservancy
- Determine possible conflicts in cohabitation between livestock and large predators

2

Study Area

CHAPTER 2
STUDY AREA

2.1 Topography

The Roodewalshoek Conservancy, encompassing a surface area of approximately 20 km^2, is an important corridor-area for leopards and brown hyaena moving between the surrounding areas. The study area is situated along a subsidiary road perpendicular to the R37 between Lydenburg and Burgersfort, approximately 12 km NNW from Lydenburg in Mpumalanga province (Fig. 2.1) and borders with Thaba-Tholo Private Game Reserve on the western perimeter. The conservancy perimeter is unfenced, allowing free movement of predator and prey alike, and internally houses 1 m high cattle fences which surrounds different livestock-camps in the area. About six farm houses can be found, two of which is permanently occupied. The only other infrastructure present in the area includes roads accessible mainly by off-road vehicles. The valley encompassing the conservancy has a north to south orientation with slopes facing predominantly east or west (Fig. 2.2). This valley forms part of the catchment area of the Olifants River system, however, it has not officially been classified as such and is therefore not under the proper conservatory measures needed for catchment areas. Altitudes encountered in the conservancy ranges from approximately 1 100 to 1 800 m above sea level.

This area is uniquely situated in the ecotone of the Sekhukhuneland Center of Plant Endemism and the Lydenburg Center of Plant Endemism (Fig. 2.3). The Lydenburg Centre of Plant Endemism encompasses the region between the Sekhukhuneland Centre of Plant Endemism to the west and the Wolkberg Centre of Plant Endemism to the east (Fig. 2.3). It has an Afromontane flora linking it northwards to the Zimbabwean Highlands and southwards to the southern Drakensberg mountain range. A total of 2 266 species and 51 endemic plant taxa have been identified (Emery *et al.*, 2002) and endemism is prevalent within the families Ericaceae, Gesneriaceae, Asteraceae, Orchidaceae and Iridaceae in increasing order of abundance.

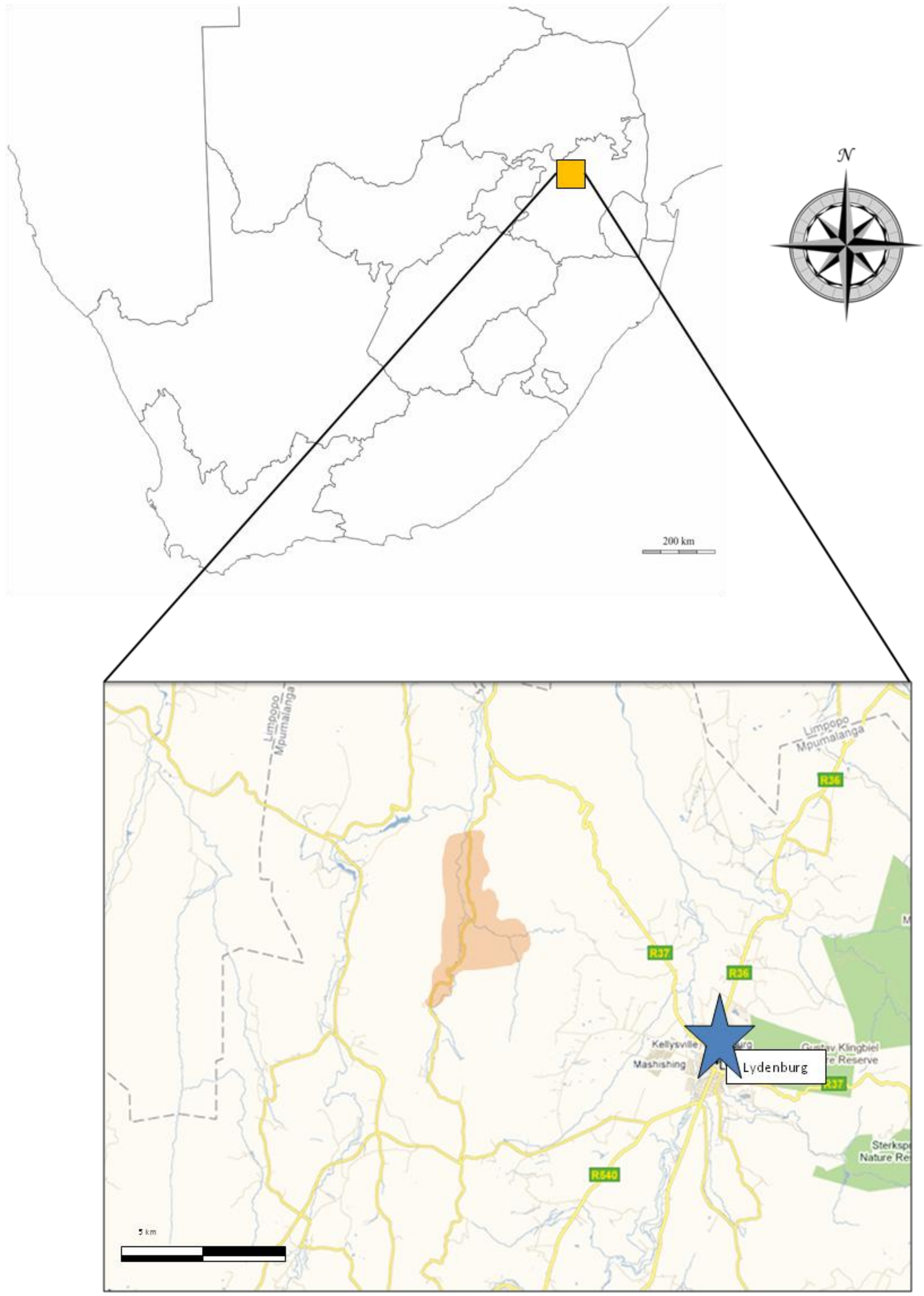

Figure 2.1 Location of the Roodewalshoek Conservancy (orange area), in the Mpumalanga province. Modified from Google Map Data ©2011 AfriGIS (Pty.) Ltd.

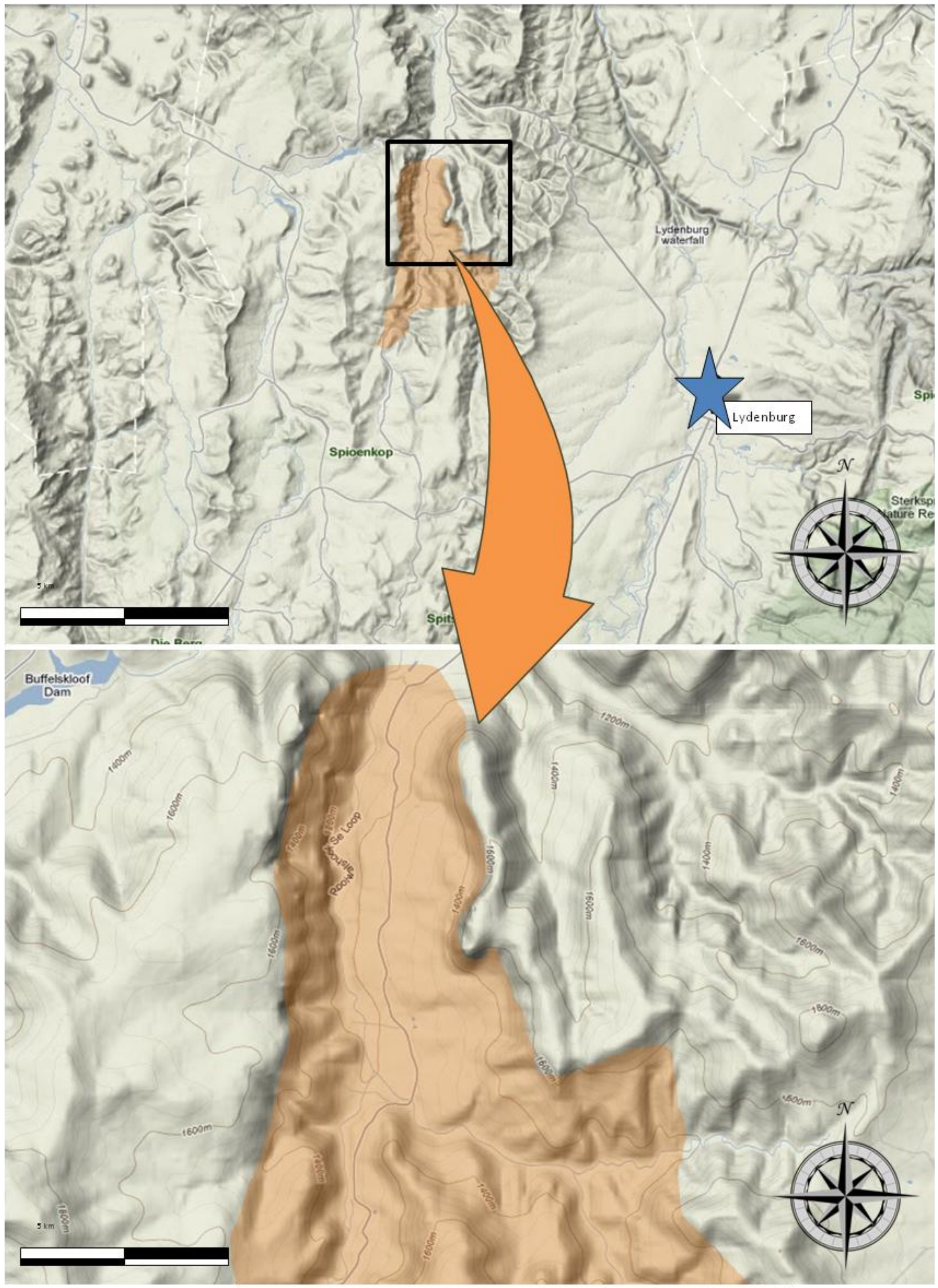

Figure 2.2 Topographical context of the study site (orange area) with altitudinal ranges from 1 100 to 1 800 m above sea level. Modified from Google Map Data ©2011 AfriGIS (Pty) Ltd.

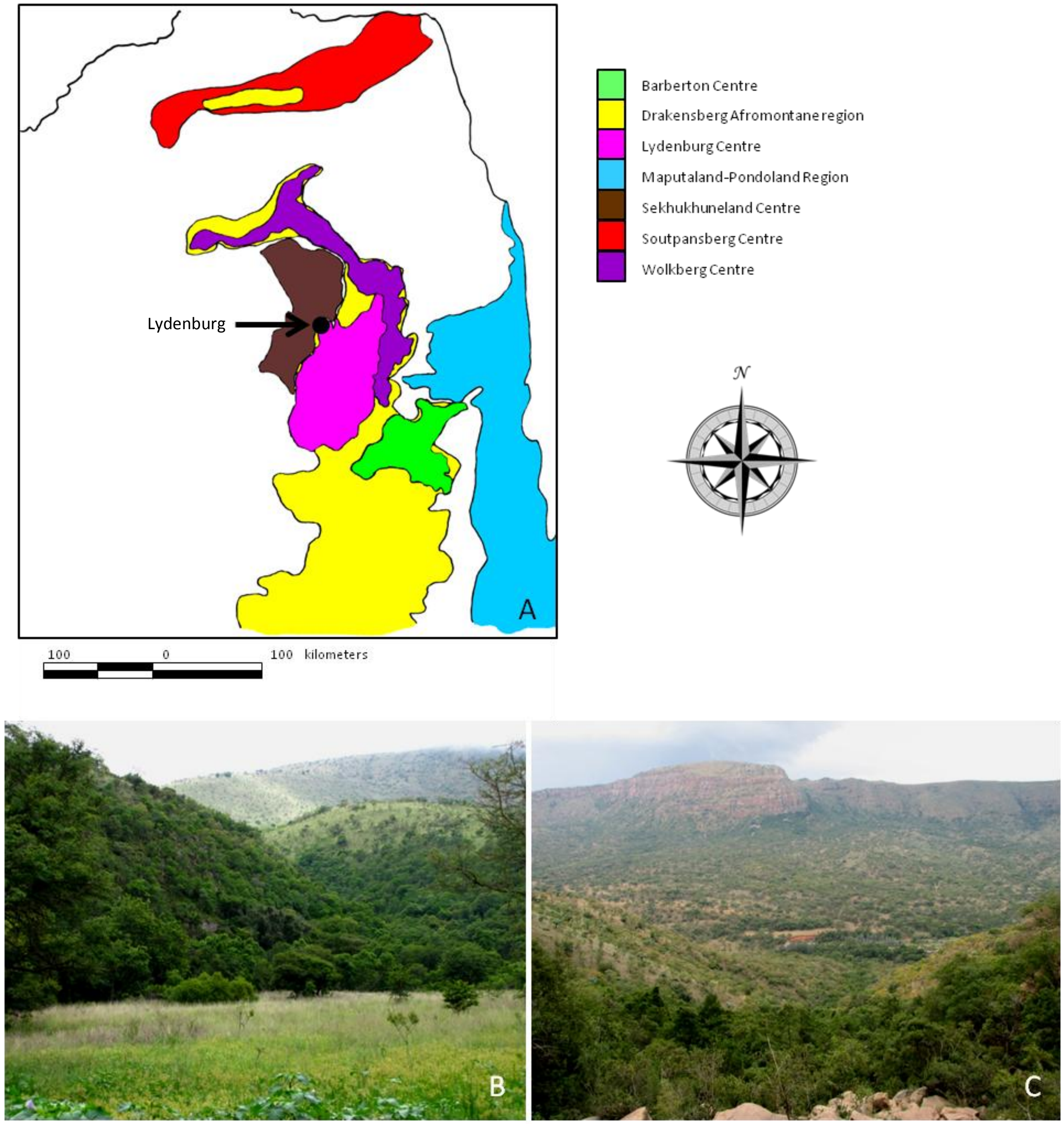

Figure 2.3 Floral characteristics of the Roodewalshoek Conservancy. **A,** plant Centres of Endemism in North Eastern parts of South Africa redrawn from Schmidt *et al*. (2002); **B,** domination of Lydenburg Thornveld on the east and west facing slopes of the conservancy; **C,** remnants of Northern Afromontane Forest found as small patches in deep, smaller valleys.

According to Emery *et al.* (2002), 46% of Mpumalanga's flora is contained within the Lydenburg Centre of Plant Endemism, which covers only approximately 9% of the surface area of the province. Mucina *et al.* (2006) found high concentrations of local or regional endemics in the mountainous areas surrounding Lydenburg. The Sekhukhuneland Centre of Plant Endemism falls in the rainfall shadow of the Drakensberg escarpment and shows a greater degree of aridity than the areas to the east with vegetation adapted accordingly.

2.2 Climate

Monthly rainfall is relatively irregular on a year to year basis and the average minimum and maximum temperatures remain relatively mild in summer (November to March) and winter months (May to August). The Roodewalshoek Conservancy is situated in a summer rainfall region and receives most of its precipitation from October to January (Fig. 2.4) with an average annual precipitation of 342 mm. Maximum temperatures can reach up to 29°C from September to March and temperatures as low as 0°C with frequent frost are encountered from May to August. The average annual maximum temperature is 27°C and the annual average minimum temperature is 16°C. The average monthly maximum temperature is 24°C, the average minimum temperature is 10°C and monthly rainfall records show average records of 28 mm.

2.3 Vegetation

The study area encompasses a combination of several habitat types, including Lydenburg Montane Grassland, Sekhukhune Montane Grassland and Lydenburg Thornveld. The grassland areas can be found spreading out from the top of the valley cliffs outwards from the study area and the thornveld habitat is most prevalent closer to the riverine areas, where it denses into deciduous riparian forest (*vide* Fig. 2.3). Remnants of Afromontane forest patches can be found in the deeper, smaller valleys (*vide* Fig. 2.3).

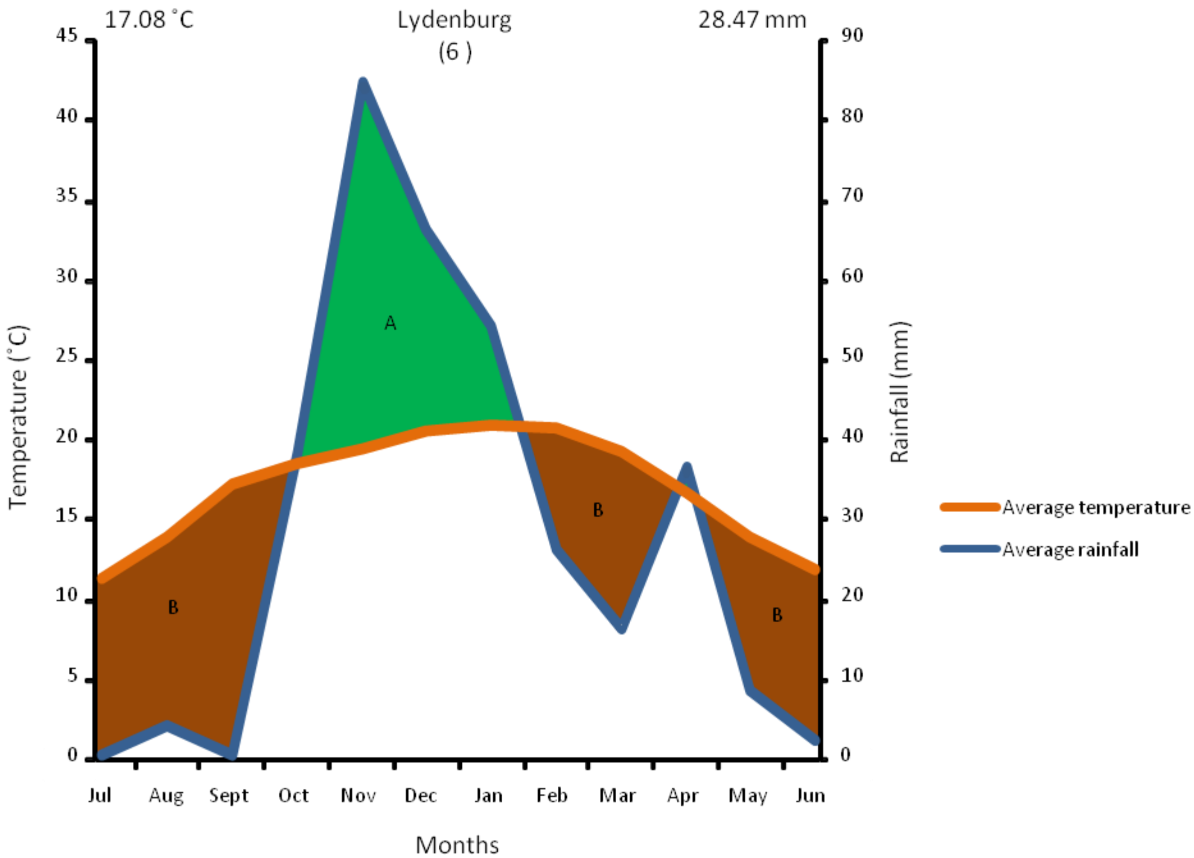

Figure 2.4 Climate diagram of Lydenburg, Mpumalanga according to the method of Walter (1964). Numbers between brackets indicate years of observation. Average annual temperature and rainfall is indicated on the top-left and top-right, respectively. **A,** wet season; **B,** dry season.

Small forests and shrub-like thickets are common along faults, drainage lines (Fig. 2.5) and narrow diabase dykes, which are relatively common in this region. Almost a quarter (23%) of this vegetation type has been transformed with mostly alien plantations (20%) and cultivated lands (2%). Dense, sour grassland occur on the slopes of mountains and hills, with scattered clumps of shrubs and trees in sheltered habitats (Fig. 2.4). Northern Afrotemperate Forest patches are restricted as small patches to mountain valleys and low ridges at high altitudes and are relatively species-poor (*vide* Fig. 2.3). Most forest patches occur at altitudes ranging between 1 450 and 1 900 m above sea level, with some outliers occurring between 1 100 and 1 800 m. The open plains are characterised by turf and clay soils between the hills where dense, tall grassland can be found (Mucina *et al.*, 2006). The foothills and plains areas of the study area are dominated by frost-hardy woodland (Fig. 2.5). This type of vegetation structurally comprises closed grassland which is almost always wooded, and sometimes being densely wooded in rocky areas. According to Mucina *et al.* (2006) wooded areas occur less densely in frost-ridden valleys where *Acacia karroo* are still able to persist.

2.3.1 Centres of Plant Endemism

2.3.1.1 Lydenburg Centre of Plant Endemism

A. Geology

The Lydenburg Centre of Plant Endemism is geologically located on the Pretoria Group, which predominantly comprises quartzite, shale and small quantities of andesite with diabase intrusions (Emery *et al.*, 2002). The base of the Pretoria Group is formed by pale-weathering shales and overlying quartzite (Norman & Whitfield, 2006). The region includes high-altitude plateaus, mountain peaks and slopes, undulating plains, hills and deep valleys. Soil of this region is mostly derived from quartzite and shale, as well as dolomites and lavas of the Pretoria Group of the Transvaal Supergroup (Mucina *et al.*, 2006). Occasional thin quartzite bands can be seen on the surface as they are sandwiched between the predominant shales. Intrusive diabase and rounded boulders are common (Norman & Whitfield, 2006).

Figure 2.5 Vegetation types of the Roodewalshoek Conservancy. Riverine areas characterized by deciduous riparian forest during **A,** lush, green summer and **B,** dry, pale winter as well as frosty, hardy woodland in **C,** plains and **D,** mountain slopes.

B. Vegetation

A high number of endemic plant taxa are confined to the surrounding Lydenburg and Sekhukhuneland Centres of Plant Endemism (Emery *et al.*, 2002) and the greater Lydenburg area represents a unique area of plant endemism (Van Wyk & Smith, 2001). Mucina *et al.* (2006) suggested that the regions bordering arid savanna regions have the highest vegetation activity from February to April and it is likely to be the situation in the conservancy. The Lydenburg Centre of Plant Endemism, as well as the Barberton and Wolkberg Centres are incorporated by the Drakensberg Afromontane Region (*vide* Fig. 2.3). This region is discontinuous and incorporates an area of about 84 500 km² in southern Africa with plant-endemism around 75% (Emery *et al.*, 2002).

2.3.1.2 Sekhukhuneland Centre of Plant Endemism

A. Geology

The area is transected by major chains of hills and has a north-south orientation, creating moderately steep slopes facing predominantly east or west. Dense, sour grassland occur on the slopes of mountains and hills, with scattered clumps of shrubs and trees in sheltered habitats. This centre of endemism is linked to special substrates, among which rare ultramafics and quartzites play a major role (Mucina *et al.* 2006). The region is characterized by heavy-metal soils that are derived from predominating pyroxenite, norite and anorthosite formations. It forms part of the Bushveld Igneous Complex that has ultramafic layers (Emery *et al.*, 2002). The area mostly overlies the mafic intrusive rocks of the Main and Upper Zones of the Rustenburg Layered Suite, an economically important part of the Bushveld Igneous Complex (Mucina *et al.*, 2006). Surface mining of outcrops of vanadium and chromite by strip or opencast mines occurs at a rapid rate and is resulting in large-scale habitat loss (Emery *et al.*, 2002).

B. Vegetation

The Sekhukhuneland Centre of Plant Endemism is situated westward from the Lydenburg Centre of Plant Endemism (*vide* Fig. 2.3) and not incorporated by the Drakensberg Afromontane Region. The open plains are characterized by turf and clay soils between the hills and dense, tall grassland can be found here. Encroachment by indigenous microphyllous tree species is common in some places. Endemism is high in woody and herbaceous plants and is represented in the family Anacariaceae, Euphorbiaceae, Lamiaceae and Liliaceae.

2.4. Conservation concerns

The report by Emery *et al.* (2002) found that the areas surrounding Lydenburg can be classified as part of the sites that harbors the highest concentration of biodiversity in Mpumalanga. Approximately 25% of the Lydenburg Centre of Plant Endemism has been transformed, of which approximately 19% of transformation occurred due to afforestation. An estimated 30% of the Sekhukhuneland Centre of Plant Endemism is under subsistence or commercial cultivation and vast areas are being mined for vanadium by using strip-mining techniques. Many farmers in the area have, however, embarked on ecotourism initiatives that aids in the conservation of this vegetation type (Mucina *et al.*, 2006). This Centre of Botanical Endemism is not formally protected by any nature reserves and only approximately 2% of the Lydenburg Centre is under formal protection (Emery *et al.*, 2002). Rutherford *et al.* (2006) states that the Sekhukhune Plains Bushveld is heavily degraded in places and overexploited for mining, urbanization and cultivation. Invasion by alien species and encroachment of indigenous microphyllous trees is common throughout the area. About 25% of the area has been transformed to be mainly under dry-land subsistence cultivation.

Poaching of potential prey and of predator species is increasing in the area due to the increasing demand of an expanding bushmeat and muthi trade (Fig. 2.6). Currently a relatively small area is under pressure from chrome and platinum mining activities, which however, is very likely to expand in the near future. There is much degradation of the remaining vegetation and widespread erosion up until the level of forming dongas. However, many farmers in the area have embarked on ecotourism initiatives, which aids in the conservation of this unique area.

Figure 2.6 Poaching poses a large threat to herbivores and snares like shown by red arrows in **A,** is not uncommon. **B,** camera traps also did great service in elucidating poacher activity in the study area.

3

Materials and Methods

CHAPTER 3
MATERIALS AND METHODS

3.1 Surveying Methods

3.1.1 Camera Traps

The choice of a site for the location of a camera trap station should be evaluated thoroughly (O'Connell & Bailey, 2011). Because leopards live at relatively low densities, the probability of one encountering a camera trap is low. Large felids are known to make use of roads to patrol their home ranges or to locate prey (Karanth *et al.*, 2006; Karanth & Chundawat, 2002). Camera traps were operated during a period of two years from January 2009 to December 2010. The locality of each camera trap station was chosen in such a way as to maximize the possibility of detecting leopards and brown hyaenas, therefore these stations were set mainly along trails and roads that were most likely to be frequented by these carnivores, irrespective of habitat type. Other station localities included areas with good visibility, areas where signs of predator activity were encountered and areas where the topography channeled the animals in that area past a certain point. At one specific camera trap station, located in riverine bush habitat, regular predator activity was observed and hence traps were placed on both sides of the trail in order to capture both sides of one individual. Camera traps were placed in a spatial arrangement of 33 camera trap stations in an area of approximately 20 km^2 (Fig. 3.1). Karanth *et al.* (2011) noted that baits and lures can be used effectively to potentially increase photo-capture possibilities in big cat studies, but the current study has had no success with this method in the Roodewalshoek Conservancy.

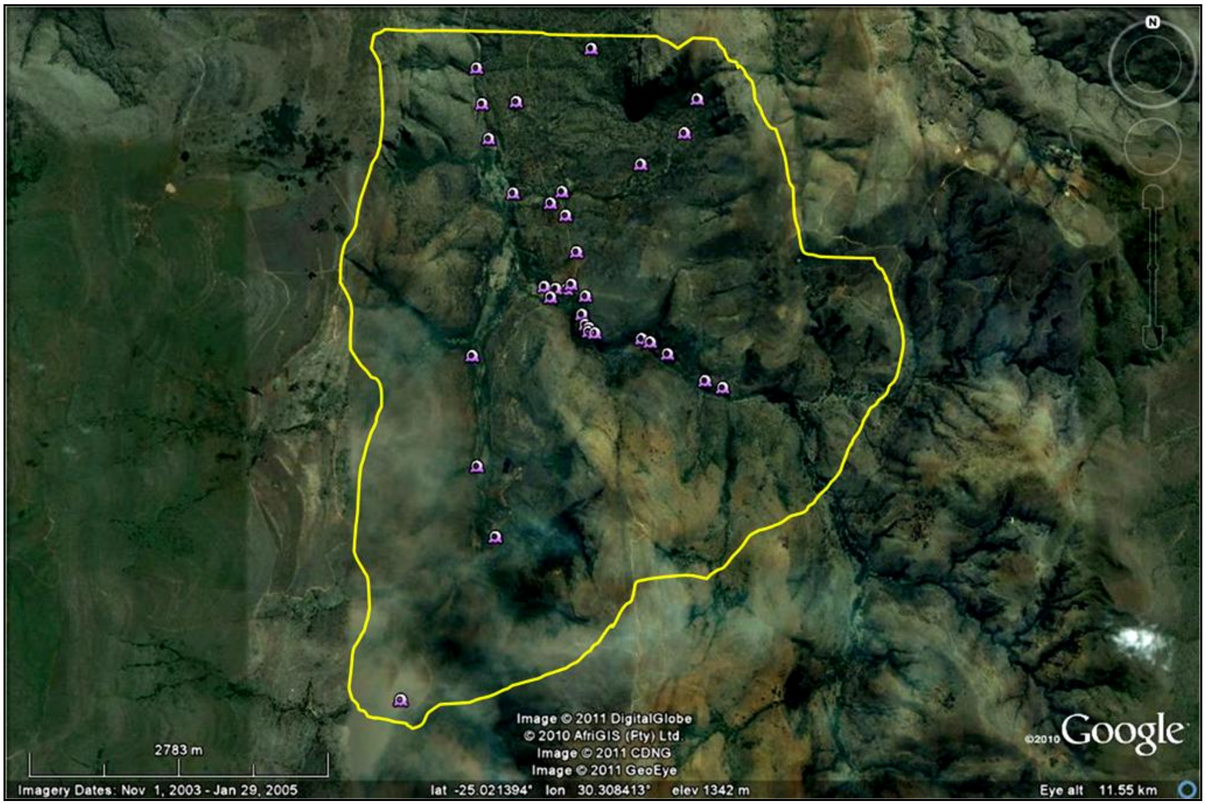

Figure 3.1 Placement of digital camera traps in the Roodewalshoek conservancy over a period of two years from January 2009 to December 2010. Yellow line, conservancy border.

At first several different models of camera traps were used including the Wildview® Xtreme 5, Cuddeback® Capture, Cuddeback® Capture IR, Cuddeback® EXcite and Scout Guard® SG 550 IR (Table 3.1). Due to night photo clarity and fast trigger speed, the Cuddeback® Captures proved to be the most effective camera traps and were therefore used for the remainder of the study. Infrared cameras proved ineffective in terms of distinguishing between individual leopards and brown hyenas because most of the images were out of focus. The presence of a flash did not appear to disturb the animals and several individuals from different species showed awareness towards the camera traps.

Table 3.1 Technical information of camera traps used during the study.

Type of Camera trap	Trigger speed (seconds)	Resolution (Megapixel)	Flash type
Wildview® Xtreme 5	1.50 – 3.00	5	Strobe
Cuddeback® Capture	0.30	3	Strobe
Cuddeback® Capture IR	0.30	3	Infrared
Cuddeback® EXcite	0.75	2	Strobe
Scout Guard® SG 550 IR	1.20	3	Infrared

Each camera trap was equipped with a uniquely labeled 1GB SanDisk® memory card and a set of 1.2 Volt GP® rechargeable NiMH 7000 mAh D-cell batteries, which were recharged by means of solar power and a Vanson® Universal Battery Charger. In order to maximize the possible number of photographs that could be captured the camera trap stations were checked at a frequency of three to seven days to ensure that the batteries are still functioning. Visits to the sampling sites were limited as much as possible in order to minimize the amount of human disturbance at the site which may have a negative impact on the natural activity of the two target species.

Each leopard and brown hyena possesses an asymmetric pelage pattern that is distinct to each individual (Jackson *et al*., 2006). The camera taps were therefore orientated at a degree of 45˚ to 90˚ to the anticipated travel path in order to be able to capture full-on lateral photographic data. Camera traps were set up by means of fastening it against a tree trunk at a height of 0.5 to 1 m above the ground and leaved branches were used to camouflage the camera trap by being positioned so that it will break up the outline of the equipment. In order to maximize the area of movement-detection, the camera traps were fastened against trees that were closer than three meters from the anticipated travel path. Sometimes fence posts also proved useful for the setup of a camera trap. Coordinates for each camera trap station were obtained with the aid of a GPS (*vide* Fig. 3.1).

3.1.2 Field Observations

Field observations were carried out over a two-year period from the start of 2009 to the end of 2010 on a quarterly basis during summer, autumn, winter and spring. Each visit to the Roodewalshoek Conservancy was spent setting up and managing camera trap sample stations while observational sampling were carried out early morning or late afternoon either on foot or by four-wheel drive vehicle with the visual aid of a 8 x 42 National Geographic™ binoculars. Only potential prey species larger than 2 kg in weight were observed to trigger camera traps, and thus only these species were documented. Number of individuals, gender and age-category, such as adult or juvenile, of all animals were noted on a standardized form. Any additional information for identification purposes, such as unique scars, territorial, anti-predator and reproductive behaviour were included when observed. The coordinates of each species were recorded with the aid of a Garmin eTrex Legend® C Global Positioning System. Field surveys in search of brown hyaena and leopard tracks were mainly focused on the existing off-road vehicle roads as well as well-defined game trails in the conservancy, since these animals use such paths relatively often when present in the area. Coordinates of all observed tracks as well as the bearing thereof were recorded.

3.1.3 Tracks and Signs

In order to try to distinguish between individual predators based on their pugmarks, one has to use as many variables per pugmark as possible. Therefore, pugmarks of both leopards and brown hyenas were measured as shown in Figure 3.2 by means of calibrated vernier calipers. Only the padded parts of the pugmarks of brown hyenas were measured, excluding the markings left by nails from the measurement.

3.2 Calf Losses

Instances of calf predation from 2005 until 2008 were obtained from logbooks held in the conservancy. Each instance of calf predation from 2009 and 2010 was recorded on a standardized form noting the date, number of calves taken and the suspected predator. Losses where no predator could be positively identified were noted as such. For each instance of calf predation, the date of occurrence was correlated with the moon phase and precipitation of that day. Where possible, the responsible predator species was identified. Instances where it was uncertain which predator species was responsible were noted as such. These instances of calf predation were not included in data analysis of determining the predator species responsible for the most calf losses in the conservancy.

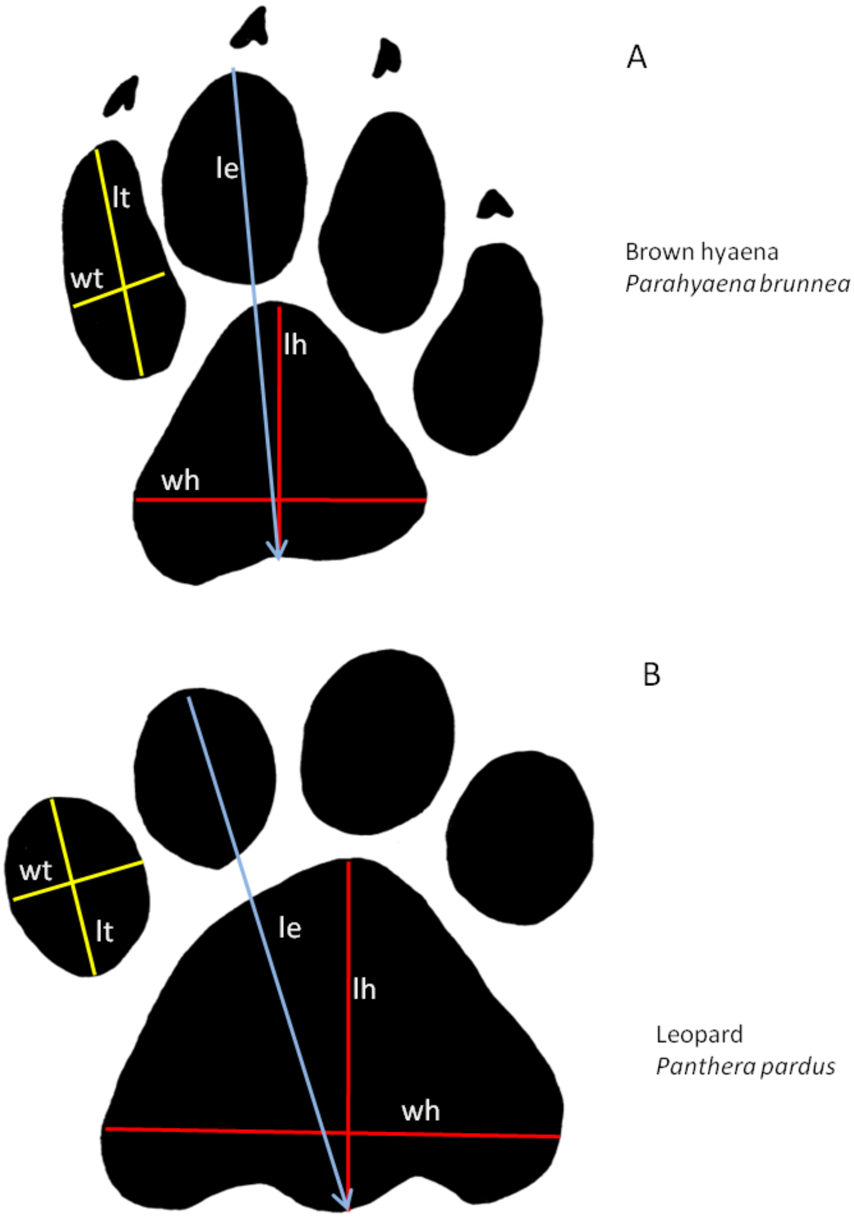

Figure 3.2 Tracks of **A,** brown hyaena and **B,** leopard redrawn and measured from gypsum casts made during the study. Abbreviations: **lh,** length of heel pad; **wh,** width of heel pad; **lt,** length of toe pad; **wt,** width of toe pad; **le,** length from the anterior tip of each toe pad to the center outline of the third evagination of the posterior heel pad.

3.3 Photographic Data

Each photograph of a predator was examined by focusing on the unique markings of each individual. The clarity of the photo and the orientation of the animal towards the camera were taken into account based on guidelines that were modified from Jackson *et al*. (2006). These guidelines suggested by Jackson *et al.* (2006) include:

a) A photograph that was poorly taken and out of focus, from which only the species could be ascertained, were only recorded as the species being present with no extra information.
b) Identification was based firstly on unique anatomical features such as a missing tail or unique scarring. Each individual brown hyena was further identified based on stripe patterns on fore and hind limbs (Fig. 3.3). Similarly, individual features of each leopard consisted of uniquely arranged groups of spots and rosettes or uniquely shaped rosettes and spatial arrangement on the face, neck, flanks, hindquarters, forelimbs, hind limbs and the dorsal surface of the tail (Fig. 3.4).
c) Each individual was assigned with at least one primary feature such as a unique spot pattern on each of the lateral flanks and two secondary features such as unique spot pattern on the legs, hindquarters, neck and face. Pelage patterns from both sides of one individual are needed in order to ensure a positive initial identification (Fig. 3.3 and Fig. 3.4).
d) The identification of at least three different corresponding features, containing one primary and two secondary features was considered efficient in order to ascertain the identity of an individual (Fig. 3.4).
e) Whenever an initial capture of an individual could not be positively matched with a previously photographed individual, the photograph was considered an initial capture of a new individual.
f) The recapture of an individual is defined as a photo where the individual could be positively identified as a previously photographed individual.

Each photograph was given a unique code and linked with the coordinates of the camera trap station, date and time of the photograph as well as the moon phase at the given time of record. The directional movement of predators was also noted.

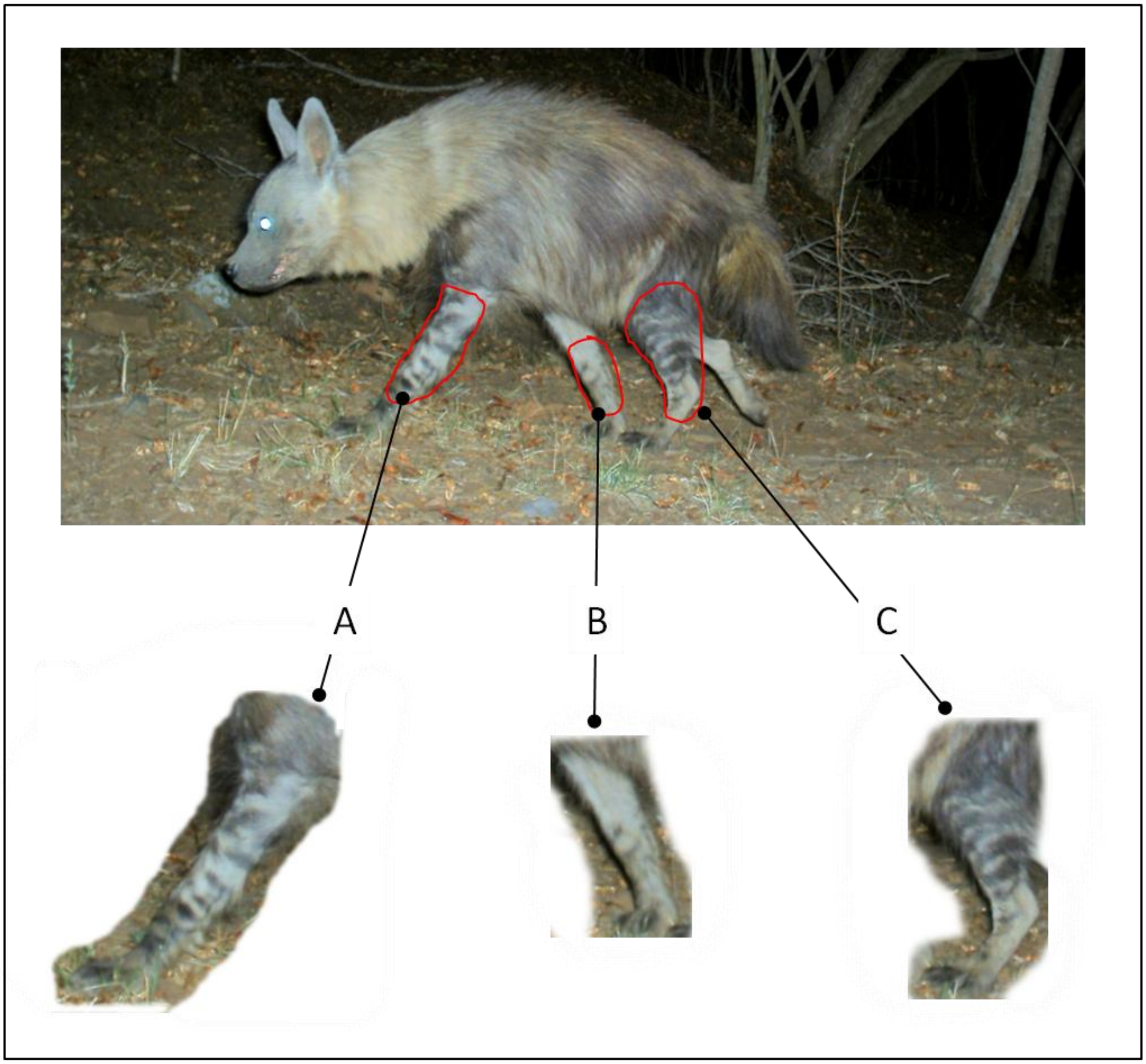

Figure 3.3 Unique stripe arrangements (areas encircled with red) of adult brown hyaenas on the **A,** fore limbs, **B,** inner limbs and **C,** hind limbs used for identification of individual animals.

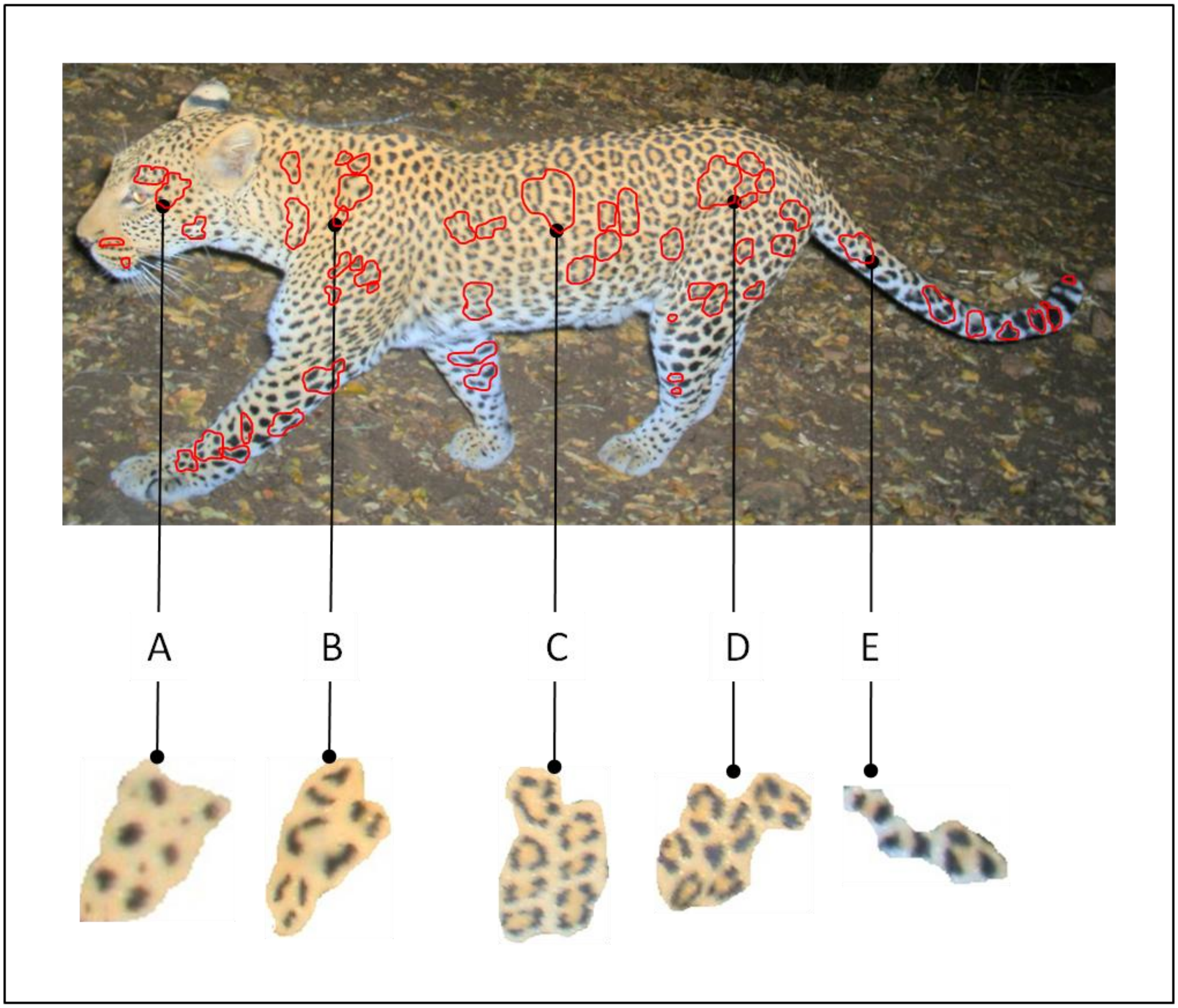

Figure 3.4 Unique spot and rosette arrangements (areas encircled with red) of leopards on the **A,** face, **B,** fore limbs and fore quarters, **C,** lateral flanks, **D,** hind quarters and hind limbs and **E,** tail used for identification of individual animals.

3.4 Moon Phases, Intensity and Circadian Rhythm Defined

In order to assess the possible influence of the intensity of moonlight on the presence or activity of potential prey and predators investigated in the Roodewalshoek Conservancy, the moon cycle was divided into a dark phase and a light phase. The dark phase of the moon was thus defined as the period from the first night of the Last quarter phase to the last night of the New moon phase, and the light phase was defined as the period from the first night of the First quarter phase to the last night of Full moon. Circadian, lunar and monthly rhythms, presence or activities were represented as the percentage of the number of observations per relevant specified period of each prey and predator species and collectively for small, medium-sized and large predators. Data used to analyze nocturnal activity patterns stretched from 18:00 to 06:00 for species which were nocturnally active. In order to assess the possible influence of the intensity of moonlight on the rates of calf predation, the moon cycle was divided into a dark phase and a light phase. Lunar and monthly patterns of calf predation were represented either as the percentage of the number of calves lost per relevant specified period or as the percentage of the number of attacks on calves per specified period.

3.5 Analytical Methods

Observations of brown hyaenas were based on camera trap and spoor data, which constituted 81% and 19% of observations, respectively. Observations of leopards were also based on camera trap and spoor data, which constituted 72% and 28% respectively, while other species were only recorded via camera traps. According to Bridges & Noss (2011) behavioural and activity patterns lend themselves particularly well to graphical representation and a number of publications relied on the inference drawn from proportional comparisons. Thus the average percentage of observations of species, as recorded with camera traps as well as through field observations, were represented in histograms according to the specific cyclical requirement such as time of day or month of the year. Microsoft Access 2007 was used to construct a database and consequent pivot charts were used to summarize all relevant information. Pearson correlation coefficients were used to test ecological relationships. Statistical correlation, regression analyses and construction of graphs were conducted with the aid of Microsoft Excel 2007.

4

Prey Ecology

CHAPTER 4
PREY ECOLOGY

4.1 Introduction

The behaviour and distribution of prey populations have a great influence on the quality of a predator's habitat and the health of predator populations in a given area. Collecting data on the ecology of the prey available to a predator is therefore essential to gaining knowledge on the ecology of the predator. It is of vital importance to understand the ecological requirements of a species in order to maintain successful conservation of that species (Balme *et al.*, 2007). The effect of terrain and habitat structure upon the distribution of a prey population is profound and ungulates will prefer the types of habitat which best answer to their habitat requirements (Maheshwari, 2006). In consequence, predators are also common in these habitat types because their requirements of food and habitat structure are met in these areas (Bakker, 1983; Kruuk, 1986; Woodroffe, 2001; Carbone & Gittleman, 2002).

Mills (1992) stated that the elucidation of the feeding ecology of large carnivores can potentially contribute a great deal in understanding their behavioural ecology. Ray *et al.* (2005) found that large carnivore density is correlated with the availability of prey in a given area and according to Breuer (2005) carnivores seem to consume the most abundant prey species in their area. A study conducted by Wegge *et al.* (2009) has contradicted the suggestion by Breuer (2005) and found that predation is highest among the most preferred prey independent of the density of such species. Cooper *et al.* (2007) stated that predation plays a key role in shaping mammalian communities by decisions and choices of both predators and prey species. Prey activity patterns, spatial distribution and availability can influence hunting success and prey selection

(Fuller *et al.*, 1992; Henschel & Skinner, 1990). Thus, resource selection by carnivores seems to be driven by prey abundance (Litvaitis *et al.* 1986; Murray *et al.* 1994; Pike *et al.* 1999; Palomares *et al.* 2001; Spong 2002) as well as landscape attributes (Stephens & Krebs 1986; Hopcraft *et al.*, 2005; Hebblewhite *et al.*, 2005). Hayward & Kerley (2005) summarized these two factors in the hypotheses that predators will select hunting areas where the risk of injury during the hunt and energy expenditure will be at its minimum.

Griffiths (1980) debated that the optimization approach of predators may not be as easily employable as was first assumed. This approach, which by definition concerns the costs and benefits associated with feeding (Griffiths, 1980), has been difficult to prove due to the difficulty associated with actually defining the costs and benefits involved. Estimated costs can be defined as the time spent in handling of the prey, the effect of the costs on the predator's growth rate and the energetic costs of the movement by the predator in order to search for prey (Stein, 1977; Elmer & Hughes, 1978; Griffiths, 1980). Several researchers (FitzGibbon & Fanshawe, 1989; Karanth & Sunquist, 1995; Bothma & Walker, 1999; Radloff & du Toit, 2004; Carnaby, 2006) suggested that predators exercise energy maximization by selectively hunting for prey type, age, body condition and gender. Carnaby (2006) further suggested that predators would regard animals without weapons such as horns, as preferred prey.

In general, prey tends to face more than one natural predator during their lifetime and therefore they must display anti-predator strategies that serve as the best form of protection against the hunting strategies of several predators (Schultz *et al.,* 2004). According to Ward *et al.* (2000) prey species which forage individually, can and will modify their behaviour in response to interference and perceived risk from predators. It was suggested by Estes (1991) and Carnaby (2006) that antelopes live in groups in order to minimize predation rates on the group and according to Schultz *et al.* (2004), predation rates decline with decreasing density of groups of prey species in a given area and with increasing group size. It would therefore seem that predation avoidance could be the primary advantage of being social.

Antelopes can follow two main types of anti-predator strategies, namely passive and active. Passive anti-predator behaviour is exhibited by most antelope species that have camouflaging coloration that allows them to blend into their surroundings and to confuse predators (Carnaby, 2006). The main form of passive defense by social species is strength in numbers. The active type of defense includes for example different patterns of flight response such as zigzagging and high jumping, which helps the antelopes to confuse predators (Estes, 1991). Antelopes also make use of alarm calls (Estes, 1991; Apps, 2000; Skinner & Chimimba, 2005; Carnaby, 2006) while females of most species will eat the afterbirth and bodily excretions of their young in order to hide their scent from potential predators.

Sharp hooves and horns are effective weapons during an attack. Carnaby (2006) pointed out that most of the antelope where both sexes are equipped with horns prefer open habitat areas or they might be nomadic in nature. He suggested that the females of such antelope species need horns to defend their offspring and themselves. According to Carnaby (2006) it would be easier for species that occupy densely vegetated habitats to hide away from predators and he suggested that horns could be a great disadvantage when moving through dense undergrowth. Carnaby (2006) concluded that females of species living in habitats of dense vegetation have no need for horns since they, and their offspring, can rely on camouflage to avoid detection by predators. It was also suggested by Carnaby (2006) that the males still need horns for territory and dominance disputes and to better their mating opportunities.

Estes (1991) suggested that the habitat preferences of prey species that prefer open habitats make such species more vulnerable to predation. Carnaby (2006) added that the social structure of ungulates can be viewed as the result of preferred habitat, diet and body size and he further suggested that open habitat types allow for greater movement and therefore favors larger groups of animals. East (1984) suggested that predator-prey relationships can be related to rainfall and vegetation productivity in African savannas. A theory suggested by Carnaby (2006) also stated that the more heavily the diet of a species depends on browsing, the less gregarious the species would be. Thus, it would seem that species occurring in habitat without dense cover tend to have larger herds, providing strength in numbers. It is also evident that small ungulates tend to have a solitary nature and occur in densely vegetated habitats, while the larger ungulates tend to favour open habitats where strength in numbers protects them against predators (Carnaby, 2006).

4.2 Prey Species: General Overview

Antelopes that were recorded in the study area seemed to show a relatively even distribution of solitary and gregarious species (Table 4.1), with the majority of antelopes being mixed feeders preferring dense, wooded habitats, using a passive form of anti-predator behaviour. During the study 16 potential prey species (>2 kg) were recorded through camera traps and field observations in the Roodewalshoek Conservancy (Table 4.2), of which one, the Helmeted Guineafowl *Numida meleagris* (Linnaeus, 1758), will not be discussed in this thesis. The remaining species are represented by the orders Ruminantia, Lagomorpha, Primates, Tubulidentata, Artiodactyla and Rodentia. According to Estes (1991), Apps (2000), Robinson (2000), Skinner & Chimimba (2005), and Carnaby (2006), five of the observed potential prey species namely the cane rat *Thryonomys swinderianus* (Temminck, 1827), Cape porcupine *Hystrix africaeaustralis* Peters, 1852, Jameson's Red rockrabbit *Pronolagus randensis* Jameson, 1907, bushpig *Potamochoerus porcus* (Linnaeus, 1758) and the aardvark *Orycteropus afer* (Pallas, 1766) are strictly nocturnal. The scrub hare *Lepus saxatilis* F. Cuvier 1823, common grey duiker *Sylvicapra grimmia* (Linnaeus, 1758), klipspringer *Oreotragus oreotragus* (Zimmermann, 1783), mountain reedbuck *Redunca fulvorufula* (Afzelius, 1815), bushbuck *Tragelaphus scriptus* (Pallas, 1766) and the greater kudu *Tragelaphus strepsiceros* (Pallas, 1766) are diurnal and nocturnal and four species, namely the vervet monkey *Cercopithecus aethiops* (Linnaeus, 1758), Chacma baboon *Papio ursinus* (Kerr, 1792), impala *Aepceros melampus* (Lichtenstein, 1812) and the warthog *Phacochoerus aethiopicus* (Pallas, 1766) are strictly diurnal (Table 4.2).

Table 4.1 Ecological separation of antelopes in the Roodewalshoek Conservancy

Category	Solitary	Gregarious
Total number of potential prey species	7	8
Size		
Small (1 - 10 kg)	3	2
Medium (10 - 50 kg)	3	3
Large (>50 kg)	3	1
Habitat preference		
Open	2	3
Dense	7	5
Diet		
Primarily grass	1	0
Mixed/browse/other	6	8
Anti-predator strategy		
Staying hidden / flight into cover	6	6
Avoid cover / flight into the open	1	2

Table 4.2 Potential prey species recorded in the Roodewalshoek Conservancy. Compiled from Estes, 1991; Apps, 2000; Skinner & Chimimba, 2005; Carnaby, 2006. M, male; F, female.

Species	Size (kg)	Habitat requirements	Social organization	Active time of day	Breeding season	Anti-predator strategy	Importance as prey species: Leopard	Importance as prey species: Brown hyaena
				Small species				
				Order Rodentia				
Cane rat *Thryonomys swinderianus* (Temminck, 1827)	M: 3.2-5.27 F: 3.4-3.8	Reed beds or thick tall grass near water	Social (?)	Crepuscular & Nocturnal	August-December	Flight into cover	Preferred	Preferred
Cape Porcupine *Hystrix africaeaustralis* (Peters, 1852)	10-24 with F>M	Any habitat type except true deserts	Monogamous pair Territorial	Nocturnal	August-January	Flight into cover	Unusual	Rare
				Order Lagomorpha				
Scrub hare *Lepus saxatilis* (F. Cuvier 1823)	1.5-4.5 F>M	Savanna woodland with mixed grass and scrub. Avoids areas of open grass and true deserts	Solitary	Nocturnal & Diurnal	Year-round but peak September-February	Zig-zag flight into cover	Preferred	Preferred
Jameson's Red rockrabbit *Pronolagus randensis* (Jameson, 1907)	1.8-3	Rocky areas	Solitary	Nocturnal	Year-round	Zig-zag flight into cover	Preferred	Preferred

Table 4.2 Continued

				Order Primates				
Vervet monkey *Cercopithecus aethiops* (Linnaeus, 1758)	5-9	Edge species associated with riverine vegetation. Wooded habitats except true rainforest	Gregarious, highly social Territorial	Diurnal	September-December	Sentinel system identifying predator, eliciting appropriate anti-predator response	Preferred	Rare
				Medium sized species				
				Order Ruminantia				
Bushbuck *Tragelaphus scriptus* (Pallas, 1766)	M: 40-80 F: 25-60	Thick, dense cover and forest edge	Solitary Non-territorial Sedentary	Nocturnal & Diurnal	Births peak in wet season	Freeze and race for nearest dense cover at last moment	Preferred	Preferred
Common duiker *Sylvicapra grimmia* (Linnaeus, 1758)	M: 12.9-18.7 F: 13.7-20.7	Broad spectrum of habitats where there is enough vegetation cover for concealment	Monogamous Territorial	Diurnal & Nocturnal	Year-round with peak in summer.	Crouching or flight into denser cover	Preferred	Preferred
Klipspringer *Oreotragus oreotragus* (Zimmermann, 1783)	M: 11.6-18 F: 15.9	Steep, rocky mountainous terrain with cliffs	Monogamous pair Territorial	Diurnal & Nocturnal	Year-round	Flight into cliffs for better vantage point	Preferred	Occasional
Mountain reedbuck *Redunca fulvorufula* (Afzelius, 1815)	M: 22-38 F: 19-35	Rolling, grassy hills, suitable floodplain and montane habitats	Social Territorial	Nocturnal & Diurnal	October-January	Crouching or flight into cover	Preferred	Occasional

Table 4.2 Continued

Impala *Aepceros melampus* (Lichtenstein, 1812)	M: 53-76 F: 40-53	Ecotone species. Light woodland with little undergrowth and grassland of low to medium height	Social Seasonally territorial	Diurnal	November-January	Flight by means of visual display called high-jumping	Preferred	Occasional
				Order Primates				
Chacma baboon *Papio ursinus* (Kerr, 1792)	M: 27-44 F: 14-17	Savanna and arid zones wherever enough water, trees & cliffs occur	Gregarious, highly social Non-territorial	Diurnal	Year-round	Sentinel system identifying predator, eliciting appropriate anti-predator response	Unusual	Rare
				Large species				
				Order Artiodactyla				
Bushpig *Potamochoerus porcus* (Linnaeus, 1758)	54 – 115	Habitat with enough concealment e.g. wooded habitats, lowland and montane forests	Gregarious, highly social Non-territorial	Nocturnal	October-November	Flight into concealment followed by feinted/actual attack	Preferred	Rare
Warthog *Phacochoerus aethiopicus* (Pallas, 1766)	M: 62-100 F: 45-71	Open savanna	Social Sedentary	Diurnal	October-December	Flight to underground refuge followed by feinted/actual attack	Occasional	Rare

Table 4.2 Continued

Warthog *Phacochoerus aethiopicus* (Pallas, 1766)	M: 62-100 F: 45-71	Open savanna	Social Sedentary	Diurnal	October-December	Flight to underground refuge followed by feinted/actual attack	Occasional	Rare
				Order Ruminantia				
Greater Kudu *Tragelaphus strepsiceros* (Pallas, 1766)	M: 190-315 F: 120-215	Thicket and bush habitat with adequate cover	Social Non-territorial Sedentary	Diurnal & Nocturnal	January-March	Crouch, sneak away silently. Takes flight at last moment	Occasional	Rare
				Order Tubulidentata				
Aardvark *Orycteropus afer* (Pallas, 1766)	40-100	Main requirement: supply of termites & ants as food source	Solitary Territorial	Nocturnal	May-August	Flight into underground refuge	Occasional	Occasional

4.3 Results

4.3.1 Monthly Presence of Prey Species

The presence of recorded prey species in sampled areas showed a monthly variation, with some prey species present all year round while others showed definite periods of occurrence. Rainfall seemed to have some influence on the occurrence of such species, with a weak positive correlation (R^2 = 0.1612; r = 0.4056) found between the presence of prey species and precipitation. During the summer months (September to March) a weak negative correlation (R^2 = 0.0832; r = -0.2885) was calculated between occurrence of prey and predators. However, during winter (April to August) a stronger negative correlation (R^2 = 0.1025; r = -0.3202) was calculated between the occurrence of prey and predators in sampled areas. Most small potential prey species was observed continuously during the winter months and only sporadically during summer (Fig. 4.1). Medium potential prey species which occurred on a constant basis throughout the year in the study area include bushbuck, Chacma baboons and common grey duikers (Fig. 4.2). Sporadic occurrence of impala and mountain reedbuck were encountered mostly during the mid-summer months, especially during December, while only impala were present during the end of winter and the onset of spring. All species classified as large prey were continuously present throughout the year, except for the aardvark which showed a sporadic presence in sampled areas and were mostly observed during mid-summer (Fig. 4.3).

Social species, including the bushpig, cane rat, Cape porcupine, Chacma baboon, greater kudu, impala, mountain reedbuck and warthog only occurred sporadically during the year (Fig. 4.1 to Fig. 4.3). Similar intermittent incidences of occurrence were observed for solitary species with the exception of common grey duikers which were present all year round. During late summer (March) and mid-winter (June) the presence of different kinds of prey were the lowest with almost half (44%) of observed species absent from the conservancy at these times (Fig 4.1 to 4.3). The highest incidence of prey occurrence was observed to be during late autumn (April and May) and mid-summer (November and December). Overall, Chacma baboons, common grey duikers and bushbuck (Fig. 4.2) were most frequently present, while vervet monkeys *Cercopithecus aethiops* (Linnaeus, 1758), Jameson's red rockrabbit *Pronolagus radensis* Jameson, 1907 and cane rats were rarely encountered.

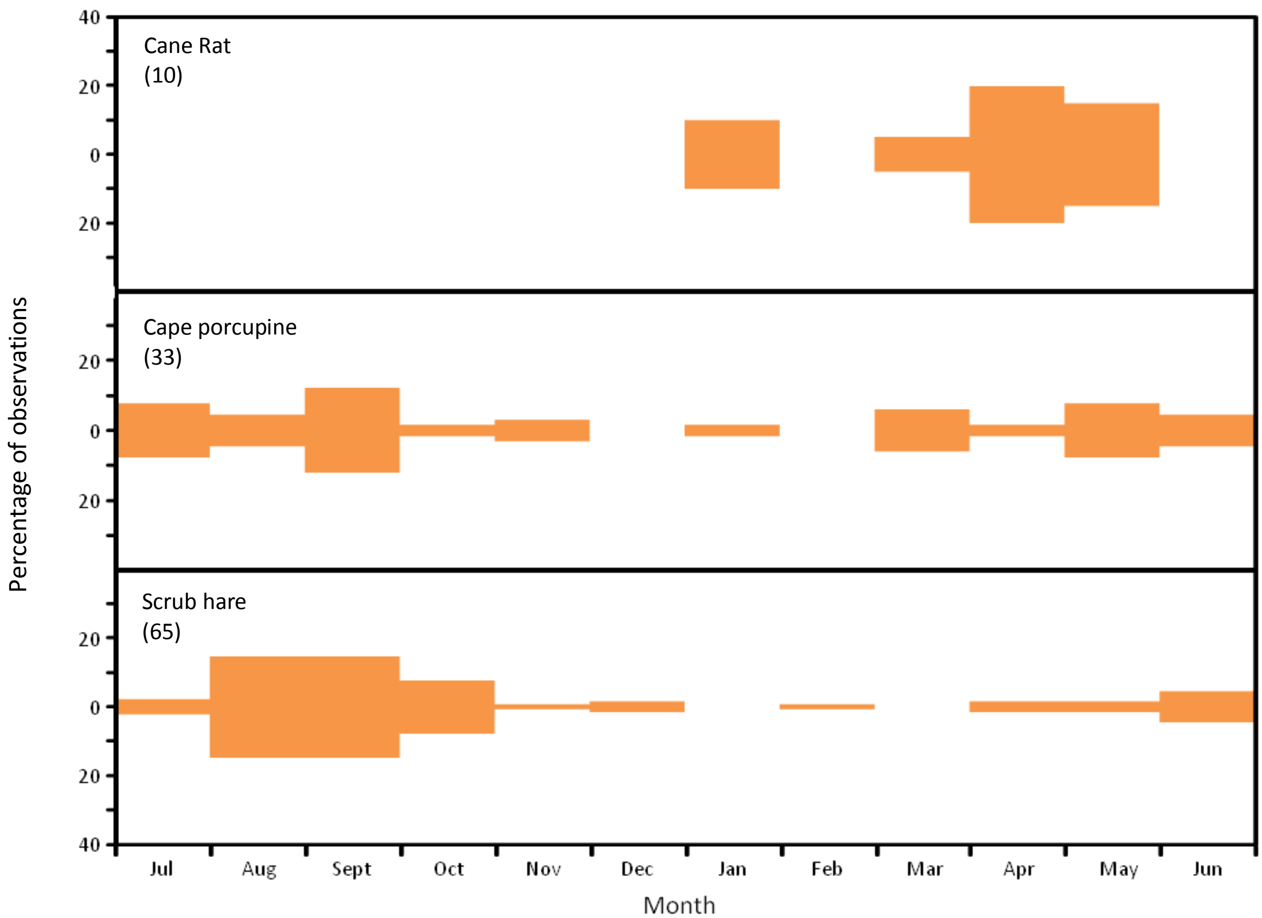

Figure 4.1 Monthly presence of small potential prey species in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations.

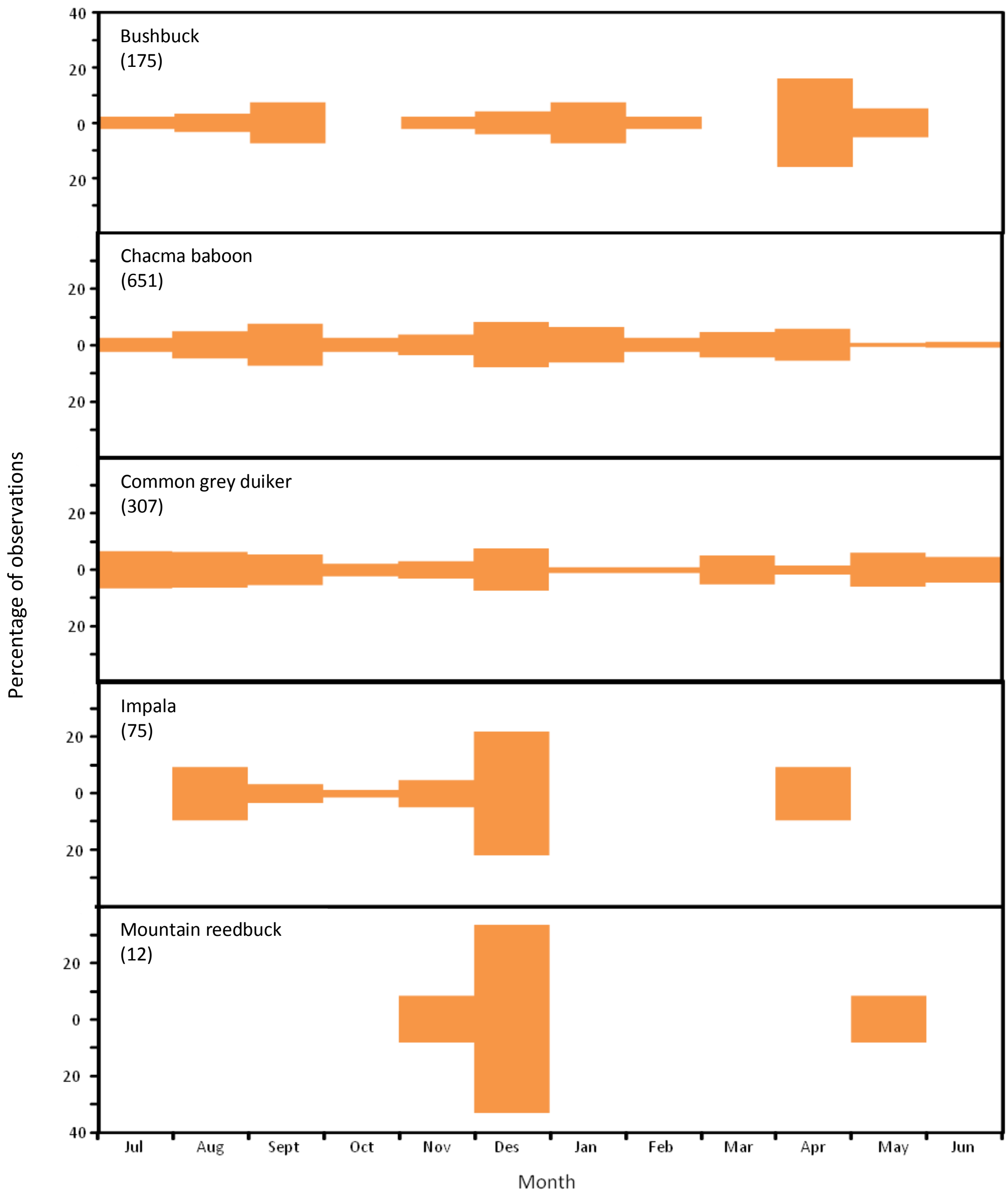

Figure 4.2 Monthly presence of medium potential prey species in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations.

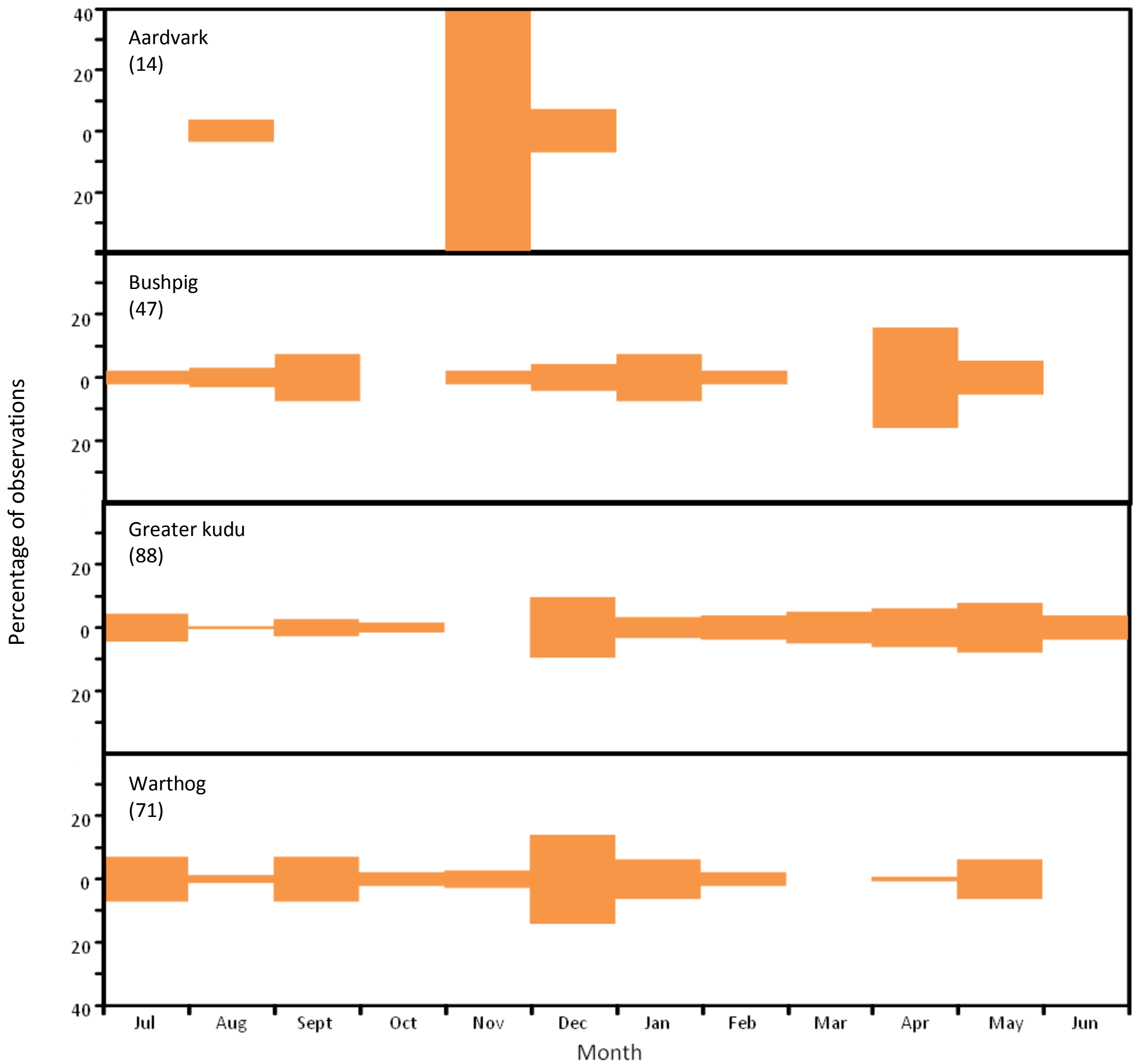

Figure 4.3 Monthly presence of large potential prey species in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations.

4.3.2 Circadian Rhythms of Prey Species

Circadian rhythms of both diurnal and nocturnal prey species in sampled areas showed definite periods of activity. All small prey species are nocturnal. Cane rats and Cape porcupines displayed some periods of inactivity, while scrub hares were continuously active (Fig. 4.4). In contrast with small prey, most medium prey species were active during the day, with the exception of bushbuck, common duikers and to a lesser extend mountain reedbuck which displayed nocturnal activity as well (Fig. 4.5). Of all large prey species only greater kudus and warthogs were diurnally active, while aardvark and bushpigs were observed to be active from early evening to early morning. Warthogs, usually described as a strict diurnal species, showed some activity well into the hours after dark and early mornings before sunrise. Not only did the periods of activity of most diurnal prey species match, assemblages where different species were seen together were also noted. Baboon troops, accompanied by common grey duikers, bushbuck, impala and sometimes various ungulate species were observed.

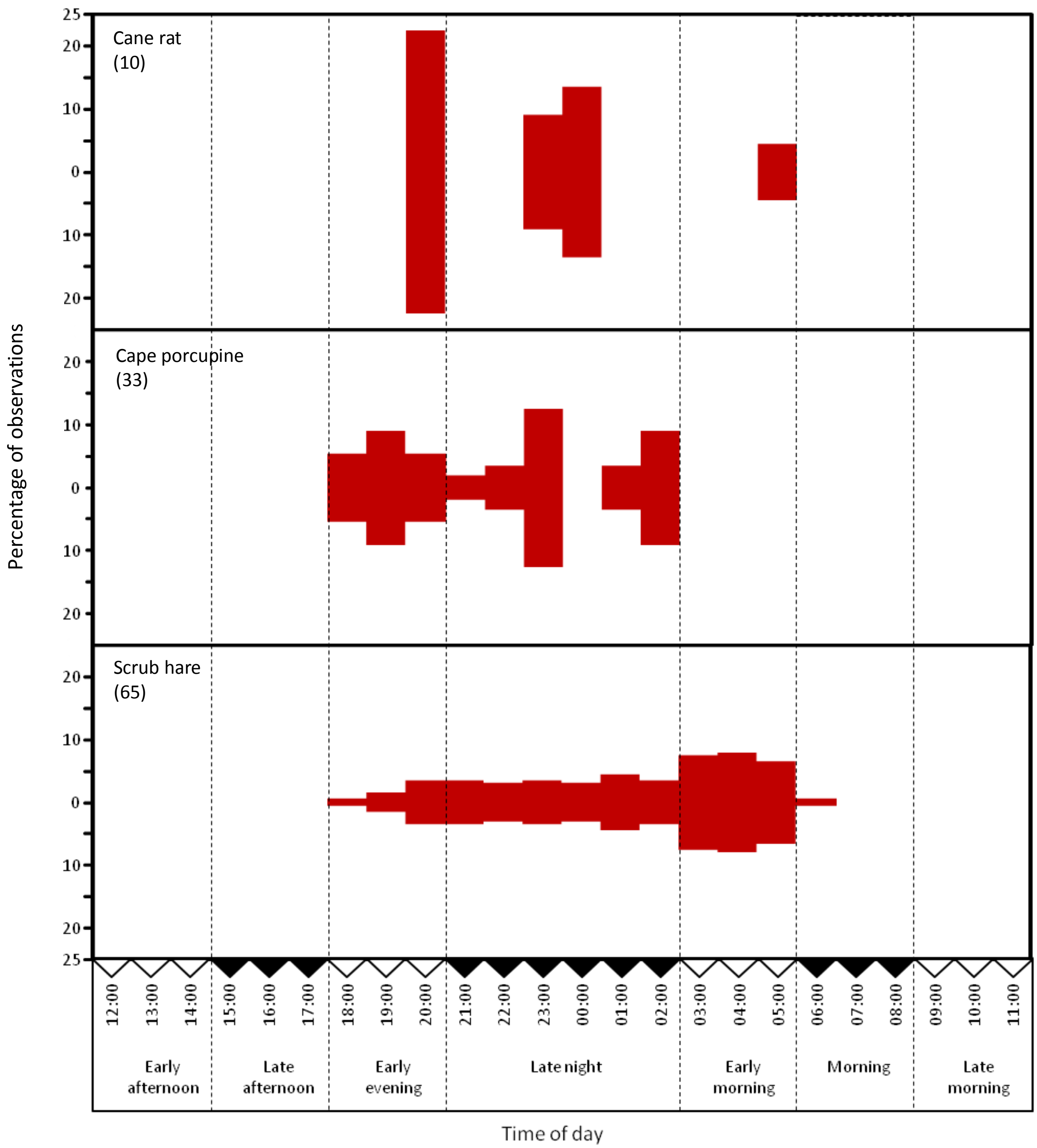

Figure 4.4 Circadian rhythm of small prey species in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations.

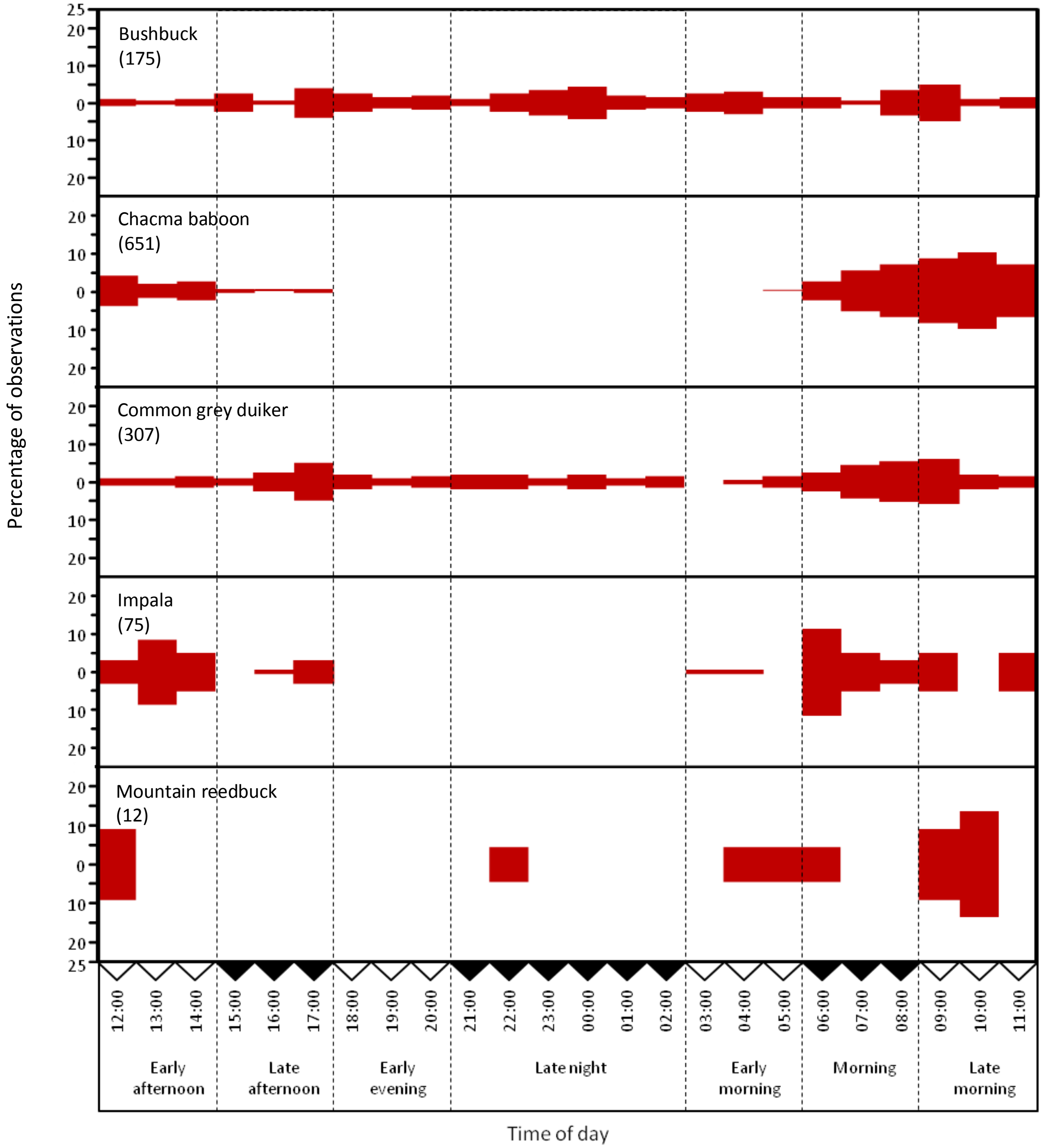

Figure 4.5 Circadian rhythm of medium prey species in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations.

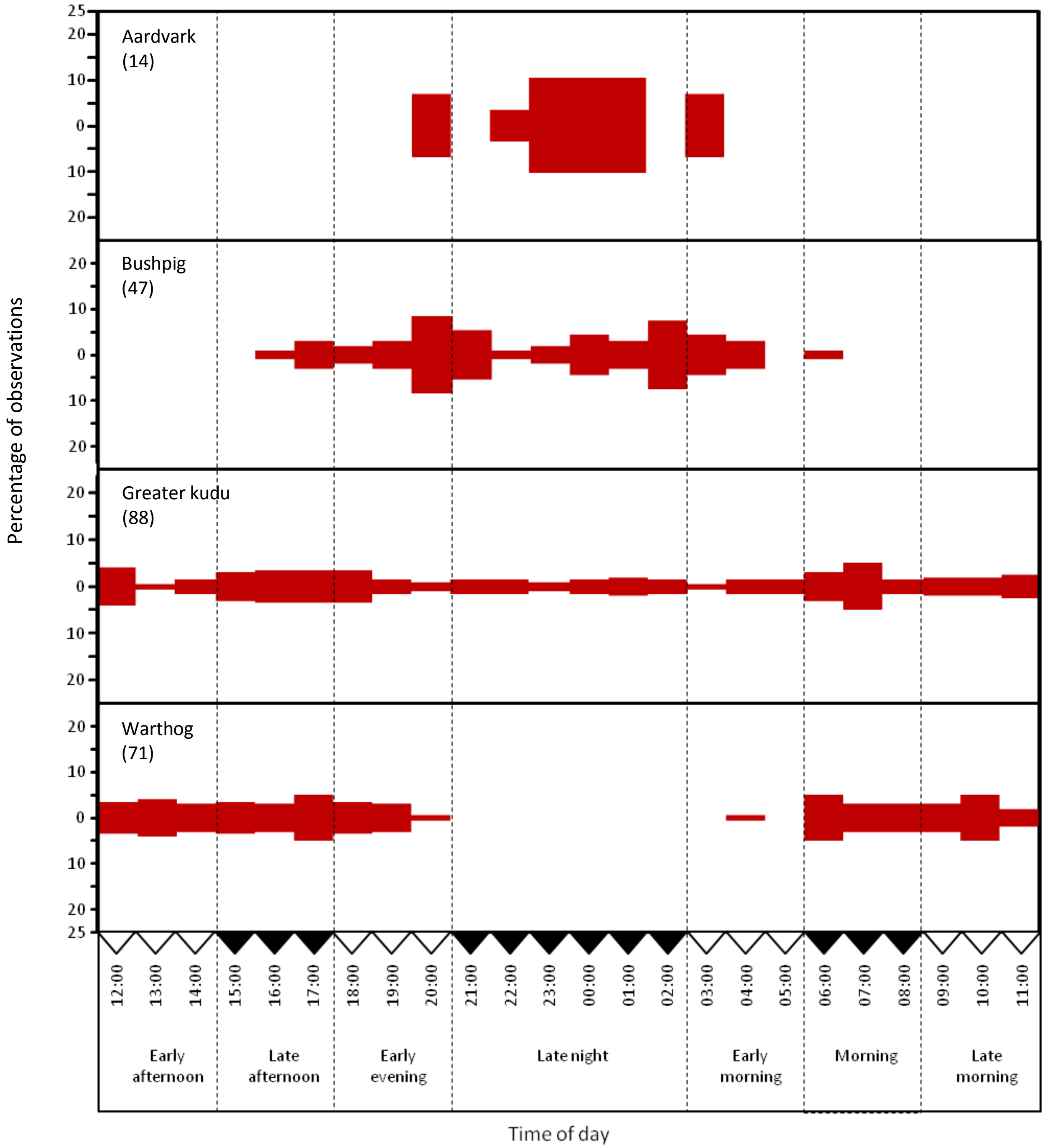

Figure 4.6 Circadian rhythm of large prey species in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations.

4.3.3 Potential Prey Activity as it Relates to the Lunar Cycle

The nocturnal activity of prey species in sampled areas seemed to differ according to changes in moonlight intensity. Some species did not show a definite preference for specific moonlight intensity while others showed definite periods of increased activity during different stages of the moon cycle. A general trend observed was that these animals increased their nocturnal activity as moon light intensity increases from the New Moon to First Quarter phase, followed by a gradual decrease in activity as moonlight intensity decreases towards Last Quarter. However, no statistical correlation could be found between the nocturnal activity of prey species and moonlight intensity ($R^2 = 0.0798$; $r = 0.2825$).

All small prey species, with the exception of cane rats, occurred continuously irrespective of moonlight intensity (Fig. 4.7). Most cane rats were only active when moonlight intensity was low. The majority of medium sized prey species were observed when moonlight intensity is high (Fig. 4.8). Although bushbuck and common grey duikers were both active during all different moonlight intensities, both these antelope species were most active when moonlight intensity was high. However, mountain reedbuck were solely active during times of high luminescence. In general, no definite preference for a specific light phase of the moon could be identified for large prey species (Fig. 4.9). Bushpigs and greater kudus were present during all moon phases, while aardvark seemed to avoid high moonlight intensities.

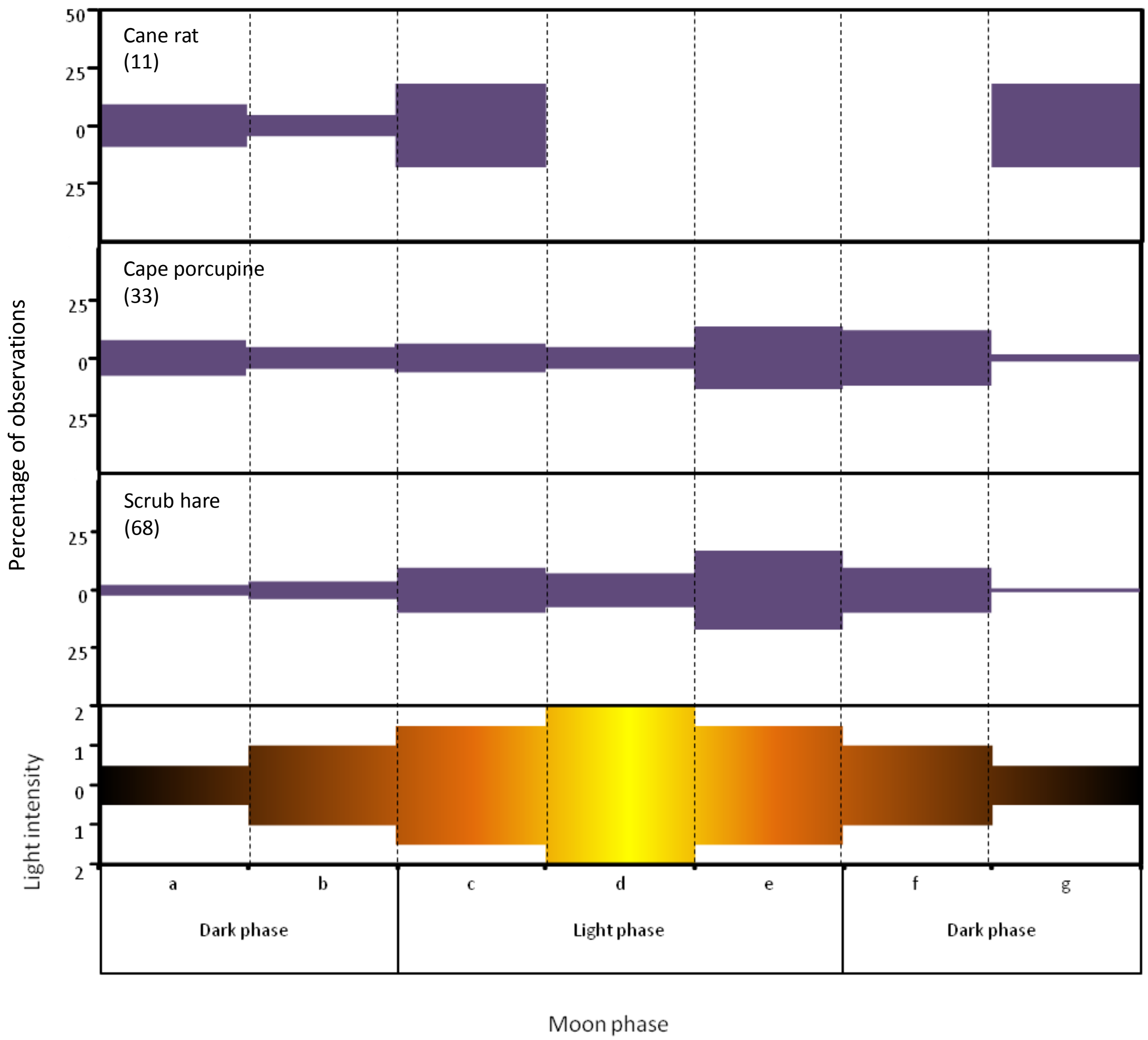

Figure 4.7 Nocturnal activity of small potential prey species during periods of lunar light in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. **a,** period from new moon to 3rd night after new moon; **b,** period from 4th night after new moon to night before first quarter; **c,** period from first quarter to 5th night after first quarter; **d,** period from 6th night after first quarter to 3rd night after full moon; **e,** period from 4th night after full moon to 7th night after full moon; **f,** period from last quarter to 5th night after last quarter; **g,** period from 6th night after last quarter to night before new moon. Numbers between brackets indicate number of observations.

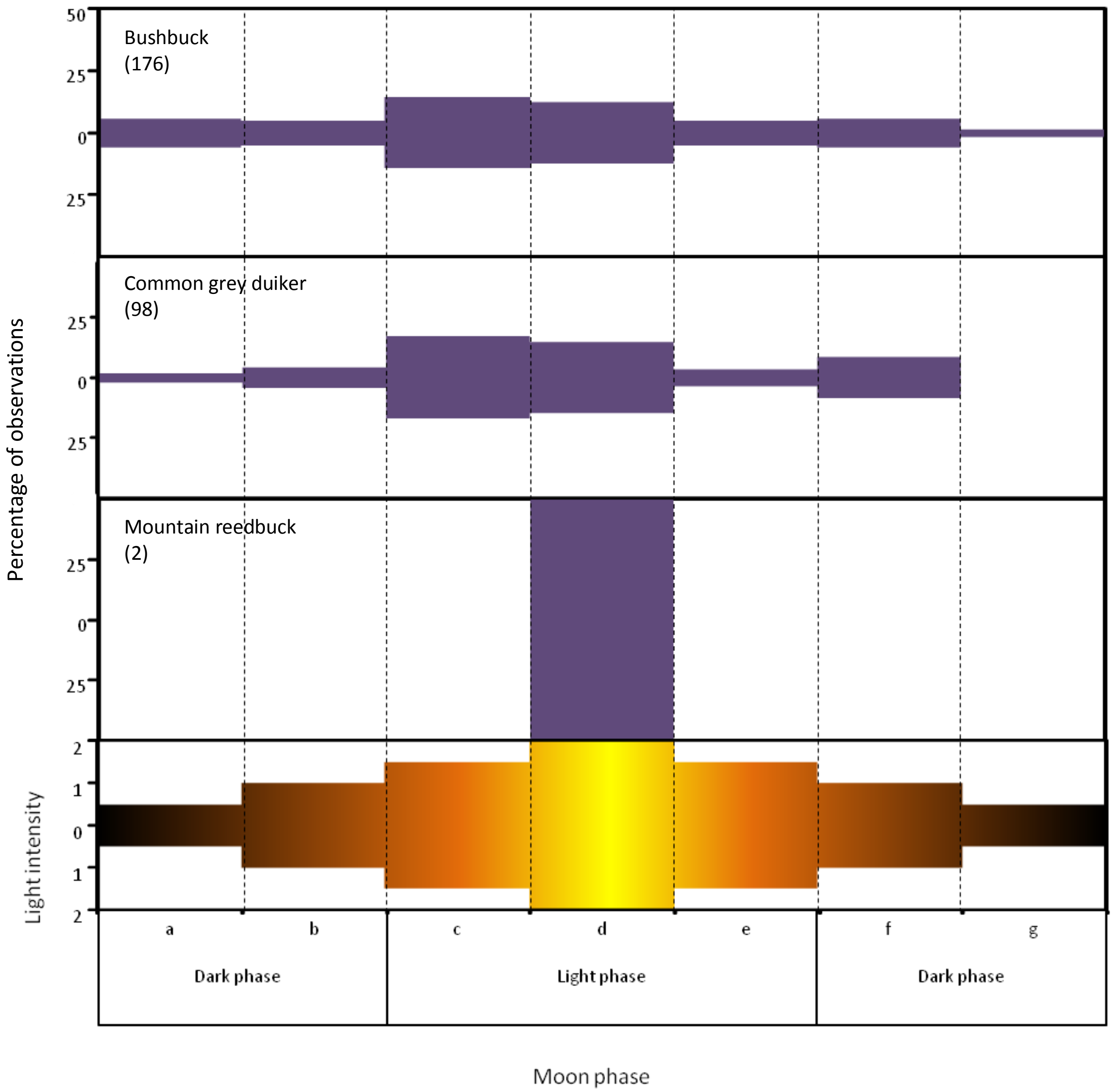

Figure 4.8 Nocturnal activity of medium sized potential prey species during periods of lunar light in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. **a,** period from new moon to 3rd night after new moon; **b,** period from 4th night after new moon to night before first quarter; **c,** period from first quarter to 5th night after first quarter; **d,** period from 6th night after first quarter to 3rd night after full moon; **e,** period from 4th night after full moon to 7th night after full moon; **f,** period from last quarter to 5th night after last quarter; **g,** period from 6th night after last quarter to night before new moon. Numbers between brackets indicate number of observations.

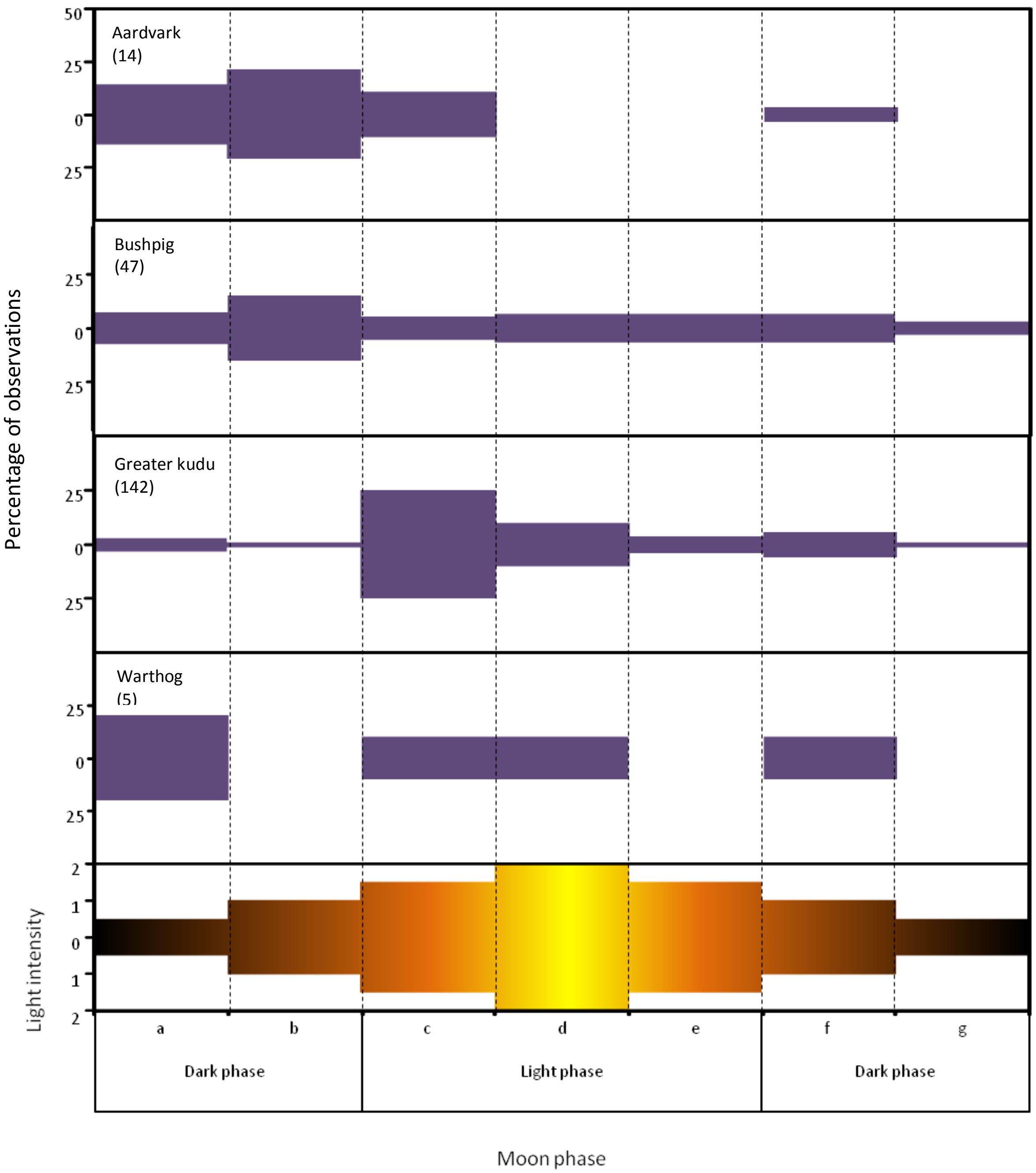

Figure 4.9 Nocturnal activity of large potential prey species during periods of lunar light in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. **a,** period from new moon to 3rd night after new moon; **b,** period from 4th night after new moon to night before first quarter; **c,** period from first quarter to 5th night after first quarter; **d,** period from 6th night after first quarter to 3rd night after full moon; **e,** period from 4th night after full moon to 7th night after full moon; **f,** period from last quarter to 5th night after last quarter; **g,** period from 6th night after last quarter to night before new moon. Numbers between brackets indicate number of observations.

4.4 Discussion

Prey availability and the ecology of available prey species dictate the ecology of predators in a given area (Bakker, 1983; Kruuk, 1986; Henschel & Skinner, 1990; Fuller *et al.*, 1992; Mills, 1992; Woodroffe, 2001; Ray *et al.*, 2005; Cooper *et al.*, 2007). Different factors respectively contribute to a varying degree to prey-selection by predators (FitzGibbon & Fanshawe, 1989; Estes, 1991; Karanth & Sunquist, 1995; Bothma & Walker, 1999; Radloff & du Toit, 2004; Schultz *et al.*, 2004; Carnaby, 2006). Physical prey size, social structure, anti-predator behaviour and preferred habitats (Estes, 1991; Carnaby, 2006) play very important roles in that social antelope species in open habitats are more conspicuous to a predator, but have more strength in the number of vigilant eyes compared to solitary antelopes that occupy dense habitats.

The main forms of passive anti-predator defence are camouflage and strength in numbers (Estes, 1991; Skinner & Chimimba, 2005; Carnaby, 2006) and both of these strategies were successfully displayed by potential prey species in the conservancy. Social species in the conservancy were found more frequently in the less dense areas where they can easily spot a predator, while solitary prey species occurred more frequently in dense riparian forest where they rely heavily on camouflage to remain hidden. It was suggested by Balme *et al.* (2007) that reduced detectability of prey in dense vegetation can lead to a smaller number of prey animals killed in habitats with dense cover compared to habitats with intermediate cover. All the potential prey species displayed effective active anti-predator strategies. Impala, common grey duikers, bushbuck and occasionally mountain reedbuck foraged in the presence of a Chacma baboon troop, which can be interpreted as a cooperative effort to better detect the presence of a predator.

Leopards and brown hyenas are nocturnal predators and were also observed as such in the conservancy. They rarely showed signs of activity during daylight hours. These two species are also opportunistic hunters and considered to have a catholic diet

(Mills, 1978; Owens & Owens, 1978; Mills, 1982; Hes, 1991; Hopcraft *et al.*, 2005; Al-Johany, 2007; Bothma & Le Riche, 1984; Mills, 1994; Bailey, 1995). This may play a role in dictating the behavioural patterns of some especially the medium sized ungulates since they comprise a big proportion of the diet of these predators (Hes, 1991; Bailey, 1995; Hart *et al.*, 2008). Maude (2005) and Georgiadis *et al.* (2007) suggested that predators tend to prey more often on the most abundant prey species in their area.

The most abundant species in the conservancy included Chacma Baboon (n = 658), common grey duiker (n = 309), greater kudu (n = 271), bushbuck (n = 175) and impala (n = 75). Medium sized mammals feature prominently in the diet of leopards and brown hyenas (Mills, 1982; Bothma & Le Riche, 1984; Hes, 1991; Estes, 1991; Mills, 1994; Bothma & Walker, 1999; Chauhan *et al.*, 2000; Kuhn, 2008) and prey are influenced by habitat type (Chauhan *et al.*, 2000; Carnaby, 2006). According to Hayward *et al.* (2006), the leopard's preferred prey species include animals with a body mass of 10 – 40 kg which in the Roodewalshoek conservancy include impala, bushbuck and common grey duiker. Although the greater kudu was classified as a rare prey item for leopards and brown hyaenas, this antelope species exhibited nocturnal behavior in the conservancy, which means that kudu juveniles could be regarded as potential prey for these carnivores. Therefore, most abundant prey available was Chacma baboons, common grey duikers, bushbuck, impala as well as juvenile greater kudus. The collective social composition of these prey species seems to be equally solitary and social and also equally diurnal and nocturnal. Common grey duikers and bushbuck showed both diurnal and nocturnal activity, which would probably make these antelope species more vulnerable to predation by nocturnal predators compared to the diurnal Chacma baboons and impala.

Peaks in hourly activity throughout the day were unique to each species, although some species showed activity peaks during the same periods. Bushbuck, impala and warthog showed increased activity during the early morning, indicating that these species utilize the first light of day to move between feeding localities. Therefore early morning seem to be the best time to observe or record bushbuck, impala and warthogs. Except for the warthog, these animals are of medium size and regarded as preferred prey species. The behaviour to be active during the early mornings can be to avoid potential contact with nocturnal predators. Activity of nocturnal prey species aardvark, Cape porcupine, bushbuck, and common grey duiker, seemed to peak during the late hours of the night and this would then be the best time of day to record and observe these animals. These species are not highly social, occur mostly in densely vegetated habitats and tend to rely mostly on camouflage to avoid predation. It would therefore be more beneficial to these species to be active when visibility is low and the chances of a predator detecting them are reduced.

Prey were observed more often during the drier months in the sampled areas and the reason for this may be that they are more dependent on the water provided by the perennial river during this time of year. It may also be a result of reduced chances of being observed due to thicker vegetation in summer and better visibility stemming from drier vegetation during winter. During December, most prey species give birth to their young and it seems that they prefer to do so in this area which provides ample cover and easily accessible water (Fairall, 1968). In accordance to the findings of Bailey (1995) and Augustine (2002), impala seemed to prefer more densely vegetated habitats during the dry season and this may be due to the fact that they tend to feed on browse more during this time.

Moonlight intensity plays a vital role in the activity of nocturnal prey species (Van Rensburg, 1965). In general, prey increased their nocturnal activity from the New Moon to the First Quarter phase of the moon, while a decrease in activities are noticeable towards the Last Quarter phase. High luminescence will increase visibility for both predators and prey and both kinds must avoid visual detection by the other. Low luminescence will result in poor visibility for both predators and prey. It would therefore seem that most nocturnal prey species prefer to be active when visibility is moderate, enabling them to better detect predators while the possibility of being detected is decreased. Leopards and brown hyena prefer to hunt medium sized prey (Mills & Mills, 1978; Owens & Owens, 1978; Mills, 1982; Bothma & Le Riche, 1984; Skinner & Chimimba, 2005; Hes, 1991; Estes, 1991; Mills, 1994; Bothma & Walker, 1999; Carnaby, 2006). In the Roodewalshoek Conservancy seemingly preferred prey species occur abundantly and the effect of the activity patterns of these prey species on the activity patterns of leopards and brown hyenas will be discussed in Chapter 6.

5

Leopards, Brown hyaenas and Other Carnivores

CHAPTER 5
LEOPARDS, BROWN HYAENAS AND OTHER CARNIVORES

5.1 Introduction

Little doubt exists regarding the existence of interspecific competition in natural communities (Connell, 1983; Schoener, 1983; Gurevitch, *et al*., 1992; Denno, *et al*., 1995; Grover, 1997) and that this competition serves as an important determinant in the overall composition of natural communities (Cody & Diamond, 1975; Diamond & Case, 1986; Morin, 1999). However, uncertainty still remains about the biological influences lessening or intensifying competition between species, and the impact thereof on population densities and the community structure in an area (Chesson & Huntley, 1997; Gurevitch *et al*., 2000). According to Chase *et al.* (2002), predation is only one of the factors that have a major impact on competitive interactions between species.

The population distribution and behaviour of potential prey species have a significant influence on the quality of habitat available to a predator and therefore indirectly affects the health of predator populations in an area. Spatial arrangement, availability and activity patterns of prey species have been known to not only influence the selection of preferred prey, but also the hunting success of predators (Fuller *et al*., 1992; Henschel & Skinner, 1990). Habitat structure of an area has an effect on the spatial distribution and activity of potential prey species. This will then influence the types of preferred habitat of predators (Bakker, 1983; Kruuk, 1986; Woodroffe, 2001; Maheshwari, 2006). Eleven carnivore species were recorded to be present in the Roodewalshoek conservancy, including the leopard and brown hyaena (Table 5.1).

Small predators with a body mass smaller than 10 kg, included the African civet *Civettictis civetta* (Schreber, 1776), honey badger *Mellivora capensis* (Schreber, 1776), large-spotted genet *Genetta tigrina* (Schreber, 1776), marsh mongoose *Atilax paludinosus* (G. Cuvier, 1829) and the slender mongoose *Galerella sanguinea* (Rüppel, 1836). Medium sized predators, species ranging in weight from 10 to 30 kg, included the Cape clawless otter *Aonyx capensis* (Schinz, 1821), caracal *Felis caracal* (Schreber, 1776), serval *Felis serval* (Schreber, 1776), side-striped jackal *Canis adustus* (Sundevall, 1846). The only large carnivores recorded in the Roodewalshoek conservancy, with weight larger than 30 kg, was the leopard and the brown hyaena (Table 5.1). Of all eleven carnivorous species encountered in the Roodewalshoek Conservancy, only two, the Cape clawless otter and the brown hyaena are presumed to be social. Detailed information on the ecological characteristics of carnivores is summarized in Table 5.1.

Table 5.1 Ecological characteristics of carnivores present in the Roodewalshoek Conservancy summarized from Estes, 1991; Apps, 2000; Skinner & Chimimba, 2005; Carnaby, 2006. M, male; F, female.

Species	Size (kg)	Habitat requirements	Social organization	Active time of day	Breeding season	Diet	Hunting strategy
Small predator species							
African civet *Civettictis civetta* (Schreber, 1776)	7-20	Most habitat types	Solitary Territorial Sedentary	Nocturnal	August-January	Insects, invertebrates, vertebrates up to the size of new-born antelope, carrion, fruit, vegetables	Run & pounce predator that uses death shake to kill prey
Honey badger *Mellivora capensis* (Schreber, 1776)	8.0-14.5	Very dry to wet conditions, only absent from true deserts	Monogamous pairs	Diurnal & Nocturnal	Summer months	Opportunistic insectivore and carnivore – catch insects to young of large vertebrates, carrion, fruit. Specialize in feeding on bees and bee-larvae	Forage thoroughly, relying on sense of smell to detect prey
Large-spotted genet *Genetta tigrina* (Schreber, 1776)	M: 1.4-3.2 F: 1-2.5	Forests, arid bush and forest fringes with adequate drinking water	Solitary Polygynous Presumed territorial	Nocturnal	August-March	Insects, small mammals, invertebrates, frogs, birds, fruit	Stalk, rush & pounce, kills with several bites
Marsh mongoose *Atilax paludinosus* (G. Cuvier, 1829)	2.5-5.0	Near water and areas with sufficient cover	Solitary Territorial	Nocturnal & Crepuscular	August-February	Snails, freshwater crabs, frogs, fish, insects, marsh birds, eggs, reptiles, worms, carrion	Wade & grope in shallow water. Detect prey with hands
Slender mongoose *Galerella* sanguinea (Rüppel, 1836)	M: 0.5-0.7 F: 0.3-0.5	Forest fringes, woodland scrub and grassland with enough cover	Solitary Polygynous Territorial	Diurnal	October-March	Small vertebrates and insects	Chase & pounce predator. Does not administer death shake to kill prey
Medium sized predator species							
Cape Clawless Otter *Aonyx capensis* (Schinz, 1821)	M: 10-18 F: 12-16	Small & large streams, lakes, ponds, swamps	Presumed social Clan hold territory	Diurnal & Nocturnal	Year-round, peak at end of dry season	Crabs, frogs, fish, insects, snakes, waterbirds, molluscs	Probe & grasp prey with hands

Table 5.1 Continued

			Medium sized predator species				
Caracal *Felis caracal* (Schreber, 1776)	M: 12-18 F: 8-13	Arid bush & savanna, rocky hills, mountainous areas with enough cover	Solitary Territorial	Nocturnal & Crepuscular	October-February	Small to medium sized mammals, birds, reptiles	Stalk & pounce followed by suffocation by means of a throat-bite
Serval *Felis serval* Schreber, 1776	M: 10-18 F: 8.7-12.5	Near water in grassland savanna, marshland, montane grassland, along edges of forests	Solitary Territorial	Diurnal & Nocturnal	Births peak during wet season	Specialize in catching rodents and birds that live in tall grass. Birds up to the size of flamingos, snakes, lizards, frogs, fish, insects, young of small-medium sized antelope	Stalk & pounce followed by suffocation by means of a throat-bite
Side-striped jackal *Canis adustus* (Sundevall, 1846)	M: 7.3-12 F: 4.3-10	Woodland, grassland, marshes with good ground cover, montane habitats	Monogamous Territorial pairs	Nocturnal	August-October	Small mammals, fruit, insects, carrion	Rush & grab
			Large predator species				
Brown hyaena *Parahyaena brunnea* (Thunberg, 1820)	35-50 F>M	Dry savanna areas	Social Clan defends territory	Nocturnal & Diurnal	Year-round	Opportunistic predator of vertebrates up to the size of young of large mammals. Invertebrates, insects, birds, plant material, carrion	Rush & grab
Leopard *Panthera pardus* (Linnaeus, 1758)	M: 35-65 F: 25-58	Any habitat type with enough cover and a variety of small-medium sized mammals	Solitary Territorial	Nocturnal & Crepuscular	Year-round	Medium sized antelopes, young of larger antelopes, small vertebrates, birds, small carnivores, reptiles	Ambush & stalk, kills prey with bite to throat or nape of neck

5.2 The Leopard *Panthera pardus pardus* (Linnaeus, 1758)

5.2.1 Taxonomic Notes

Class: Mammalia Linnaeus, 1758

Order: Carnivora Bowdich, 1821

Family: Felidae G. Fischer de Waldheim, 1817

Genus: *Panthera* Oken, 1816

Species: *P. pardus* (Linnaeus, 1758) Pocock, 1916

Sub-species: *P. pardus pardus*

The leopard was originally described by Carl Linnaeus in 1758 as *Felis pardus* from a specimen collected in Egypt. It was first placed in the genus *Panthera* by R.I. Pocock in 1916 (Bothma & Walker, 1999). The first known felids date back 40 million years ago to the upper Eocene era. Representatives of the modern cats, subfamily Felinae, have existed since the Miocene, 24 million years ago (Estes, 1991). From then on, until a few million years ago, saber-toothed cats dominated the family. Modern big cats arose as predators on modern ungulates and the golden cat *Profelis aurata* (Temminck, 1827) and the caracal *Felis caracal* (Schreber, 1776) are considered to be survivors of an earlier radiation (Estes, 1991). The leopard, along with the jaguar (*P. onca*) (Linnaeus, 1758), tiger (*P. tigris*) (Linnaeus, 1758), lion (*P. leo*) (Linnaeus, 1758) and snow leopard (*P. uncia*) (Schreber, 1775), consist of the relatively young felid genus *Panthera* (Uphyrkina *et al.,* 2001) thought to have diverged 2 to 3 million years ago from a common ancestor (Johnson & O'Brien, 1997). Fossil evidence as old as 1.5 to 2.0 million years suggest that leopards were once more widely distributed than today (Maheshwari, 2006), reflecting the astounding adaptiveness of these animals. Uphyrkina *et al*. (2001) estimated an origin for modern leopard lineages to be 470 000 – 825 000 years ago in Africa, which was followed by migration into and across Asia approximately 170 000 – 300 000 years ago. The discussion around subspecies is controversial (Hes, 1991). Fossil records for leopards and other cats belonging to the genus *Panthera*, together with the extensive geographical distribution of leopards and varying morphological characteristics led to the naming of 27 subspecies in early taxonomic descriptions (Uphyrkina *et al.,* 2001). Currently however, according to Miththapala *et al.* (1996) and Uphyrkina *et al.* (2001), there are nine recognized subspecies of leopards namely:

Panthera pardus delacourii Pocock, 1930 from southeast Asia into southern China

Panthera pardus fusca (Meyer, 1794) on the Indian sub-continent

Panthera pardus japonensis (Gray, 1862) in northern China

Panthera pardus kotiya Deraniyagala, 1956 in Sri Lanka

Panthera pardus melas (Cuvier, 1809) in Java

Panthera pardus nimr (Hemprich & Ehrenberg, 1833) in Arabia

Panthera pardus orientalis (Schlegel, 1857) from the Russian Far East, Korean peninsula and north-eastern China

Panthera pardus pardus (Linnaeus, 1758) in Africa

Panthera pardus saxicolour Pocock, 1927 in Central Asia

No other large African carnivore is as shy, secretive and elusive as the leopard (Hes, 1991; Hancock, 2000; Bothma & Walker, 1999). Bailey (1993) stated that the leopard is the least studied of all African mammalian species and Maheshwari (2006) added that it is less studied than any other big cat such as lions. Up until the 1970's the leopard remained relatively unstudied in the wild (Eisenberg & Lockhart, 1972; Schaller, 1972; Muckenhirn & Eisenberg, 1973; Guggisberg, 1975) and the first intensive study was carried out by Hamilton (1976) in Kenya. From the 1980's to the present, leopards were studied on a more ongoing basis by numerous researchers (Bothma & Le Riche, 1984; Le Roux, 1984; Norton & Lawson, 1985; Bothma & Le Riche, 1986; Norton & Henley, 1987; Le Roux & Skinner, 1989; Hes, 1991; Mills & Biggs, 1993; Bailey, 1993; Bothma, & Le Riche, 1995; Miththapala, *et al.,* 1996; Chauhan *et al.* 2000; Hancock, 2000; Henschel, 2001; Henschel & Ray, 2003; Hunter *et al.,* 2003; Uphyrkina & O'Brien, 2003; Balme & Hunter, 2004; Santiapillai & Jayewardene, 2004; Bothma 2005; Hayward *et al.,* 2006; Bothma & Bothma, 2006; Maheshwari, 2006; Schwarz & Fischer, 2006; Balme *et al.,* 2009), mostly inside conserved areas where these animals are more easily observed.

5.2.2 Physical Appearance

The leopard is the largest spotted cat in Africa (Skinner & Chimimba, 2005). These animals are also the least specialized of the big cats and have an incredible ability to live in extremely diverse habitats not favoured by most other predators (Norton *et al*., 1986; Bailey, 1993; Mills & Biggs, 1993; Mills & Hes, 1997). Leopards are highly adaptable and can even reside close to human settlements (Athreya & Belsare, 2007). Leopards are territorial, solitary carnivores and typical cat, associating only with other conspecifics in the form of mating partners during the mating season and young cubs until the cubs are independent (Estes, 1991; Hes, 1991; Bailey, 1993). They are mainly nocturnal and show a preference for thickets (Mills & Biggs, 1993; Spong *et al.*, 2000) and this stealthy animal's pelage seems ideally adapted for the dappled light of densely forested areas (Bailey, 1993). Leopards have an elongate body and limbs of moderate length. Their paws are rounded, broad and the ears are short (Maheshwari, 2006). The head is wide with short, powerful jaws and long canines (Estes, 1991; Bailey, 1993). Leopards differ highly in morphology between different geographical regions (Mills & Harvey, 2001; Uphyrkina *et al.,* 2001) with the pelage hues varying from a light tan to deep golden yellow or tawny colour (Estes, 1991; Hes, 1991; Bailey, 1993; Hancock, 2000; Uphyrkina *et al.,* 2001).

No two leopards are alike (Skinner & Chimimba, 2005) and the body of each individual is uniquely patterned with black spots on the limbs, head, hind quarters and flanks, with rosettes on the remainder of the body (Estes, 1991; Hes, 1991; Uphyrkina *et al.,* 2001; Skinner & Chimimba, 2005). Each leopard has its own unique spot pattern, as each human has a unique fingerprint (Hes, 1991). The tail is spotted or rosetted on top and it is lighter in colour underneath, usually whitish. The body colour is also lighter on the ventral parts of the animal (Estes, 1991; Skinner & Chimimba, 2005; Maheswhari, 2006). Full-grown males have a very thick muscular neck and shoulder area with a loose flap of skin dangling under the throat and running along the chest (Hes, 1991; Hancock, 2000). Males measure from 60 - 70 cm in height and weigh between 35 - 70 kg (Estes, 1991; Bailey, 1993; Stuart & Stuart, 2000; Maheshwari, 2006). Females measure 57 - 64 cm in height and weigh 28 - 58 kg (Estes, 1991; Bailey, 1993; Stuart & Stuart, 2000; Maheshwari, 2006). Leopard cubs are woolly and darkish in colour, with close-set, indistinct spots (Estes, 1991). Melanistic forms, or black leopards, occur throughout its range, mostly in humid areas (Uphyrkina *et al.,* 2001) and there are also speculations of a black leopard in the Roodewalshoek Conservancy.

5.2.3 Distribution and Habitat

Historically the leopard was once the world's most widespread solitary felid (Myers, 1976; Bailey, 1993; Skinner & Chimimba, 2005) and had a global range comprising of at least 80 countries, of which about half is located in Africa (Estes, 1991; Nowell & Jackson, 1996; Hunter *et al.,* 2003; Maheshwari, 2006; Al-Johany, 2007). The historic range of leopards spanned all north and sub-Saharan Africa, the Middle East and Asia Minor, South and Southeast Asia, extending to the Amur Valley in the Russian Far East. Island ranges included Java, Kangean, Sri Lanka, and Zanzibar (Myers, 1976; Uphyrkina *et al.,* 2001). Its current range includes much of Africa and Asia, and some relict populations are scattered through south-eastern Europe and the Middle

East (Harrison, 1968; Gasperetti *et al.*, 1985; Nader, 1989; Harrison and Bates, 1991; Al-Jumaily, 1998; Hunter *et al.*, 2003; Maheshwari, 2006). Due to their great adaptability, they inhabit virtually every African habitat and are only absent where they have been driven away by man (Bothma & Le Riche, 1984; Estes, 1991; Mills & Hes, 1997; Bertram, 1999; Spong *et al.,* 2000). Ranging from desert to rainforest and all habitats in between, these cats can be found in altitudinal gradients ranging from sea-level coastal areas to high altitude mountains above 2 000 m and even urban areas (Monod, 1965; Estes, 1991; Hes, 1991; Mills & Hes, 1997; Skinner & Chimimba, 2005; Hayward *et al.*, 2006).

In Africa, leopards appear to be least numerous in West Africa (Skinner & Chimimba, 2005). In KwaZulu-Natal, leopards occur primarily in the north-east and are sparsely distributed in the western and central parts (Skinner & Chimimba, 2005). They occur throughout Mpumalanga, the Limpopo Province, Gauteng and the North West Province, except on the highveld grassland areas in the southern parts of these provinces (Mills & Hes, 1997; Skinner & Chimimba, 2005). Sporadical occurrences have even been noted in the Free State (Skinner & Chimimba, 2005). In the Eastern Cape, leopards occur in the mountainous areas along the south coast westwards into the Western Cape and into the northern parts of the Northern Cape. Some records of leopard sightings were also reported from Lesotho (Mills & Hes, 1997; Skinner & Chimimba, 2005).

Leopards reach their highest densities in riparian zones (Bailey, 1993), suggesting that they can live wherever there is sufficient cover and adequately sized prey animals (Estes, 1991; Bertram, 1999; Sunquist & Sunquist, 2002; Skinner & Chimimba, 2005). All habitats with annual rainfall above 50 mm seem adequate to sustain leopards (Monod 1965). These cats can also infiltrate areas with less than this amount of rainfall if they keep along river courses and were thus observed in the southernmost extension of the Namib Desert along the Orange River (Stuart & Stuart, 1989; Nowell & Jackson, 1996). In general leopards seem to be associated with areas of rocky outcrops, hills, forest and mountain ranges (Skinner & Chimimba, 2005). Today, leopards can still be found in the majority of protected areas, excluding the driest desert areas (Sunquist & Sunquist, 2002).

5.2.4 Behavioural Traits

Home range sizes of leopards vary extensively between regions in African savannas (Bothma & Walker, 1999). A leopard's home range usually excludes others of the same kind and gender (Bothma & Walker, 1999) and occasional nomads will wander widely through the ranges of resident leopards (Bailey, 1993; Bothma & Walker, 1999). Both male and female leopards hold territories, which they defend against conspecifics of the same sex (Skinner & Chimimba, 2005). The core of a leopard's range is not so much actively defended against intruders but it is rather avoided by other leopards due to the presence of densely spaced scent-marks. Males may, however, sometimes engage in fierce physical fights over a range dispute (Bothma & Walker, 1999).

Leopards in areas of low rainfall have large home ranges due to the low abundance of potential prey animals throughout these areas (Bothma & Walker, 1999). Home ranges of female leopards often overlap, but there is no overlap in that of males (Estes, 1991; Bailey, 1993). Usually home ranges of males are much larger in comparison with that of females and may further overlap with home ranges of up to six females (Estes, 1991; Hes, 1991; Bailey, 1993; Bertram, 1999; Bothma & Walker, 1999; Hancock, 2000; Skinner & Chimimba, 2005). It seems that the size of a male leopard's home range is mainly determined by the number of females present throughout the area, while the size of a female's home range depend mainly on prey availability (Bothma & Walker, 1999).

The size of a typical home range, determined via radiotelemetry, have been estimated between 30 and 78 km^2 for males and only between 15 to 16 km^2 for females in protected areas (Hamilton, 1981; Bailey, 1993; Bertram, 1982; Norton & Henley, 1987). Long-term observations of individual females have shown larger home range sizes in protected areas. For example, Le Roux & Skinner (1989) estimated home range sizes of 23 - 33 km^2 in the Londolozi Private Game Reserve while Cavallo (1993) calculated areas between 37 and 38 km^2 in the Serengeti National Park. Bailey's (1993) study in the southern Kruger National park showed that the ranges of adult females seem to be centred around the most prey-rich habitat, while large male's home range also included lower quality habitats. In mountainous terrain near Stellenbosch in the Western Cape, interspersed with farms and game ranches, Norton and Lawson (1985) calculated home ranges to between 338 and 487 km^2 for both males and females. The degree of overlap between adjacent home ranges varies depending on the available food resources as well as the density of other large predators in the area (Bothma & Walker, 1999). Grown female cubs frequently establish overlapping territories on the periphery of territory held by the mother and consequently closely related females often dominate in one area (Hes, 1991).

Vocalisations and scent-markings are important means of communication and spatial arrangement of a leopard population is maintained by reducing chances of aggressive encounters between individuals (Hes, 1991; Hancock, 2000; Skinner & Chimimba, 2005). The leopard's communication system is composed of vocalizations, body postures and chemical communication (Bailey, 1993; Bothma & Walker, 1999) and they generally defend their territories by calling and demarcating the boundaries with dung, urine and tree-scratching (Estes, 1991). The white tip of the tail is often flicked and in darkness may function as a visual signal between mother and cubs (Estes, 1991). The most characteristic vocalization is a hoarse rasping "sawing" sound, which is repeated at intervals of around six minutes mostly in the early evening, just after sunset and more frequently during the dry season (Estes, 1991; Skinner & Chimimba, 2005). Leopards use all the typical feline scent-marks as a means of communication, such as spraying urine at the base of trees, bushes other objects at frequent intervals during their nightly wanderings after rubbing the head and cheeks on the same spot (Estes, 1991). Faeces are also deposited along paths and roads, in a specific position usually to be highly visible to other members of the same species (Estes, 1991). Frequently used trails are usually more thoroughly marked at trail intersections (Skinner & Chimimba, 2005).

The use of scratch trees for the purpose of scent-marking has been widely debated. One group of researchers view it only as claw-sharpening (Mondolfi & Hoogensteijn, 1986; Gorman & Towbridge, 1989; Eisenberg & Lockhart, 1972; Eisenberg, 1986) while another group suggested that tree-scratching is used as a form of scent-marking (Seidensticker *et al.,* 1973; Schaller, 1972; Eisenberg, 1970). Turnbull-Kemp (1967) believed that African leopards rarely claw or scratch trees, but Bothma & Le Riche (1995) found this practice to be relatively prevalent in leopards from the southern Kalahari savannah. By contrast, Bailey (1993) had no observation of tree-scratching in the Kruger National Park leopards. According to Estes (1991) large trees are the preferred marking posts, where the leopard will pause to sniff at previous scratch marks, stretches out along the trunk and sharpen its own fore claws.

Leopard densities vary from region to region due of differences in potential prey densities and its subsequent influence on the size of the leopard's home range (Bothma & Walker, 1999). Bailey (1993) estimated average leopard density in the Kruger National Park at 3.5 adults per 100 km^2, with much higher densities of up to 30.3 individuals per km^2 in the riparian forest zones, where high prey density occurs. In arid environments, leopard densities are low, for example Martin & de Meulenaer (1988) reported a density of 1.25 adults per 100 km^2 in South Africa's Kalahari Gemsbok National Park.

Leopards are generally more active at night than during day time hours (Bailey, 1993; Bothma & Bothma, 2006) and will also rest periodically during the night (Bailey, 1993). Environmental factors seem to influence the activity patterns of leopards and despite popular beliefs these animals are quite active during the day (Bailey, 1993; Bothma & Walker, 1999). Early mornings are usually spent lying in the sun on vantage points such as rocky ledges that presumably give a wide view of the surrounding terrain (Skinner & Chimimba, 2005). However, they usually spend the larger part of the day sleeping in a shady spot (Bailey, 1993; Bothma & Walker, 1999; Skinner & Chimimba, 2005). Normal movements seem to be largely dictated by the success or failure at satisfying its daily nutritional and mating needs. The study conducted by Bailey (1993) indicated that males exhibit a higher level of nocturnal activity than females and that activity patters are not significantly influenced by the age of an individual. In prey-rich areas, the range size and extent of a leopard's daily movements are small and the presence of cubs usually restricts a female's movements for up to six months (Bailey, 1993; Bothma & Walker, 1999; Hancock, 2000). A leopard's state of hunger significantly influences the daily distances moved and it also seems that they will move further distances in cold temperatures than in warmer temperatures (Bothma & Walker, 1999).

Leopards have a catholic diet and are generally thought to prey on medium sized ungulates, preferring species within a weight range of 5 – 40 kg (Mills & Hes, 1997; Hayward *et al.,* 2006; Schwartz & Fisher, 2006). Leopards always hunt solitarily and usually hunt at night (Skinner & Chimimba, 2005). The leopard is a stalking and pouncing specialist, and a master at concealment (Mills & Hes, 1997; Skinner & Chimimba, 2005). They will hunt mainly at night but will make full use of any opportunity, even if it is during full-blown daylight (Bothma & Walker, 1999). Although leopards are powerful and lethal hunters, they will make several unsuccessful hunting attempts during the course of their lives (Bothma & Walker, 1999).

Leopards minimize kleptoparasitism by caching carcasses in trees or underneath dense bushes (Hes, 1991; Mills & Biggs, 1993; Bertram, 1999; Hancock, 2000). Caching of kills in trees is usually not observed where leopards are the only large predator in an area (Estes, 1991). Whenever a mother and cubs congregate at a carcass, they will always take turns to feed (Hes, 1991). Motherhood seems to motivate female leopards to hunt more efficiently than other leopards (Bothma & Coertze, 2004) and females with cubs increase their hunting success, spend less energy in hunting than other leopards by regularly utilising smaller prey that are less difficult to kill and by sprinting shorter distances before making a kill (Bothma & Coertze, 2004). Bothma & Walker (1999) suggested that female leopards seem able to hunt more effectively until they reach older ages due to females having smaller teeth and feeding with more precision than males, causing less wear on their teeth. Thus females tend to usually live longer than males in the wild. The majority of old leopards die in violent conflicts or of starvation and mange also poses a great threat (Bothma & Walker, 1999).

Males and females associate only briefly to mate (Estes, 1991; Bailey, 1993; Bothma & Walker, 1999). There is no permanent pair bonding and mating follows the general cat pattern (Bailey, 1993; Bothma & Walker, 1999). During courtship the pair will remain close to each other and copulation takes place approximately every 15 minutes (Skinner & Chimimba, 2005). In general, leopards seem to have no seasonality in their reproductive season (Fairall, 1968; Bothma & Le Riche, 1984; Maheshwari, 2006), although Bailey (1993) found that mating in the Kruger National Park occurs during the extreme dry season, followed by birth peaks in unison with a peak in the birth of impalas, their main prey species in the region. Leopards in Africa and India will mate at any time of the year, and 2 - 3 cubs are usually born at a time (Estes, 1991; Hes, 1991; Skinner & Chimimba, 2005; Maheshwari, 2006).

After a gestation period of 90 - 100 days, the cubs are born in sheltered places under rocks, caves, hollow trees or in holes in the ground dug out by other animals

(Estes, 1991; Hes, 1991; Skinner & Chimimba, 2005). When a leopard cub is still small, it locates its den mainly by associated odour. Leopard cubs suffer high mortality rates and in order to avoid attracting other predators to the den while the cubs are still small, the den-location is changed every few days (Bailey, 1993; Bothma & Walker, 1999). There exists a strong, enduring maternal bond between mother and cubs (Estes, 1991) and the cubs will be taken out to a fresh kill for the first time at around two months of age (Hes, 1991). The mother leopard will leave the cubs to fend for themselves when they are between 14 and 22 months old (Estes, 1991; Hes, 1991). Reunions after this separation is not uncommon and the mother may continue to share kills with her cubs until they become fully self-sufficient (Estes, 1991; Hancock, 2000; Hes, 2001; Bailey, 1992). The continued tolerance of full-grown female offspring by the mother probably explains overlapping female ranges in an area (Estes, 1991). Furthermore, it is not uncommon for males to briefly associate with a female and young cubs (Hes, 1991; Hancock, 2000). Sexual maturity is reached at about 2.5 to 3 years of age (Estes, 1991; Hes, 1991; Bailey, 1993; Maheshwari, 2006).

5.3 The Brown Hyaena *Parahyaena* (*Hyaena*) *brunnea* (Thunberg, 1820) Hendey, 1974

5.3.1 Taxonomic Notes

Class:	Mammalia Linnaeus, 1758
Order:	Carnivora Bowdich, 1821
Family:	Hyaenidae Gray, 1821
Genus:	*Hyaena* Brisson, 1762
Species:	*Parahyaena* (*Hyaena*) *brunnea* (Thunberg, 1820) Hendey, 1974

The Hyaenidae is a somewhat small family with only four existing species presently placed in four genera (Wozencraft, 1993). The brown hyaena was first recorded in 1783 by A. Sparrmann when it still ranged around Cape Town and Table Bay (Bothma & Walker, 1999; Skinner & Chimimba, 2005). C.P. Thunberg, who has never seen a live brown hyaena during his life, described it as *Hyaena brunnea* for the first time in 1820 from a stuffed specimen with the given type locality as the Cape of Good Hope of South Africa (Skinner & Chimimba, 2005). Today the phylogeny of members of the genus *Hyaena* is a controversial subject and until the early 1970's, the brown hyaena has been classified as *Hyaena brunnea.* Palaentological evidence suggests that hyaenids first arose about 25 million years ago, during the Late Oligocene (Werdelin & Solounias, 1991). Pilgrim (1932), Ewer (1955), Thenius (1966) and Hendey (1974) all agreed that *H. hyaena* and *Parahyaena brunnea* are more closely related to one another than any of them are to *Crocuta crocuta*, but Hendey (1974) regarded *Parahyaena brunnea* and *Hyaena hyaena* as distantly related to one another sharing a more common ancestry with species of the extinct genus *Pachycrocuta* (Koepfli *et al*., 2006). In consequence of molecular analyses, Hendey (1974) created a new subgenus, *Parahyaena*, for *Parahyaena brunnea*, which had previously been classified as *Hyaena brunnea* (Thunberg, 1820). Werdelin and Solounias (1991) eventually elevated *Parahyaena* to a full generic rank. According to Bothma & Walker (1999) the brown hyaena is the rarest large carnivore in Africa.

5.3.2 Physical Appearance

The brown hyaena has the characteristic sloping-back profile shared by members belonging to the family Hyaenidae. It has strong fore quarters with long forelegs and shorter hind legs and can be classified as a medium to large sized carnivore. The brown hyaena has a shaggy dark brown to black coat with long hair exhibiting pilo-erection capabilities over most of its body, providing it with excellent thermal insulation (Estes, 1991; Mills, 1994; Bothma & Walker, 1999) and is largely without stripes, except for stripes on the legs (Mills, 1982). These patterns of the stripes on the legs are unique to each individual (Maude, 2005). The neck, shoulder and underbelly are generally light in colour. Pelage is generally thicker during winter and thin in summer time with little under fur (Mills, 1994). Female brown hyaenas are somewhat smaller than males and adult males weigh an average of 47 kg and females 42 kg (Bothma & Walker, 1999), but otherwise the two sexes look very much alike (Estes, 1991; Maude, 2005). The sexual organs of the brown hyaena are not specialized as found in the spotted hyaena *Crocuta crocuta* (Erxleben 1777), where the females have evolved a false scrotum and highly erectile clitoris (Mills, 1982). The brown hyaena is the second smallest hyaena of the four living hyaenid species alive today (Bothma & Walker, 1999). This species is very well adapted to live in environments that harbor few other large carnivores (Bothma & Walker, 1999).

5.3.3 Distribution and habitat

Brown hyaenas seem to be relatively adaptable animals and many viable populations exist outside of protected areas on agricultural land adjacent to human settlements (Skinner & Chimimba, 2005; Maude, 2005; Carnaby, 2006). The brown hyaena's distribution is limited to the drier parts of the savannas of southern Africa (Mills, 1982) and it is considered by Bothma & Walker (1999) to be the most common large carnivore in the central and southern Kalahari. Mills (1994) also stated that the largest populations can be found in the Kalahari. Brown hyaenas are endemic to the southern African sub region and historically occurred throughout the Western Cape (Skinner & Chimimba, 2005). In the northern parts of South Africa, brown hyaenas favour rocky, mountainous areas with ample bush cover (Skinner & Chimimba, 2005).

5.3.4 Behavioural Traits

Brown hyaenas live in clans and are much more social than previously thought (Bothma & Walker, 1999). Each clan has an extensive range which is defended as a territory, with the den site featuring as the centre of their society. Clan sizes may show marked fluctuations from time to time and differ from region to region, with a negative correlation between the size of the home range and the amount of available food items (Mills, 1994). The number of individuals in a clan is also usually positively correlated with the availability of food in their range (Mills, 1982; 1994; Bothma & Walker, 1999; Skinner & Chimimba, 2005). Brown hyaenas have an advanced social system similar to that of spotted hyaenas, but it is more flexible in terms of intricate relationships between members of a clan. These animals therefore have a very well developed communication system consisting of vocalizations, elaborate rituals, visual displays and extensive scent-marking, which maintains clan cohesion (Mills, 1978; Owens & Owens, 1978; Mills, 1981; Bothma & Walker, 1999). The unity within the clan is maintained by a highly ritualized greeting ceremony involving several forms of muzzle wrestling and grooming actions (Owens & Owens, 1978; Mills, 1978; Bothma & Walker, 1999). Neck-biting is often used when a new sub-adult is recruited into the clan, or when natal sub-adults are expelled from the clan. Neck-biting can also be observed as a form of ritualized fighting between members of different clans who are strange to each other (Bothma & Walker, 1999). Brown hyaenas are generally silent animals with only a small vocal repertoire and no known long-distance calls (Owens, 1978; Mills, 1981; 1982).

Scent marking by brown hyaenas occurs in the form of pastes from the anal pouch (Mills, 1982; Estes, 1991; Mills, 1994; Bothma & Walker, 1999; Skinner & Chimimba, 2005; Carnaby, 2006) and according to Bothma & Walker (1999), these pastes form the most important means of communication. Brown hyaenas use two distinct types of pastes, one of which is a long-lasting, white, lipid-rich secretion mainly used at clan faecal latrines (Mills, 1994; Skinner & Chimimba, 2005). The second component is a black, short-lasting watery secretion unique to each individual, which a foraging hyaena uses to avoid counter-productive foraging by thus identifying areas where other members of its clan have recently foraged (Mills, 1994; Bothma & Walker, 1999; Carnaby, 2006). These pastings are usually made at regular intervals by all clan members at an average of 264 pastes per 100 km, thus an intruder will be likely to encounter a fresh scent mark very soon after crossing into the clan's territory (Estes, 1991; Mills, 1994; Bothma & Walker, 1999). Defecation is also a form of marking, while urination does not seem to serve the same purpose (Mills, 1994; Bothma & Walker, 1999). According to Estes (1991) latrines of brown hyaenas are almost always associated with landmarks that stand out in their surroundings.

There usually exists little aggression between clan members and nomadic males play an important role in their society since these males are involved in most of the mating with the clan females (Mills, 1982; Bothma & Walker, 1999). Even though this species is a solitary forager, the brown hyaena display all the necessary social mechanisms for communal exploitation of a concentrated food source, such as a large carcass, as well as for socializing with other individuals (Mills, 1978; 1981; Owens & Owens, 1978; Adler, 1996). Pathways form networks throughout their home range and are maintained by pastings, usually linking carcasses up to three months old (Bothma & Walker, 1999). A clan of brown hyaenas consists mainly of a group of related individuals of both sexes, with the resident males showing little reproductive interest in any females from their own, as well as adjacent clans. Resident males are always dominated by immigrant males and mating occurs strictly between nomadic males and the resident females in the clan. A nomad will usually sire only two consecutive litters before he is replaced by a new immigrant (Owens & Owens, 1978; Mills, 1981; 1982; Bothma & Walker, 1999).

Cubs are born throughout the year, with gestation lasting about 90 days. Both dominant and subordinate females in a clan produce litters the size of one to four cubs at different times. All females will provide for and suckle cubs other than their own and cubs are weaned at around 16 months of age (Owens & Owens, 1979; Mills, 1982; Bothma & Walker, 1999). Older cubs will be provided with food at the communal den, which is brought to them by the foraging adults of the clan (Mills, 1982; 1994; Bothma & Walker, 1999). Consequently the den site of a clan is usually easily identifiable by accumulations of bones scattered around them (Mills & Mills, 1977; Owens & Owens, 1979; Lacruz & Maude, 2005) and the bone accumulation reflects the faunal composition in their range at that particular time (Skinner & Chimimba, 2005).

As with all carnivores, the range size of a brown hyaena clan's territory is determined by the resources available to them and the home range can be adjusted according to changes in the distribution and abundance of food (Mills, 1981; Skinner & Chimimba, 2005; Estes, 1991; Mills, 1994; Maude, 2005). The size of a clan's territory can range from 21.1 to 480 km^2, depending on the amount of available food, water and shelter (Owens & Owens, 1978; Bothma & Walker, 1999) and according to Skinner & Chimimba (2005) the home range of animals in the former Transvaal province of South Africa is on average 18.83 km^2.

This is a nocturnal species, predominantly a scavenger and a very inefficient hunter (Mills, 1978; 1982; Estes, 1991; Bothma & Walker, 1999; Maude, 2005). They tend to be more active soon after sundown and just before dawn. Days are commonly spent inactive in dense vegetation or burrows (Mills & Mills, 1977; Mills, 1982; Skinner & Chimimba, 2005; Mills, 1994; Bothma & Walker, 1999). Brown hyaenas cover great distances in search for food and they can travel up to 54.4 km in less than 14 hours (Mills, 1978; 1994). In areas where they occur mutually with larger predators such as lions, the kills made by these more efficient predators are a very important source of food for the hyaenas (Mills, 1982; Bothma & Walker, 1999). When a group of brown hyaenas congregates at a large carcass, they would typically feed in turns with individuals breaking off pieces of the carcass to carry off to feed elsewhere or to cache for later use (Mills, 1978; Owens & Owens, 1978; Mills, 1981; Estes, 1991; Mills, 1994; Skinner & Chimimba, 2005).

5.4 Predator Interactions

Of all the carnivores observed in the conservancy, the only competition might be between leopards and brown hyaenas due to similarities in their behaviour and feeding ecology. There also exists a possibility of resource competition between side-striped jackals and caracals due to similarities in their niche occupation. In terms of the carnivore dominance hierarchy, leopards are dominant to jackals and caracal, and are mostly dominant to brown hyaenas during one-on-one confrontations (Bothma & Walker, 1999; Carnaby, 2006). In the southern Kalahari, Brown hyenas can also often be seen following leopards, but they do not usually interfere with a kill if the leopard is still at the carcass (Mills, 1994; Bothma & Walker, 1999; Carnaby, 2006). Ecologically, the leopard and brown hyaena share many ecological traits (Table 5.2) including caching of kills, but they differ in other aspects such as social systems and hunting strategies.

Table. 5.2 Ecological traits of brown hyaena and leopard. Summarized from Estes, 1993; Apps, 2000; Skinner & Chimimba, 2005 & Carnaby, 2006.

Ecological trait	Brown hyaena	Leopard
Habitat		
Open plains to tree covered grassland	No	Yes
Bush savanna	Yes	Yes
Semidesert scrub	Yes	Yes
Woodlands	No	Yes
Diet		
Fruit & plant material	Yes	No
Insects	Yes	Yes
Small vertebrates (0-15 kg)	Predator	Predator
Medium vertebrates (15-70 kg)	Predator/ scavenger	Predator
Large vertebrates (>75 kg)	Scavenger	Predator
Caching of food	Yes	Yes
Activity		
Nocturnal	Yes	Yes
Rests between peaks	Yes	Yes
Diurnal	Yes	Yes
Early morning	Yes	Yes
Late afternoon	Yes	Yes
Crepuscular	Yes	Yes
Social organization		
Social	Yes	No
Solitary	No	Yes
Territorial	Yes	Yes
Non-territorial	No	No
Feeding behaviour		
Forage/hunt in group	No	No
Forage/hunt solitary	Yes	Yes
Share food with adults of the same species	Yes	No
Protect food from adults of the same species	No	Yes

Because brown hyaenas are predominantly scavengers (Mills, 1994; Maude, 2005; Skinner & Chimimba, 2005; Carnaby, 2006), Bothma & Walker (1999) suggested that they will not have a large impact on the prey populations in their home range. When compared to the larger carnivores of southern Africa, the brown hyaena ranks low on the carnivore dominance hierarchy (Estes, 1991; Bothma & Walker, 1999), but according to Carnaby (2006) they might sometimes outrank a leopard during a one-on-one confrontation. Leopards and brown hyaenas will have little influence on the populations of the other (Mills, 1994) and one large brown hyaena may dominate a single leopard if it is a small female, or be dominated by it, if it is a large male leopard (Mills, 1994; Carnaby, 2006).

Brown hyaenas are known to follow a leopard's tracks, in order to scavenge off the kills made by the leopard and might even attempt to seize a leopard's kill (Estes, 1991; Bothma & Walker, 1999; Carnaby, 2006). Usually, however, the leopard overcomes this possible competition by caching kills it has made in trees. When a leopard and brown hyaena meet while hunting or foraging, they will often simply ignore each other (Bothma & Walker, 1999; Carnaby, 2006) and just go about their separate ways (Mills, 1994; Carnaby, 2006). The outranking predator in each case when these two species meet depends on the size of the two present parties. A large male leopard is highly unlikely to be chased from its kill by a brown hyaena, whereas a smaller female or juvenile leopard may flee when approached by the latter (Mills, 1994; Carnaby, 2006).

Brown hyaenas are dominant to caracals, which will flee from its kill when approached by a hyaena (Mills, 1994). In the Kalahari savannas there is unmistakable competition for food between black-backed jackals and brown hyaenas due to a considerable overlap in their diet and life habits (Mills & Mills, 1977; Mills, 1978; Owens & Owens, 1978; Mills, 1994). Both predators gain and loose food to each other and brown hyaenas will keep an eye on foraging jackals in case it found something to eat (Mills, 1994; Bothma & Walker, 1999).

5.5 Results

5.5.1 Monthly Presence of Carnivores

The majority of monthly observations of small predators occurred during the summer months of March, August, September and December (Fig. 5.1). African civets were most continually present of all the small carnivores and showed a fairly continual presence throughout the year. The occurrence of honey badgers peaked in mid-winter and again in early summer, but they were not observed at all in late summer during the months of February and November. Large-spotted genets were mostly absent during winter months, excluding August, as well as during late summer from January to February (Fig. 5.1). Both of the medium sized carnivores were absent during the onset of winter in May and during late summer from December to March (Fig. 5.2). Caracals were observed in the conservancy during the whole of winter, with the majority of its presence in height of winter. Side-striped jackals were mostly observed during spring and early summer from September to November (Fig. 5.2).

Large carnivores were fairly continually present in the conservancy throughout the year (Fig. 5.3), with the exception of late summer during January. Brown hyaenas and leopards also seemed to display similar patterns of presence and absence throughout the year, occurring mostly during mid- summer, autumn and mid-winter (Fig. 5.3). Large predators were continually observed in the conservancy except in late summer during the month of January. The monthly presence of large predators peaked during autumn in the months of March to April and again during mid-winter and in the height of summer (Fig. 5.4). All the other predators, which include the small and

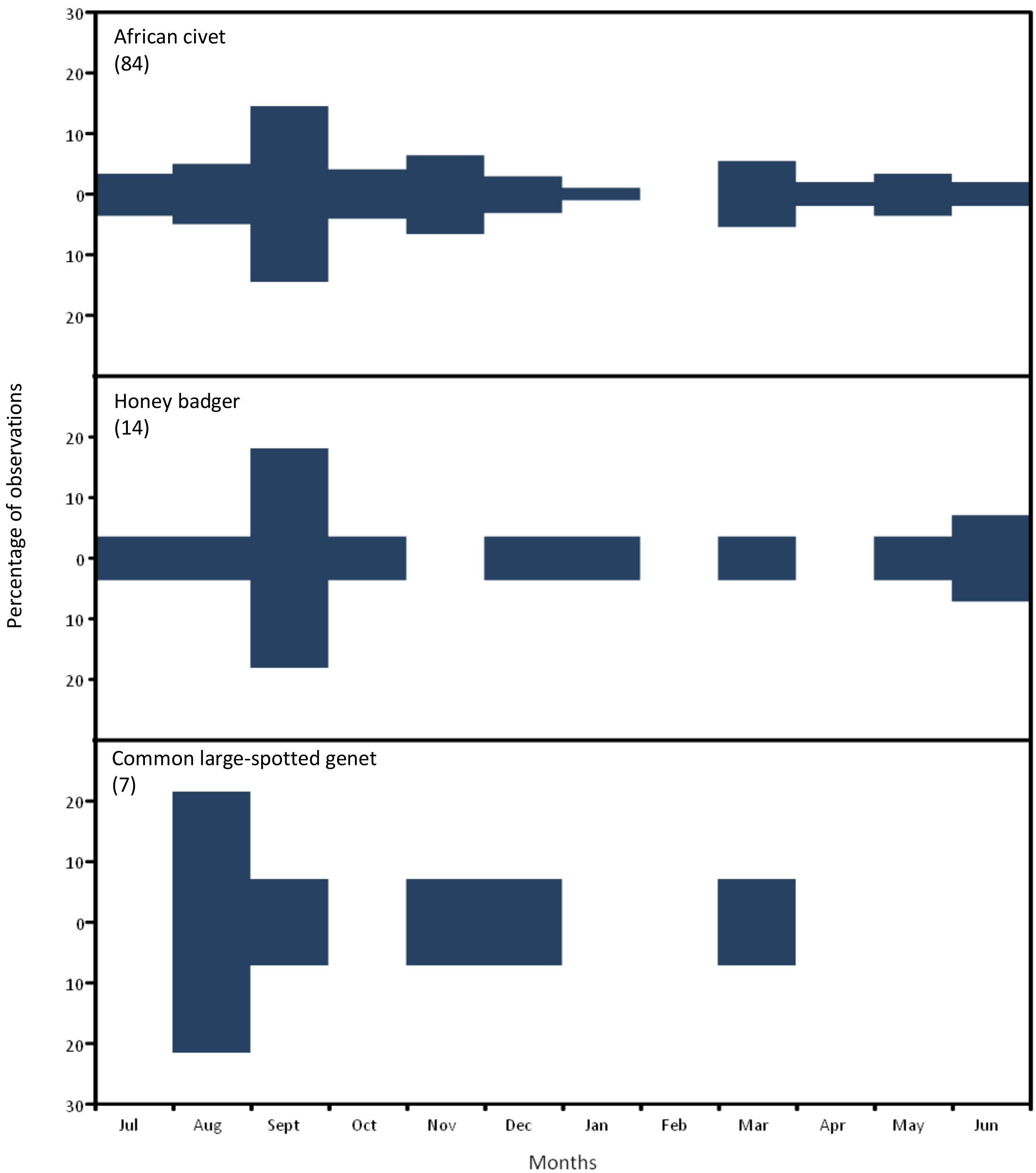

Figure 5.1 Monthly presence of small predator species in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations.

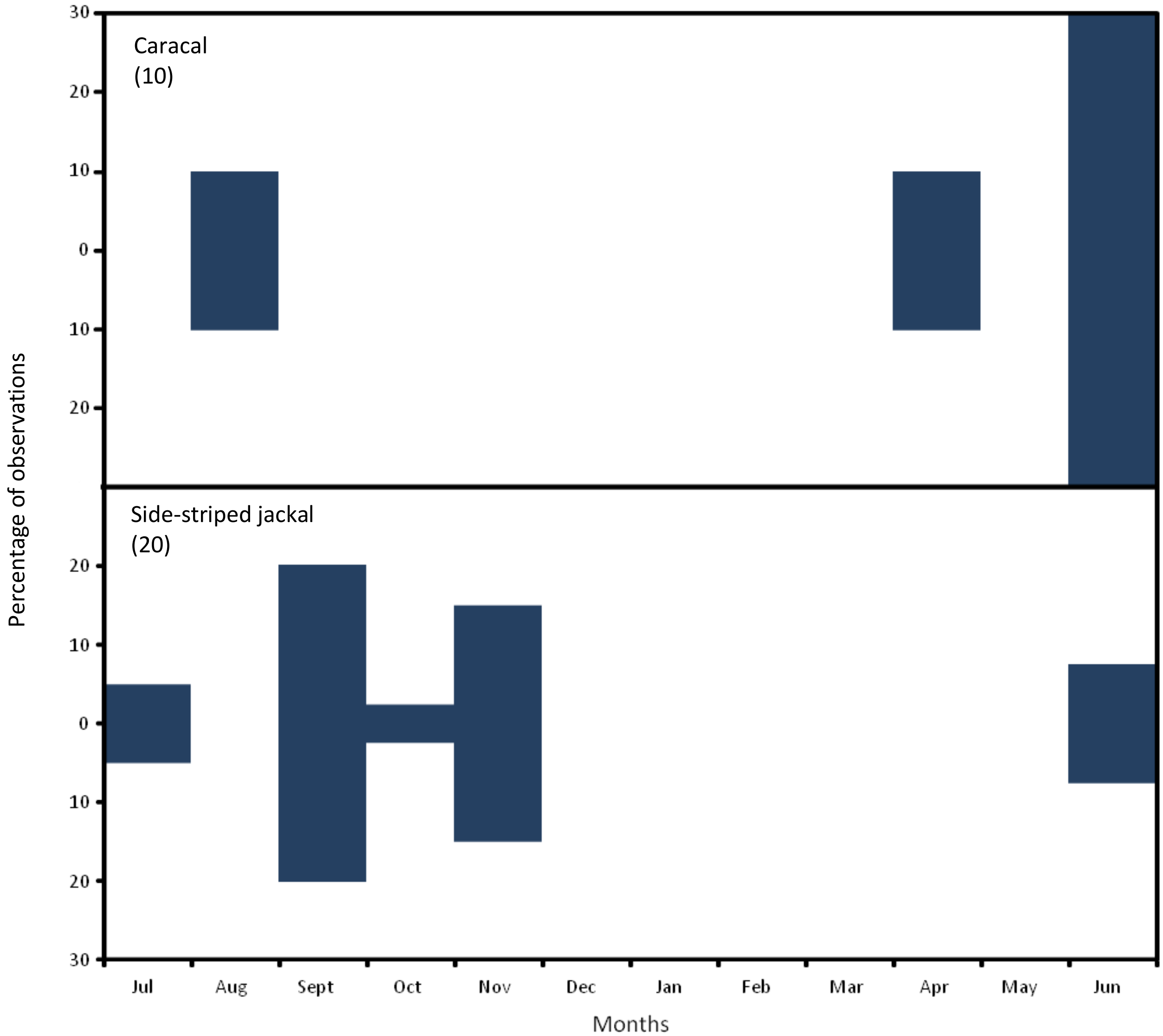

Figure 5.2 Monthly presence of medium sized predator species in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations.

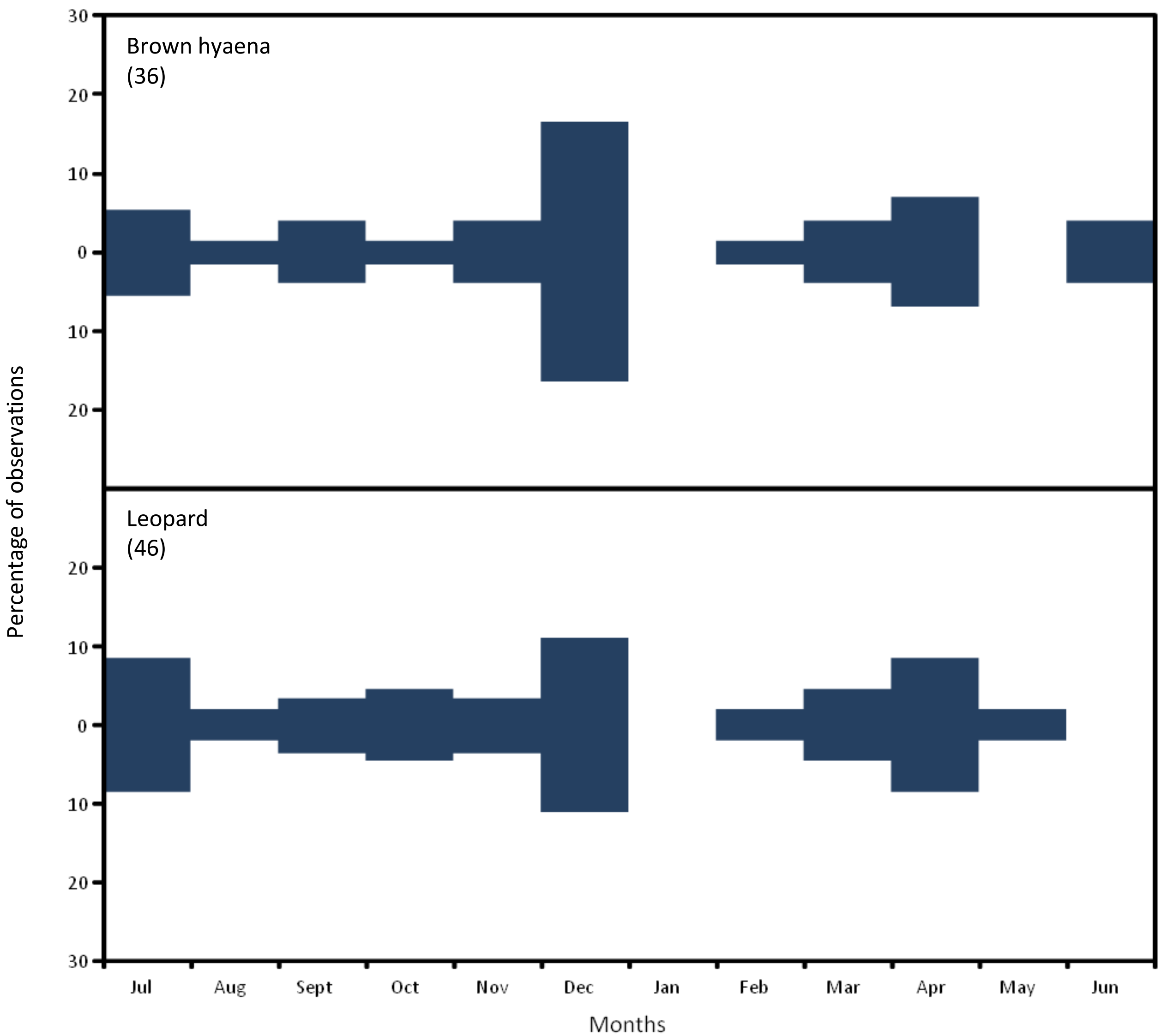

Figure 5.3 Monthly presence of large predator species in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations.

medium sized predators, were also annually persistently present except during late summer in month of February (Fig. 5.4). The monthly presence of other predators peaked in mid-winter and early spring. It is also evident that, when the presence of large predators in the study area increases, the presence of other predators decreases (Fig. 5.4). A relatively strong negative correlation (R^2 = 0.3507; r = -0.5922) was calculated between the presence of small and large carnivores during winter months. During summer a weak positive correlation (R^2 = 0.0003; r = 0.0186) was found between the presence of small and large carnivores.

As monthly rainfall increases, there is a corresponding increase in the presence of large predators and a decrease in the presence of other predators (Fig. 5.5). Except during early spring from August to September, large predator presence seemed to peak correspondingly with a peak in the number of potential prey animals observed (March to May and December) (Fig. 5.6). Three months of the year, during the mid-winter, mid-summer and the closing stages of autumn, were identified during which the presence of large predators seemed to reach a maximum, which correspond with increases in prey presence (Fig. 5.6). The only exception to this tendency was observed during the onset of summer from August to October. Potential prey and large predator presence peak during mid-summer (December), displaying a drastic decrease towards February. From then on presence of prey and predators seem to increase once more towards early autumn (April) with a steady decline to the onset of winter (Fig. 5.6).

Individuals of only certain species are represented in the analysis of individual predator data due to marked patterns displayed by these individuals. Of all African civets only six individuals were observed more than twice and these individuals showed definite periods of monthly presence and absence from the study area (Fig. 5.7). Of these six individuals, AC01 (45%), AC02 (16%) and AC04 (25%) constituted 86% of all the sightings and were more continually present in the area than other civet individuals. AC03, AC05 and AC06 were sporadically present from the end of winter to mid-

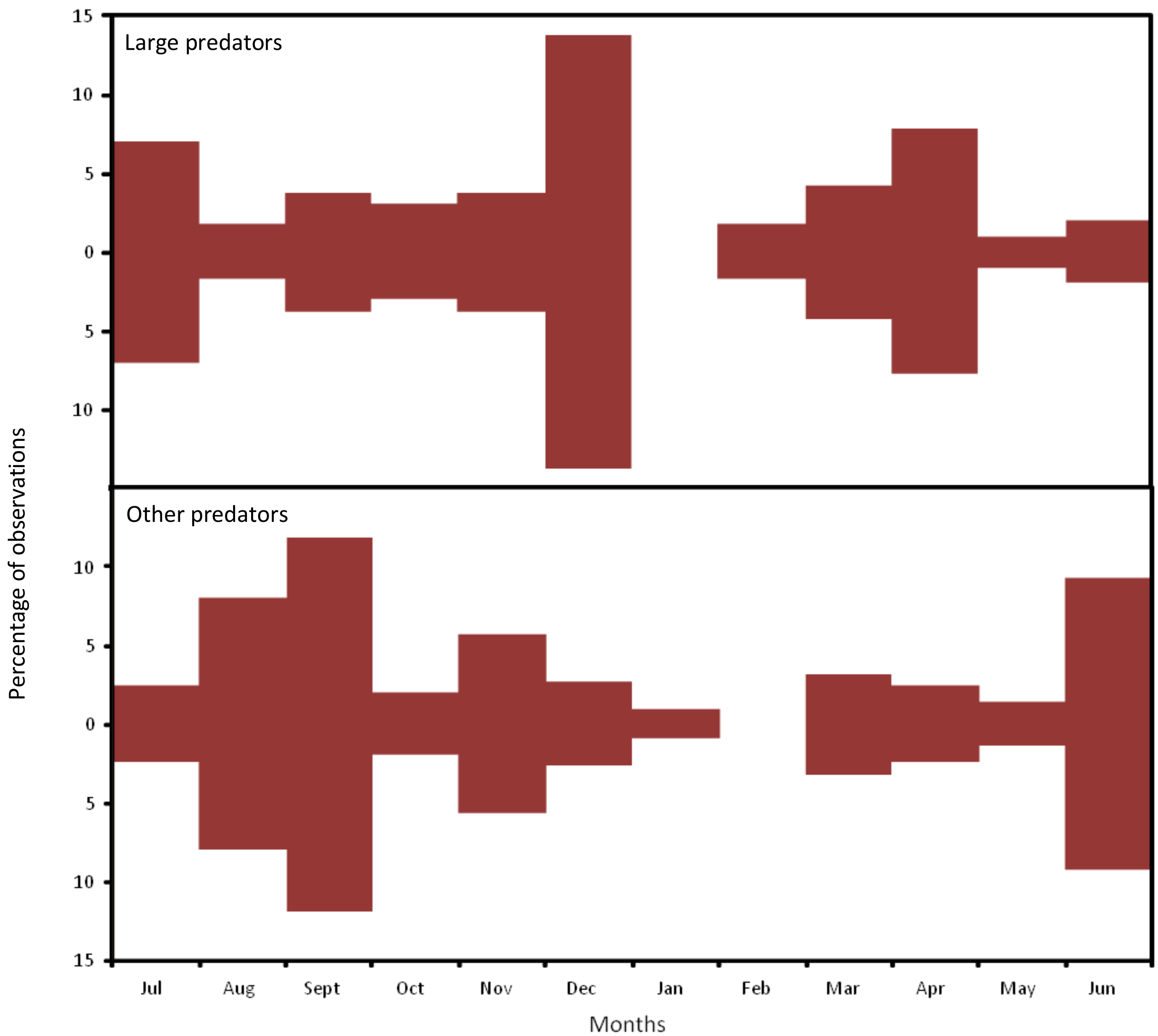

Figure 5.4 Monthly presence of large predators and other predator species in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010.

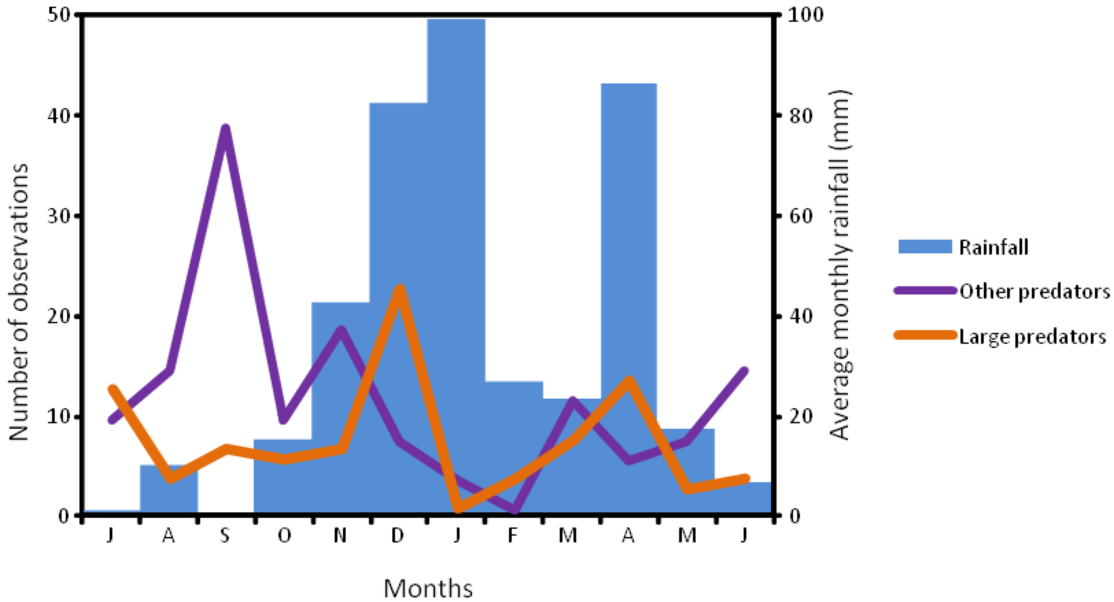

Figure 5.5 Monthly precipitation and presence of large and other predators in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010.

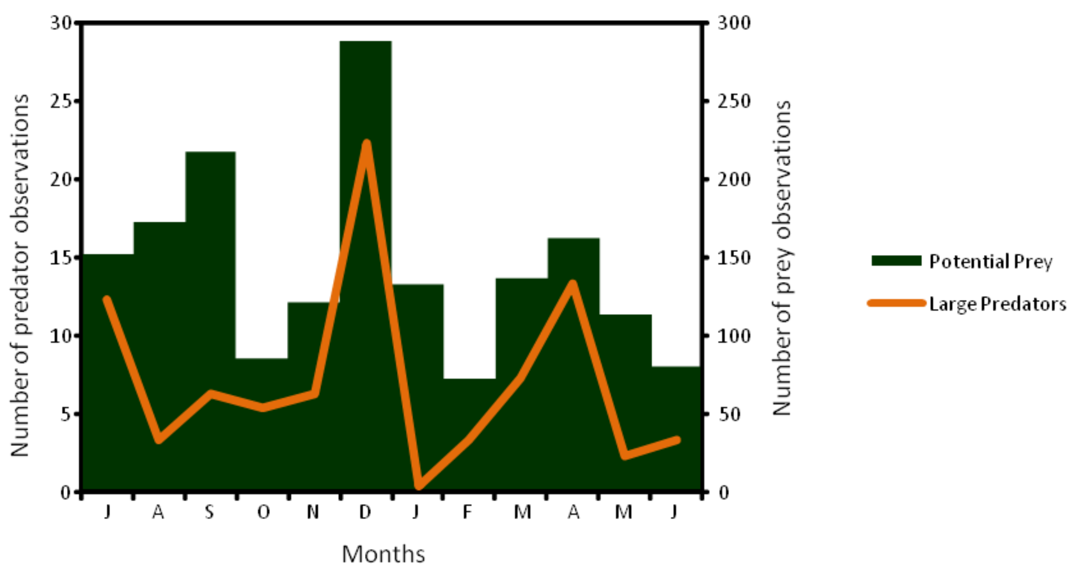

Figure 5.6 Number of prey and large predator observations in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010.

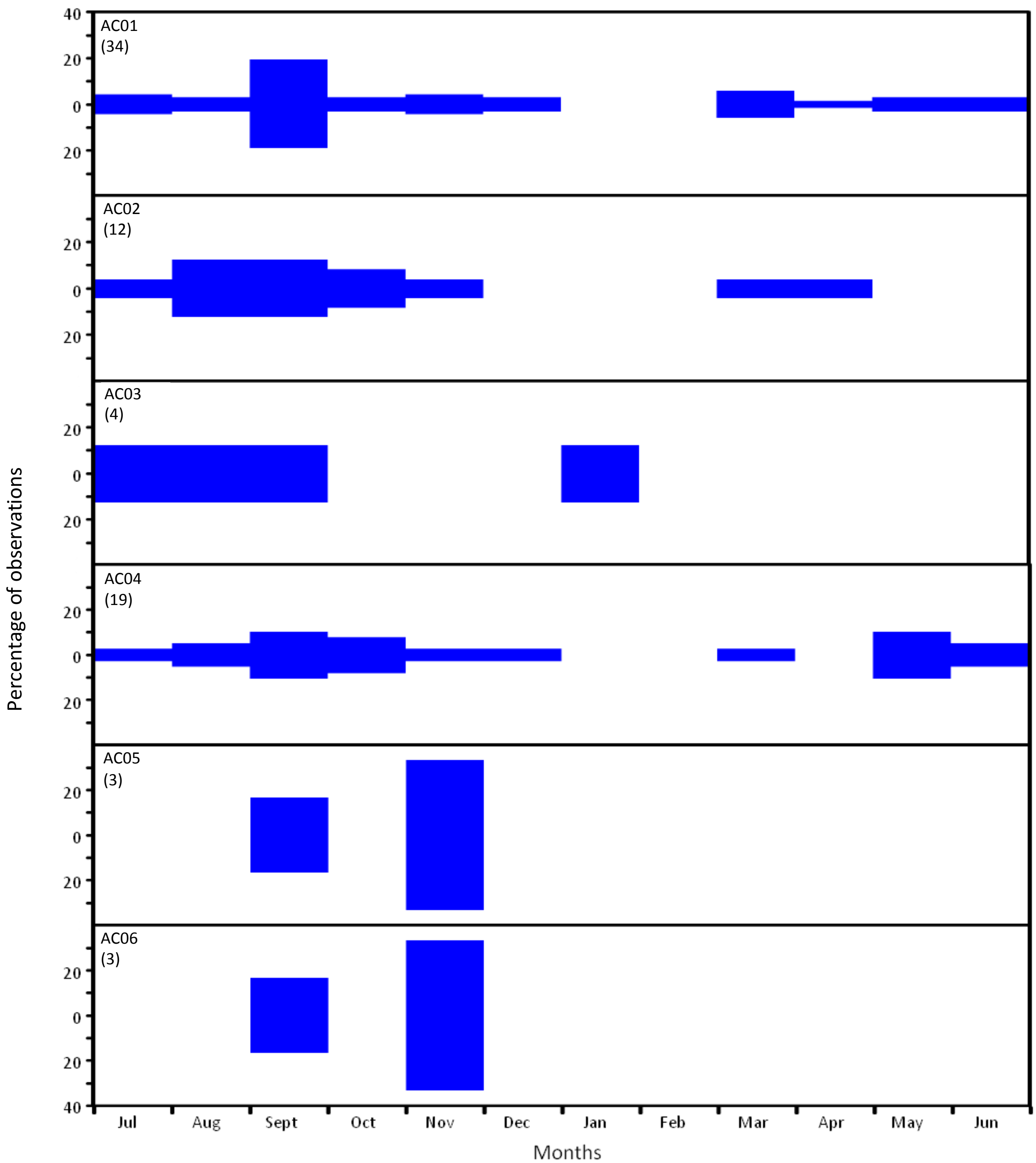

Figure 5.7 Monthly presence of individual African civets in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations.

summer, thus there is a strong possibility of resident and nomadic African civets in the Roodewalshoek conservancy.

Individual side-striped jackals did not seem to be resident and were only intermittently present in the area, with the exception of one individual (SSJ03) which occurred for three consecutive months during the onset of summer (Fig. 5.8). No resident individual brown hyaenas could be identified and brown hyaena individuals showed definite periods of presence and absence (Fig. 5.9 and Fig. 5.10). Two separate individuals were observed during late summer (March) and the onset of winter (April), three individuals were present during spring (September) and four individuals alternately visited the study area during mid-winter in the month of June (Fig. 5.9 and Fig. 5.10). This trend indicates sporadic nomadic behaviour among brown hyaenas observed in the conservancy. BH04 returned four times to the study area, which can be an indication that this area harbours a sustainable feeding site for brown hyaenas. The only instance when two individuals were ever captured at the same place on the same night at the same time, was at a greater kudu carcass, but these two individuals could not be identified.

Individual leopards also showed definite periods of presence and absence in the Roodewalshoek Conservancy (Fig. 5.11). Greater amount of avoidance among leopards were observed from spring to late summer and autumn elucidated the greatest overlap in habitat use by these individuals. Erratic encounters with two separate individuals (LF03 and LF04) where they were observed only once over a two year period, and only three accounts of LF01, is an indication that the conservancy serves as a healthy corridor for leopards moving from and towards surrounding areas of conservation. Only two individuals, one female (LF02) and one male (LM01) occupied the conservancy on a more constant basis and therefore these individuals are assumed to be the territorial female and male in the area (Fig. 5.11). None of the identifiable leopards was observed during late-summer (January) and mid-winter (June), while during the onset of autumn (April) two individuals were present in the area. In mid-summer (December) two individuals frequented the area, while three individuals were observed during late summer (March).

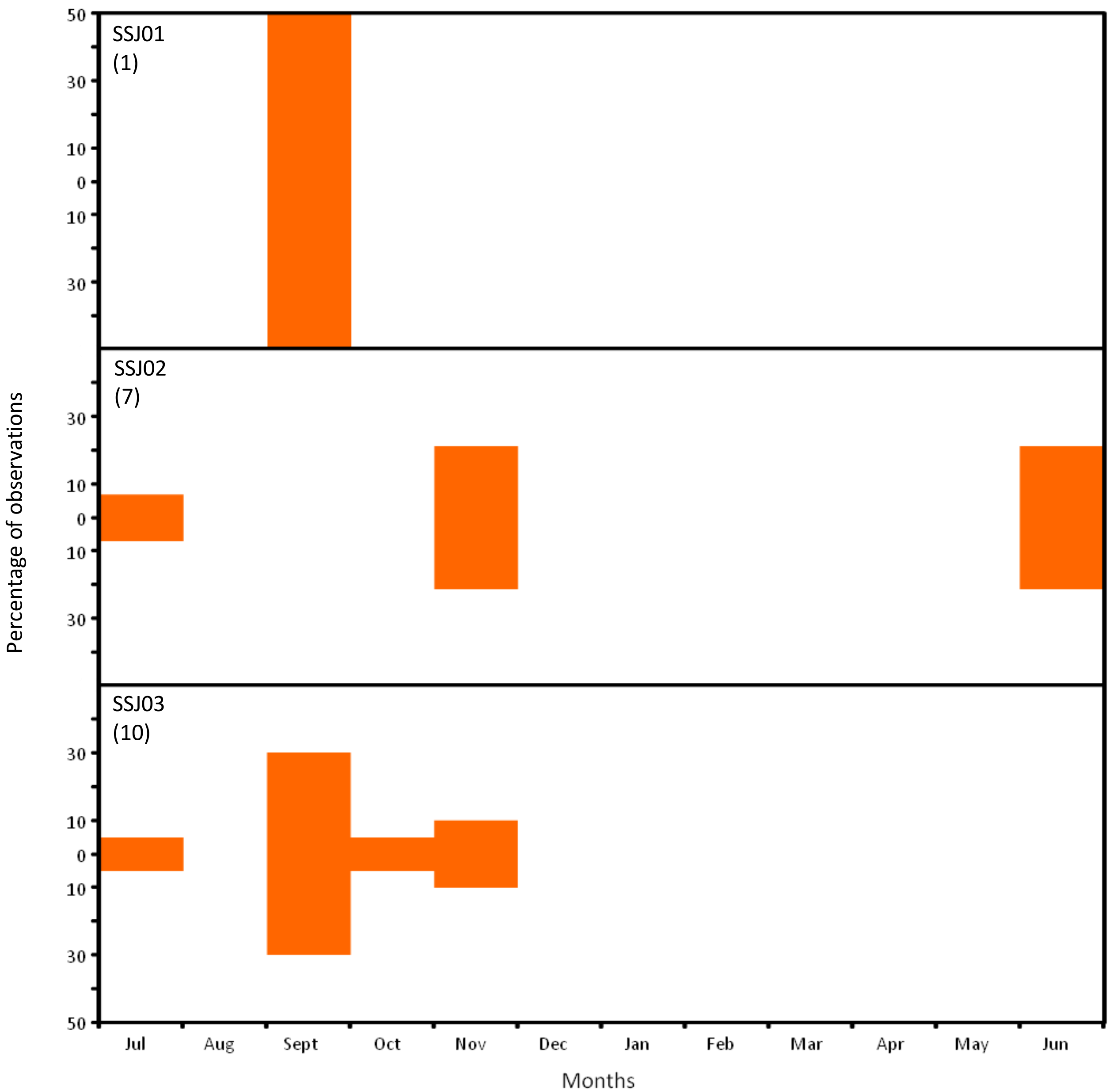

Figure 5.8 Monthly presence of individual side-striped jackals in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations.

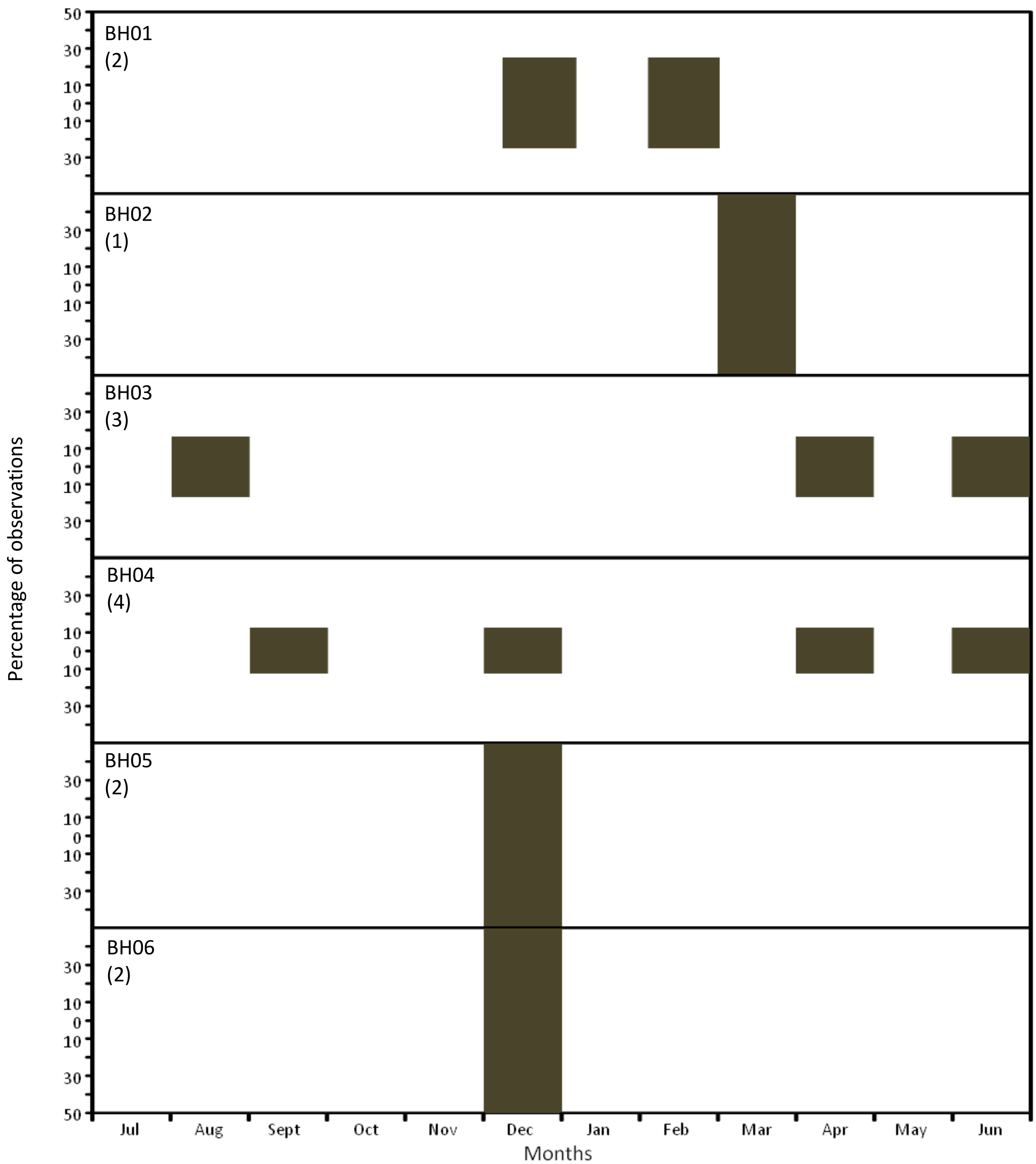

Figure 5.9 Monthly presence of individual brown hyaenas (BH01–BH06) in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations.

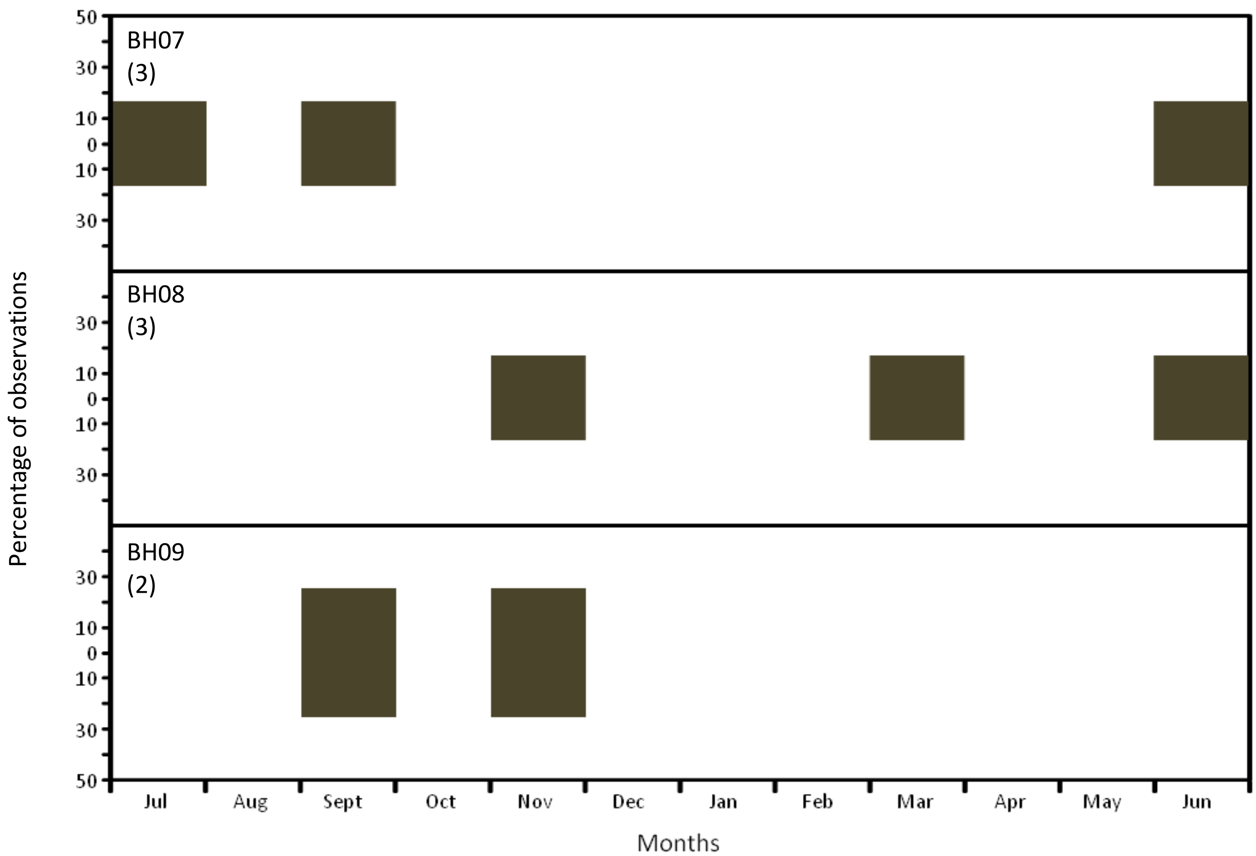

Figure 5.10 Monthly presence of individual brown hyaenas (BH07-BH09) in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations.

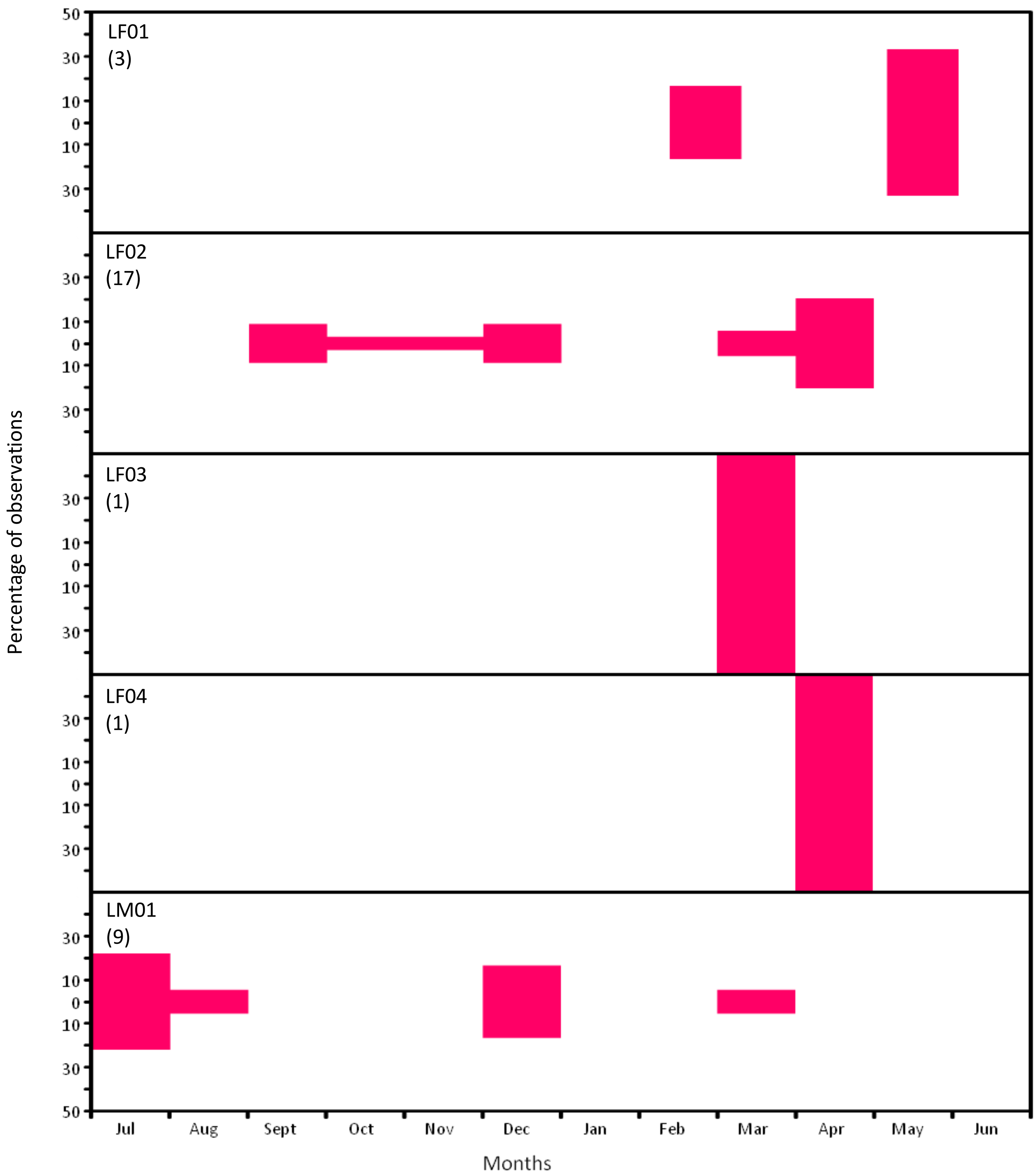

Figure 5.11 Monthly presence of individual leopards in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations. LF, female leopard; LM, male leopard.

5.5.2 Circadian Rhythms of Carnivores

Small predators in the Roodewalshoek conservancy are nocturnal (Fig. 5.12), with the majority of these predators active during the late night hours. African civets and large-spotted genets were also active in the early morning, while honey badgers were somewhat active in the late afternoon (Fig. 5.12). All the medium sized predators' activity was observed to be between 16:00 in the late afternoon and 07:00 in the morning (Fig. 5.13). Caracals showed definite periods of activity and idleness while side-striped jackals exhibited a more continual activity pattern. Caracals seemed to prefer the first stage of the early evening to be active whilst side-striped jackals are more sporadically active during the late night and early morning periods (Fig. 5.13).

Brown hyaenas were predominantly nocturnal, while leopards displayed some diurnal activity during the early afternoon and mornings after sunrise (Fig. 5.14). The hyaenas started to be active in the early evening from 19:00 until 06:00 in the morning and showed a sudden increase in activity in the early evening which gradually subsides until about midnight. After this, hyaenas became increasingly active again from the late night until daybreak (Fig. 5.14). Apart from the tendency of leopards to start their activity earlier and are active later in mornings, both of these large predators exhibit a corresponding circadian rhythm with a strong positive correlation (R^2 = 0.6419; r = 0.8012). The majority of leopard activity was between late afternoon and early morning, peaking from 20:00 in the early evening to 22:00 in the late night. Leopard activity peaks thereafter in the early morning from 03:00 to 04:00 (Fig. 5.14).

In the Roodewalshoek Conservancy the activity of large predators started in the early afternoon and continued until 08:00 in the morning whereas other predators, which included the small and medium sized predators, were observed only between late afternoon and morning (Fig. 5.15). Large predator and other predator activities reached a maximum in the early evening and again during late night, which subsides during early morning. The strongest positive correlation (R^2 = 0.7135; r = 0.8447) between large and other predator activity was found to be during early morning from 03:00 to 05:00. However, overall no correlation could be found between the daily activity of large predators and other predators.

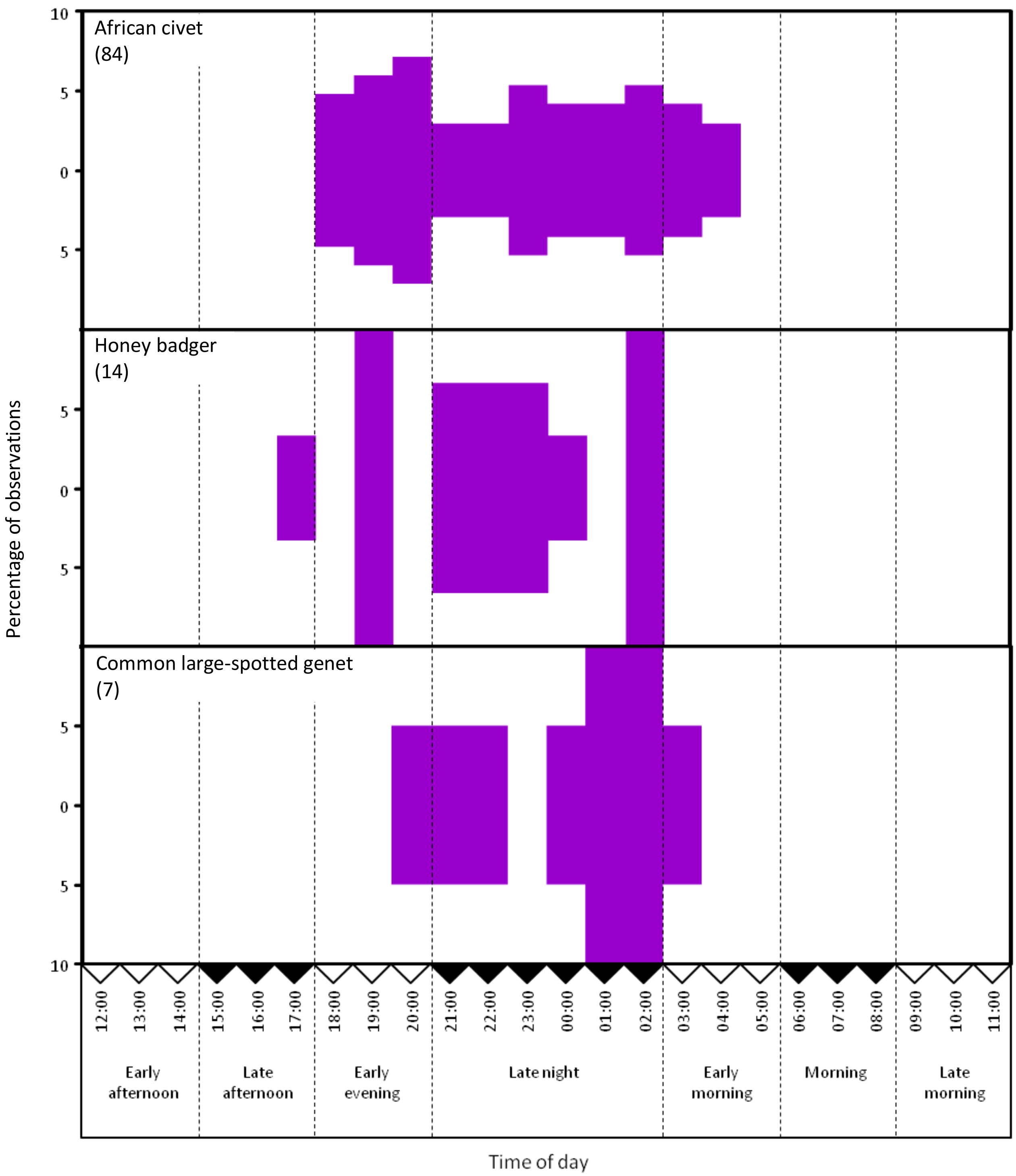

Figure 5.12 Circadian rhythm of small predators in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations.

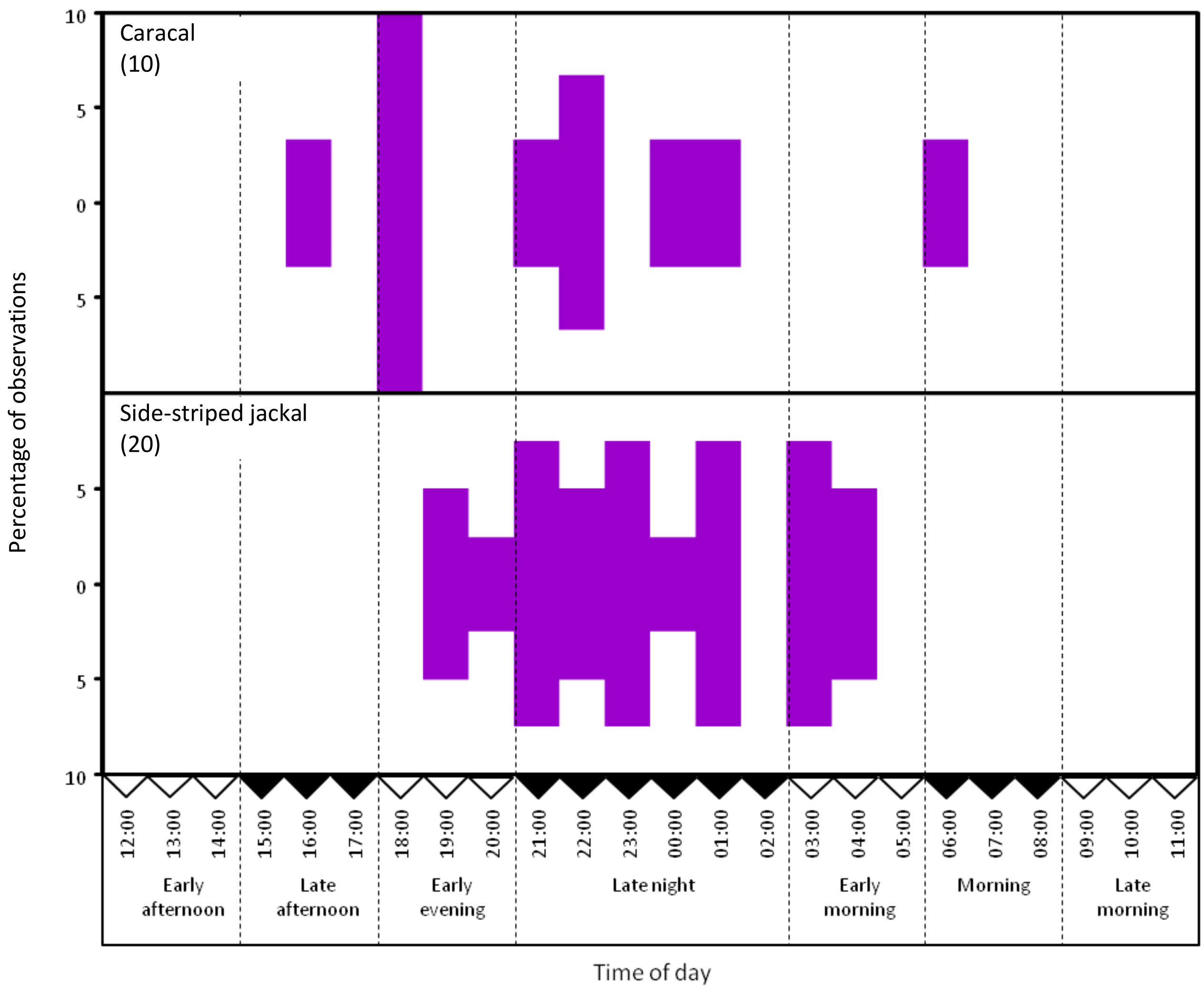

Figure 5.13 Circadian rhythm of medium sized predators in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations.

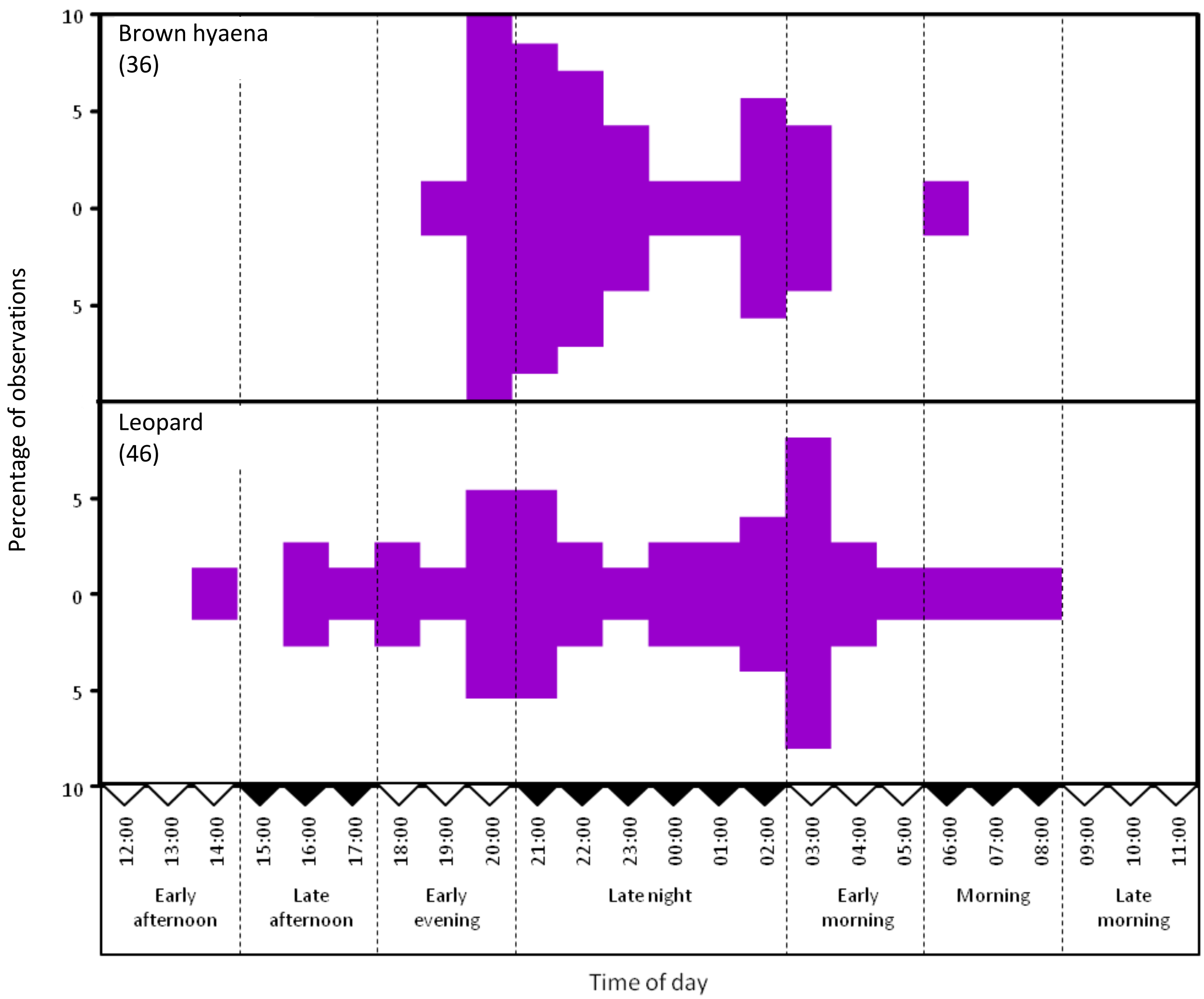

Figure 5.14 Circadian rhythm of large predators in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations.

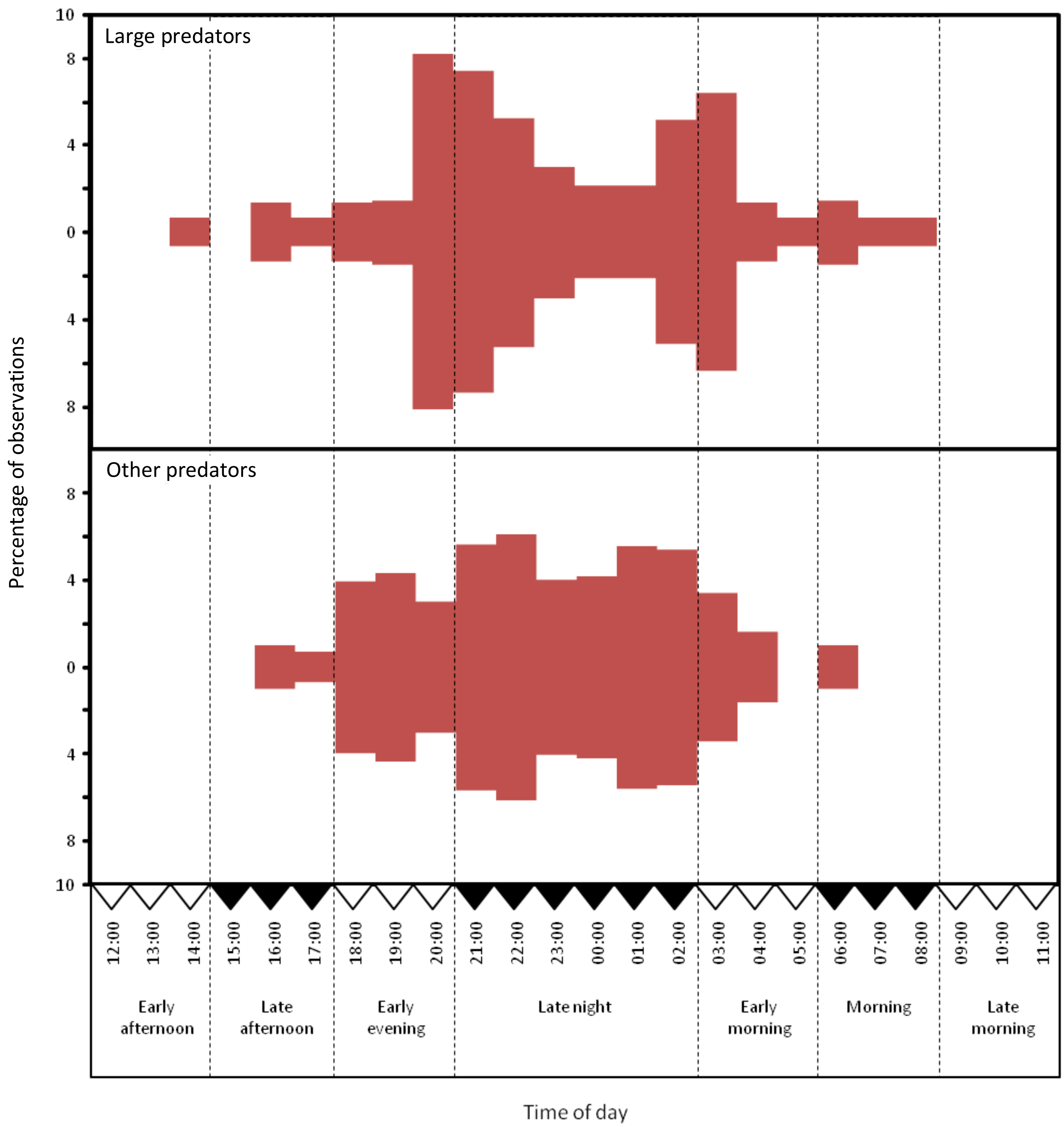

Figure 5.15 Circadian rhythm of large and other predators in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010.

5.5.3 Carnivore Activity as it Relates to the Lunar Cycle

The majority of carnivores showed a preference for either a low or high moonlight intensity, while only large-spotted genets were equally present both the dark and light phase of the moon (Fig. 5.16). Species preferring low moonlight intensity included the African civet, caracal and side-striped jackal, while the honey badger, brown hyaena and leopard were mostly observed when moonlight intensity was bright (Fig. 5.16). African civets seemed take no notice of moonlight intensity and displayed the most constant nocturnal activity pattern of all small predators. Together with honey badgers and large-spotted genets, African civets showed a decrease in activity when moonlight intensity was at its lowest (Fig. 5.17).

Both the medium sized predators were mostly present during intermediate moonlight intensity. Caracals limited their activity when moonlight intensity is low and side-striped jackals displayed limited presence when moonlight intensity is high and also when moonlight intensity is at its lowest (Fig. 5.18). Brown hyaenas and leopards exhibited very similar lunar activity patterns (Fig. 5.19). The presence of these predators peaked when moonlight intensity is high and increasing to its brightest. Leopards were observed more frequently when moonlight intensity is low, whereas brown hyaenas were observed more when moonlight intensity was intermediate (Fig. 5.19). Preference for moonlight intensity was unique to each leopard individual (Fig. 5.20). A female leopard, LF01, showed an even distribution of activity during intermediate, low and high moonlight intensity, while another female, LF02, were equally present during dark and light phase of the moon. The resident male leopard, LM01, preferred intermediate moonlight intensity and limited his activity during high and low moonlight intensity (Fig. 5.20)

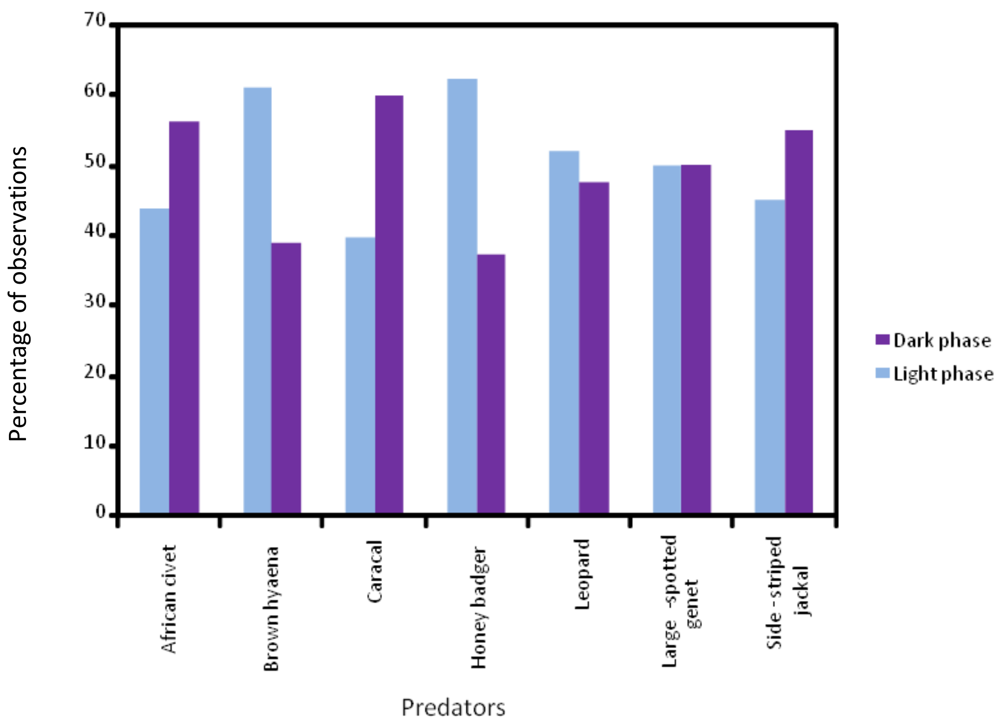

Figure 5.16 Nocturnal activity of predators during the dark and light phase of the moon in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010.

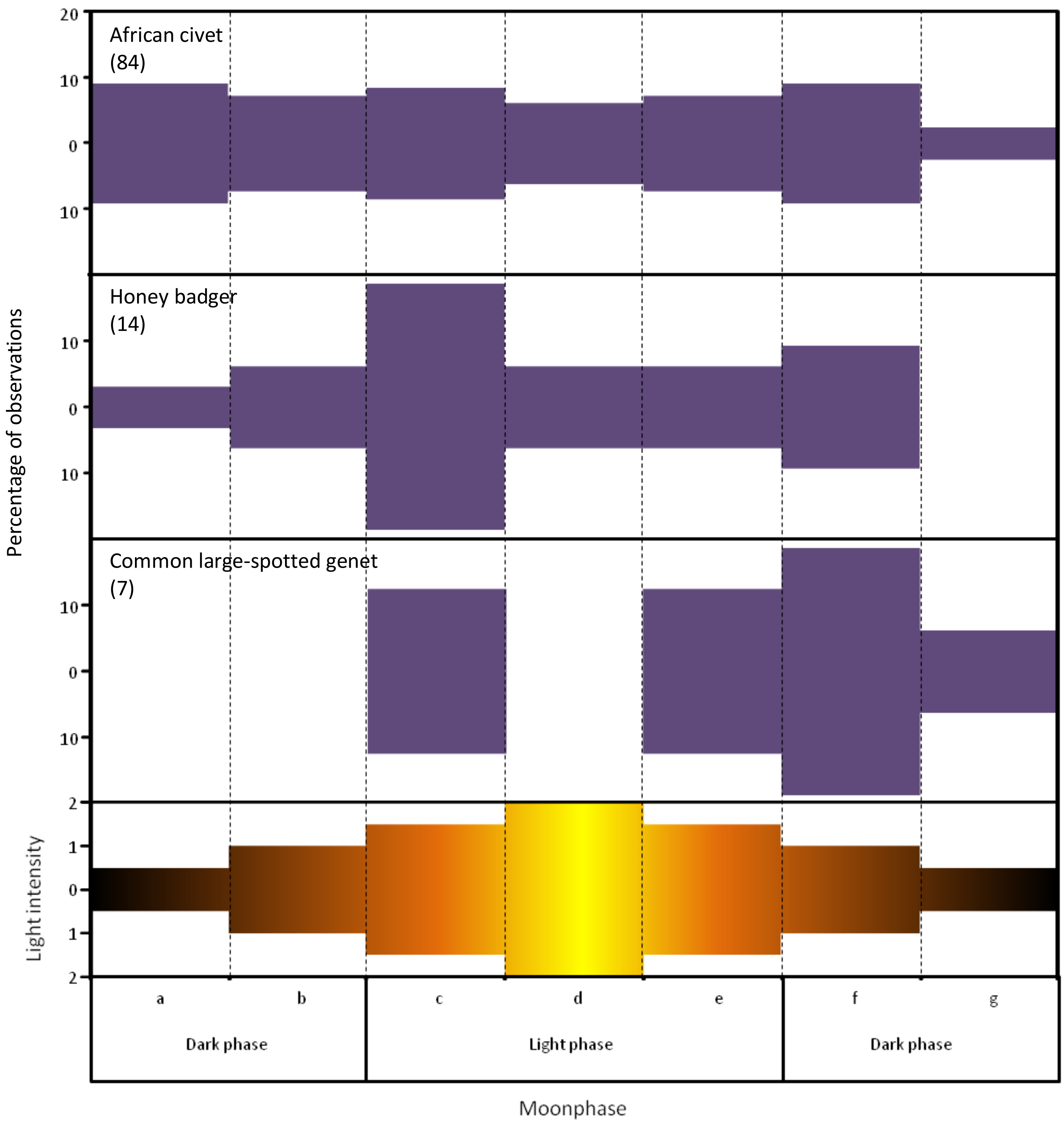

Figure 5.17 Nocturnal activity of small predator species during periods of lunar light in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. **a,** period from new moon to 3rd night after new moon; **b,** period from 4th night after new moon to night before first quarter; **c,** period from first quarter to 5th night after first quarter; **d,** period from 6th night after first quarter to 3rd night after full moon; **e,** period from 4th night after full moon to 7th night after full moon; **f,** period from last quarter to 5th night after last quarter; **g,** period from 6th night after last quarter to night before new moon. Numbers between brackets indicate number of observations.

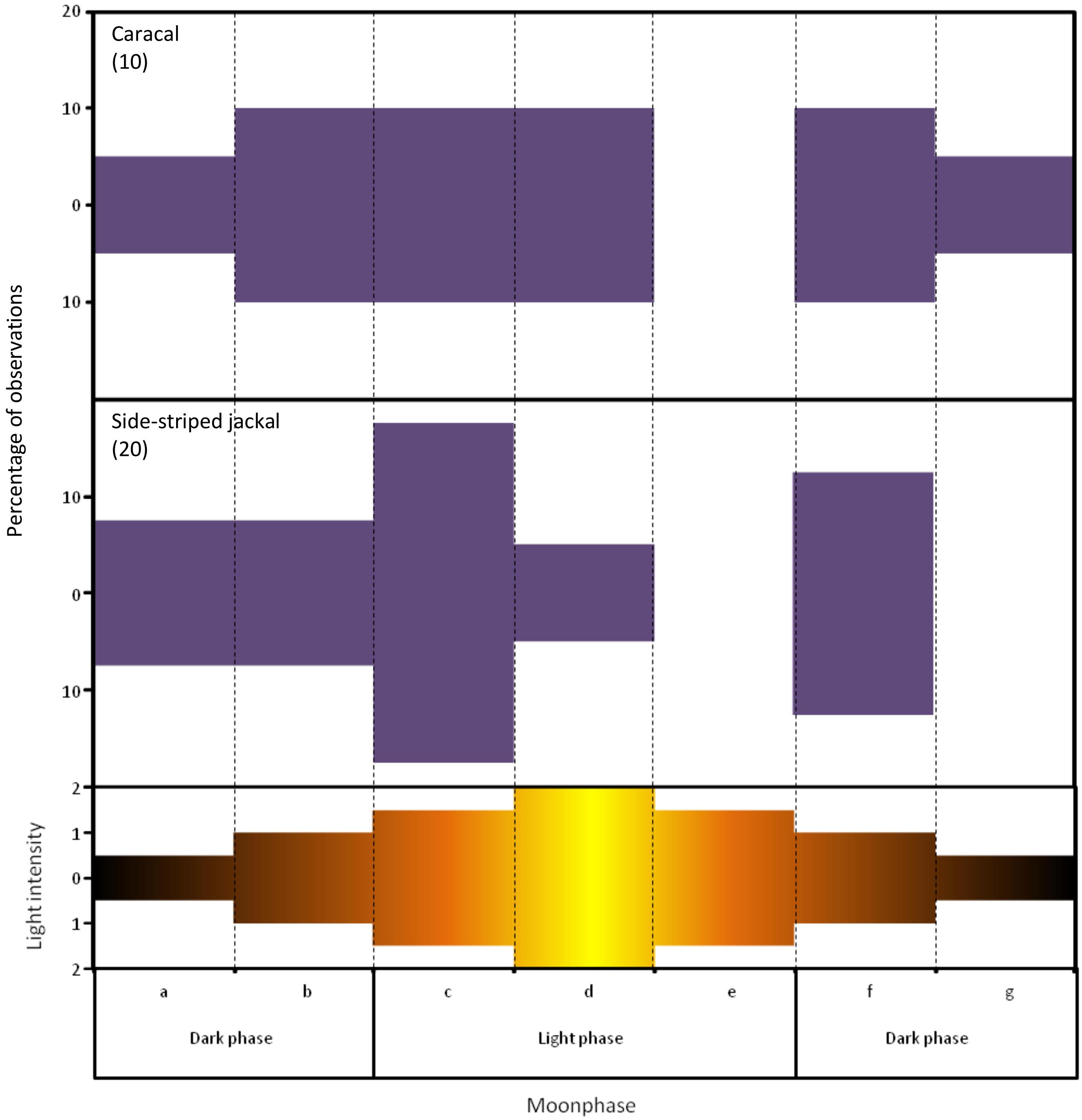

Figure 5.18 Nocturnal activity of medium sized predator species during periods of lunar light in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. **a,** period from new moon to 3rd night after new moon; **b,** period from 4th night after new moon to night before first quarter; **c,** period from first quarter to 5th night after first quarter; **d,** period from 6th night after first quarter to 3rd night after full moon; **e,** period from 4th night after full moon to 7th night after full moon; **f,** period from last quarter to 5th night after last quarter; **g,** period from 6th night after last quarter to night before new moon. Numbers between brackets indicate number of observations.

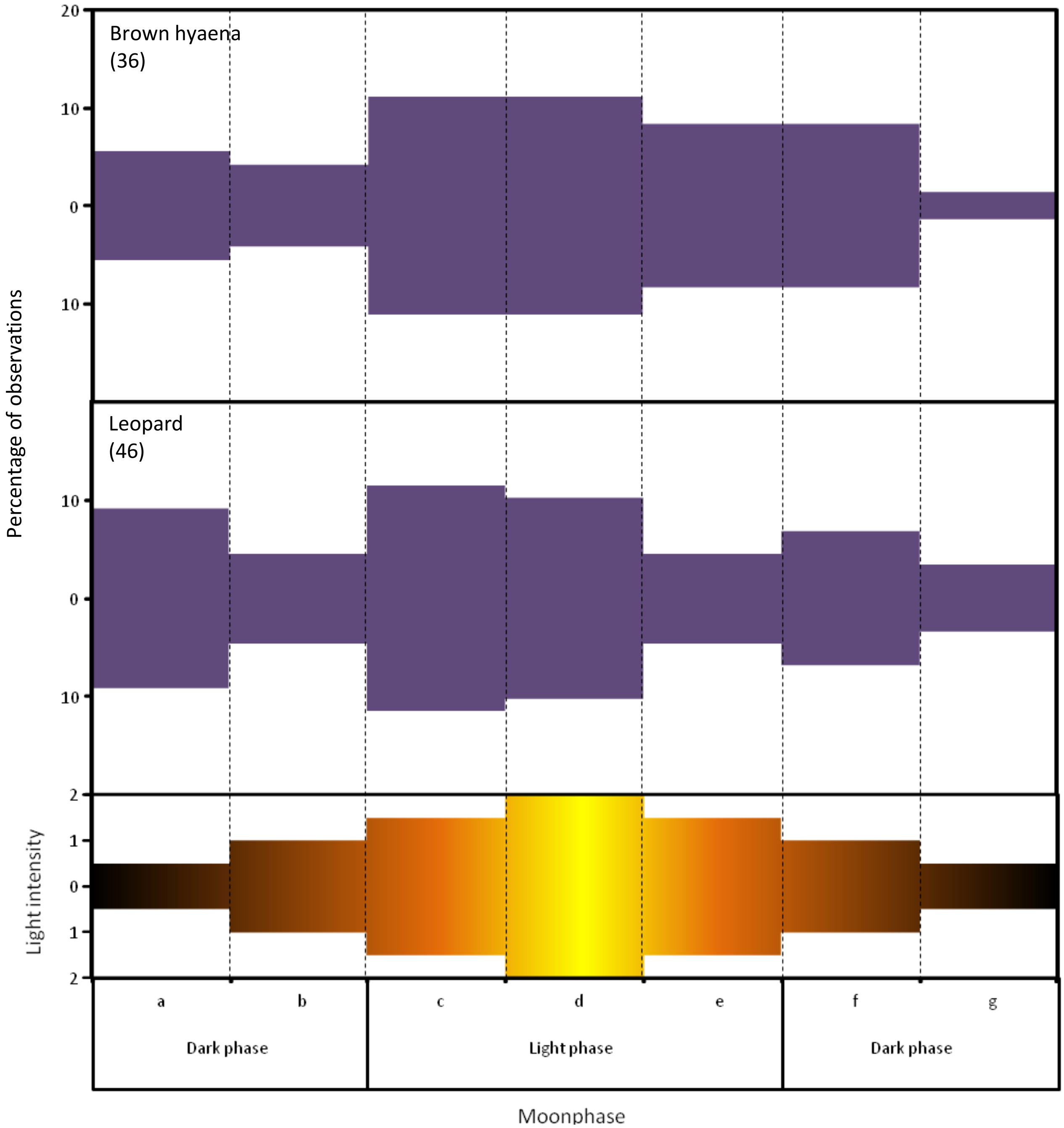

Figure 5.19 Nocturnal activity of large predator species during periods of lunar light in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. **a,** period from new moon to 3rd night after new moon; **b,** period from 4th night after new moon to night before first quarter; **c,** period from first quarter to 5th night after first quarter; **d,** period from 6th night after first quarter to 3rd night after full moon; **e,** period from 4th night after full moon to 7th night after full moon; **f,** period from last quarter to 5th night after last quarter; **g,** period from 6th night after last quarter to night before new moon. Numbers between brackets indicate number of observations.

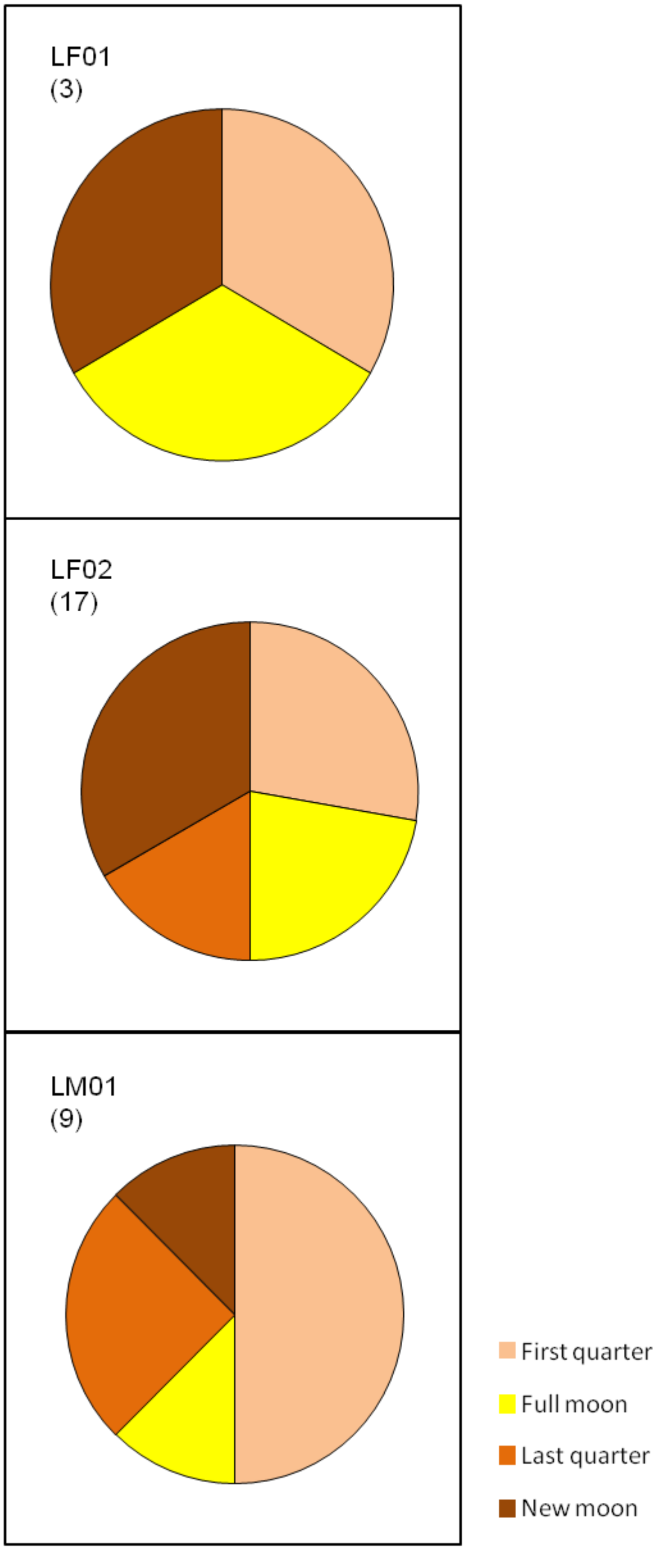

Figure 5.20 Nocturnal presence of leopard individuals during different moon phases in the Roodewalshoek Conservancy over a period of two years from January 2009 to December 2010. Numbers between brackets indicate number of observations. LF, female leopard; LM, male leopard.

5.5.4 Field Observations

Brown hyaenas and leopards usually entered the conservancy from the southern kloofs and moved northwards along the valley, using mainly riverine areas, open road and well-used game paths (Fig. 5.21). The movements of the leopards also seemed to follow a close-to weekly pattern, where they usually entered the Roodewalshoek Conservancy shortly after a weekend and leaving it then just before the following weekend starts. This may be due human activity in the Conservancy increasing drastically over weekends and the leopards may be trying to avoid this source of disturbance. Three scratch trees (Fig. 5.21) were found along the route indicated along the white arrow, where fresh scratches were found relatively frequently. One observation of an unidentified leopard occurred during late twilight in November close to one of the scratch trees, where it waited perched in another tree for three warthogs to pass underneath it and then casually jumped down to walk away at its own leisure (Johann van As, personal communication).

On another occasion an unknown leopard individual lay about 10 meters from the house, regularly calling for about 40 minutes, after which it moved northwards all along the river. During October 2009, two sets of leopard tracks (small and large) were found walking together. In all probability the smaller footprints belonged to LF02 and the large prints to LM01, which was the only male observed during the study and presumed to be the territorial male of the area. Further on, during the months following December 2009, photographical data obtained by camera traps showed LF02 first pregnant and then lactating heavily, with cub tracks also later observed in the area. One cub and LF02 were briefly seen in October during broad daylight hours close to the farm house (Gert Stoltz, personal communication). Once, while walking a circle route during field observations, fresh leopard tracks were found across footprints of the author. This indicates that these animals display some degree of diurnal activity. On the same evening, a calf was caught by a leopard.

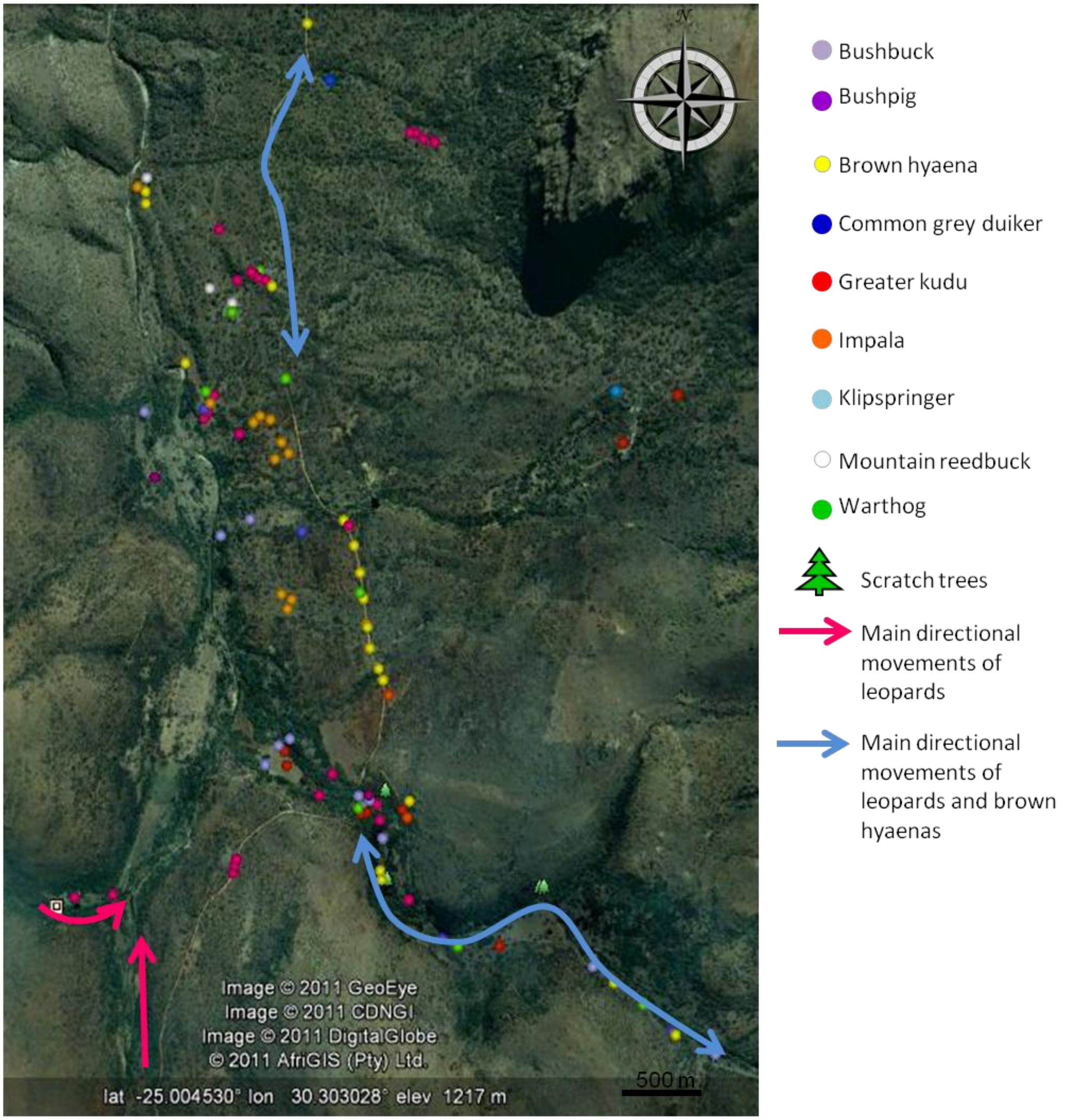

Figure 5.21 Occurrence of potential prey and large predators in the Roodewalshoek Conservancy from January 2009 to December 2010. Pink arrows, main directional movements of only leopards entering the Conservancy; Blue arrows, main directional movements of both leopards and brown hyaenas entering and moving out of the conservancy.

Neither leopards nor brown hyaenas showed interest in investigating baited camera traps. Several attempts with different types of bait were made, ranging from fish oil and aerosol spray to moving a calf left behind after a night of surplus-killing to the nearest camera trap station. Only warthogs and bushpigs showed interest in the baited sites and these sites were entirely avoided by leopards and brown hyaenas. However, when another instance of surplus-killing by a leopard took place, a camera trap was taken the following morning to the site and set up with minimal disturbance to the dead calf left behind. Then, early that evening at around 20:00, a female leopard, LF02, came to collect the calf. A male leopard, LM01, was also once photographed on the same evening when a calf was killed and partially devoured by an unknown large leopard. A local farm worker confirmed that the leopard returned the following evening to feed again on the same carcass.

Evidence of a brown hyaena following close behind a leopard was observed during November 2009, when both predators walked in the same direction along a road, approximately 150 m apart. Evidence of brown hyaena caching food in a scattered pattern inside a radius of about 500 m from a cattle carcass was also found. Femur and other large bones were hidden beneath thick tufts of grass and even wedged in underneath a flat rock. The only other observation of possible interaction between leopards and brown hyaenas were obtained with the aid of a carefully placed camera trap at a greater kudu carcass. Around 21:30, a female leopard, LF02, came to feed for 20 minutes on the carcass, ignoring the camera trap. About one and a half hours later on the same evening, a single brown hyaena made its appearance but did not feed on the carcass. Early the following evening, two brown hyaenas started feeding alternately on the carcass for about one and a half hours. Then, ten minutes after the brown hyaenas left, LF02 was observed feeding on the remains. It is, however, impossible to tell whether the brown hyaenas left due to the presence of LF02 in the immediate area, or if LF02 waited for the hyaenas to finish feeding before approaching the carcass.

5.6 Discussion

The population distribution and behaviour of potential prey species have a significant influence on the quality of habitat available to a predator, and therefore also indirectly impacts the health of predator populations in an area. Spatial arrangement, availability and activity patterns of prey have been reported to influence not only the selection of prey species, but also the hunting success of predators (Fuller *et al*., 1992; Henschel & Skinner, 1990). The most abundant medium sized prey species in the conservancy namely bushbuck, common grey duiker and impala, are also regarded as preferred prey of leopards (Hayward *et al.,* 2006). All three these prey species displayed nocturnal as well as diurnal activities.

Monthly rainfall has an effect on the vegetation composition and consequently habitat structure of an area, which in turn has an effect on the spatial distribution and activity of potential prey species. This will subsequently have an impact on the preferred habitat types of predators (Bakker, 1983; Kruuk, 1986; Woodroffe, 2001; Maheshwari, 2006). During this study, it seemed that an increase in monthly rainfall led to a decrease in the number of small predators observed. The reason for this may be that the increase of ground moisture and vegetational cover lead to increases in the biomass of potential prey species, such as small vertebrate and invertebrate fauna, leading to localized movements by small predators that move shorter distances in search of food.

On the other hand, the increase in monthly rainfall resulted in increased observations of large predators. Mills (1994) suggested that the size of a large predator's home range is negatively correlated with the amount of food items available. The reason for the increased presence of large predators during the wet season may be that, due to denser vegetation cover, sufficient prey items needed by these carnivores are more difficult to detect. This may result in these carnivores increasing daily distances moved in order to obtain sufficient nutrition. Balme *et al.* (2007) suggested that leopards prefer to hunt in habitats where prey proved less difficult to catch. The positive correlation between rainfall and large predator presence therefore suggests that these carnivores may find hunting conditions difficult during periods of dense vegetation cover.

Patterns of monthly presence and circadian rhythms of carnivores differed widely from species to species and it seemed that smaller predators tend to utilize the area more intensively in the absence of large predators and less so in the presence of their larger counterparts. This suggests that smaller predators possibly attempt to avoid predatory competition and in some cases even predation by the larger carnivores, using spatial and temporal separation, a phenomenon also found by Bridges & Noss (2011). Hodkinson *et al.* (2007) also found that the presence of leopards leads to a drop in the numbers of medium sized carnivores such as jackal and caracal in an area. According to Mills (1994), Bothma & Walker (1999) and Hodkinson *et al.* (2007), brown hyaenas also serve as an important resource competitor with jackals. The monthly pattern of the brown hyaena and leopard presence seemed to be highly similar. Since Mills (1994) found a dietary overlap between these two species and the observation of both predators sharing the same carcass during the current study might indicate a unique relationship between brown hyaena and leopard in the Roodewalshoek Conservancy. This relationship however, needs further investigation.

Van Rensburg (1965) found that moonlight intensity may influence the activity of nocturnal species. Predators in the Roodewalshoek Conservancy utilized moonlight intensity in different ways with the majority preferring to be active when moonlight intensity is moderate. While leopards and brown hyaenas are generally more often observed during the light phase of the moon, the smaller predators are in general more active during dark moonlight intensities. This may also be a form of large-predator avoidance by the smaller carnivores.

Each individual predator exhibited a unique temporal and spatial adaptation to its environment. This suggests that individuals from the same species can develop individual adaptations to the available resources and inter- and intraspecific competitions in their surroundings. It is assumed that individuals of different predator species, African civet CT01, side-striped jackal SSJ03, leopard female LF02 and leopard male LM01, which were recorded on a frequent basis during the entire study, are territorial animals in the Roodewalshoek Conservancy. No individual brown hyaena was continually present in the conservancy, suggesting that individuals utilize different areas alternately as was observed by Mills (1994), Estes (1991), Bothma & Walker (1999); Skinner & Chimimba (2005), and Carnaby (2006). It is possible that, during periods of absence from the conservancy, both small and large predators spend more time roaming the adjacent Thaba-Tholo Private Game Reserve and surrounding areas. This trend of presence and absence in an area may be indicative of core-use of home ranges by most carnivores in the Roodewalshoek Conservancy.

6

Livestock Predation

CHAPTER 6
LIVESTOCK PREDATION

6.1 Introduction

Human-carnivore conflict is a complex issue influenced by socio-political attitudes, the biology of the species of conflict as well as management action taken to reduce such conflict (Athreya & Belsare, 2007). Expanding agricultural land-use is rapidly encroaching on potential areas of wildlife dispersal and corridors, which are crucial for the integrity of conservation of large carnivores (Treves & Karanth, 2003; Santiapillai & Jayewardene, 2004). Human technological advancement and population increase is rapidly reducing and fragmenting the available habitat for large carnivores (Holmern *et al.*, 2007) and brought wildlife and people into increased contact and inevitable conflict over diminishing shared resources (Butler, 2000; Santiapillai & Jayewardene, 2004; Graham *et al.*, 2005).

Emlen (1966) and MacArthur & Pianka (1966) suggested that predators select prey based on the energy gained from prey, the time searched in order to find prey and handling costs, such as risk of injury inflicted by prey (Sunquist and Sunquist, 1989). Temple (1987) added that the degree of prey vulnerability could also be a determining factor in prey selection. MacArthur & Pianka (1966) hypothesized that predators in productive environments tend to be more selective when choosing a prey object than predators in unpredictable environments. According to Bothma & Coertze (2004) and Hayward & Kerley (2005) predators will select habitats in which to hunt where energy requirements can be met with minimum energy expenditure and Maheshwari (2006) added that predators prefer habitat types which harbor the least difficult obtainable prey. It was suggested by Carbone and Gittleman (2002) that the presence of carnivores in an area is closely related to the prey biomass in an area and therefore prey density seems to be a fundamental determinant of carnivore density between and within species.

6.2 Livestock Predation: An Overview

The most common source of man's conflict with predators is livestock depredation (Skovlin, 1971; Denney, 1972; Freedman, 1989; Lawson, 1989; Mills, 1991; Newmark *et al.,* 1993; Oli *et al.,* 1994; Du Toit, 1995; Kreuter & Workman, 1996; Weber & Rabinowitz, 1996; Kharel, 1997; Mishra, 1997; Ciucci & Boitani, 1998; Conner *et al.,* 1998; Linnell *et al.*, 1999; Mizutani, 1999; Vitterso *et al.,* 1999; Kangwana & Mako, 2001; Linnell *et al.* 2001; Treves *et al.,* 2002; Linnell & Broset, 2003; Linnell *et al.,* 2003; Marker *et al.,* 2003a; 2003b; Ogada *et al.*, 2003; Polisara *et al.,* 2003; Santiapillai & Jayewardene, 2004; Treves *et al*., 2004; Herfindal *et al.,* 2005; Marker *et al*., 2005; Ray *et al.*, 2005; Woodroffe *et al.,* 2005; Al-Johany, 2007). This results in the experience of substantial economical losses by the affected farmers (Van Bommel *et al.,* 2007). Livestock predation and the feeding ecology of large carnivores have been studied in many areas where humans and carnivores are forced to share living space (Kruuk, 1980; Skinner *et al.*, 1980; Rabinowitz, 1986; Hoogestejin *et al.*, 1993; Karanth *et al.,* 1999; Rasmussen, 1999; Hoogestejin, 2000; Funston *et al*., 2001; Marker *et al.*, 2003a; 2003b; Hemson, 2003; Bagchi & Mishra, 2006; Hemson *et al.,* 2009). This conflict can have a substantial disproportionate effect on the affected rural community (Dar *et al.*, 2009) since those who live closest to the source of carnivores will be more severely affected (Skinner *et al.,* 1992; Butler, 2000; Holmern *et al.*, 2007).

Large carnivores are especially vulnerable to conflict with humans due to their dietary requirements and the need for large home ranges, which increasingly puts them in the paths of humans (Butler, 2000; Linnell *et al.*, 2001; Macdonald & Sillero-Zubiri, 2002; Graham *et al.*, 2005). Large carnivores are therefore forced to live in extreme close proximity to humans in areas where both parties compete for space and ungulate prey species (Dar *et al.*, 2009). Depredation of livestock often results in persecution by farmers in the form of killing the perceived problem animals (Mishra, 1982; Rahalkar, 2008). However, the presence of a variety of predators in an area is indicative of a balanced system resulting from wise land-use management (Hodkinson *et al.,* 2007). In South Africa livestock depredation varies widely and the greatest losses generally occur where wild prey density is low (Ray *et al.*, 2005). Linnell *et al.* (1999) stated that domestic livestock is relatively easy prey due to their lack of virtually all ancestral anti-predator strategies and therefore represent an easier kill compared to other potential prey species of similar size. However, Polisara *et al.* (2003) found that predators often kill livestock in areas that contain adequate numbers of natural prey to sustain the resident predator community and suggested that livestock are consequentially hunted selectively rather than opportunistically. Thus any livestock farming operation has to take precautions to protect livestock from predators (Hodkinson *et al.,* 2007).

Important aspects considered when addressing human-carnivore conflict does not only include studies on the ecological patterns and drivers of livestock predation (Stander, 1997; Marker *et al.*, 2003a; 2003b; Treves *et al.*, 2004; Woodroffe *et al.*, 2007), but also address efforts to understand the driving forces and attitudes of the people who are expected by conservationists to share their land with carnivores (Zimmermann *et al.*, 2005; Selebatso *et al.*, 2008; Hemson *et al.*, 2009). Predator-prey dynamics can be affected directly as well as indirectly by the presence of cattle in the landscape (Georgiadis *et al.,* 2007). Cattle that are not placed in fenced-in areas at night will be more vulnerable to predation (Skovlin, 1971) and livestock depredation can be influenced by local environmental conditions such as abundance of natural prey (Mizutani, 1999; Polisara *et al.*, 2003) and rainfall (Patterson *et al.*, 2004; Woodroffe & Frank, 2005).

According to Linnell *et al.* (1999), it is often expected that old, unhealthy adults or inexperienced juvenile predators will prey on livestock to a greater extent than healthy adults. Several studies showed that young predators are poorer hunters, (Stirling and

Latour, 1978; Holekamp *et al.*, 1997) and Fox & Chundawat (1988), Rabinowitz (1986) and Hoogesteijn *et al.* (1993) found that older or injured predators are mostly responsible for the majority of livestock losses. However, Aune (1991) and Riley *et al.* (1994) found that most predators of livestock are in good health. Linnell *et al.* (1999) also found no evidence to support the notion that "problem individuals" exist and suggested that most individuals of large carnivore species will occasionally make use of the opportunity to kill easily accessible livestock.

Surplus-killing, where multiple prey items are killed in one event, is a highly common aspect of carnivore depredation on livestock (Andelt *et al.*, 1980; Mysterud 1980; Horstman & Gunson, 1982; Fox & Chundawat, 1988; Al-Johany, 2007). Linnell *et al.* (1999) suggested that this kind of behaviour could be a form of natural "multiple-killing" behaviour, which require more than one meal to be consumed, over a prolonged period. Thus, the killing of multiple prey items at a time can be seen as a highly effective, opportunistic adaptation. Surplus-killing is most often observed amongst smaller carnivores (Oksanen *et al*, 1985; Vander Wall, 1990; Madsen *et al.*, 1992; Macdonald *et al.*, 1994), but is not unknown in large predators (Schaller, 1972; Stander, 1997; Dale *et al.*, 1995). Well-developed anti-predator strategies of the majority of potential prey species means that the opportunity to make multiple kills presents itself very rarely and is mostly associated with unusual conditions such as severe thunderstorms (Kruuk, 1972). Livestock, which can also be viewed as a localized, unnaturally dense culmination of vulnerable potential prey lacking most anti-predator instincts, present ideal artificial circumstances that favors the predator (Linnell *et al.*, 1999).

6.3 Feeding Ecology of the Leopard *Panthera pardus* (Linnaeus, 1758)

Leopards are mainly nocturnal and show a preference for thickets (Sunquist, 1983; Estes, 1991; Bailey, 1993; Mills & Biggs, 1993; Bothma & Walker, 1999) and therefore river banks prove a very important habitat type for leopards (Hayward *et al.*, 2006). This big cat is considered to be highly opportunistic (Bothma & Le Riche, 1984; Estes, 1991; Hes, 1991; Bothma & Walker, 1999; Hancock, 2000) and will make full use of any hunting opportunity, even during daylight hours (Hes, 1991; Bothma & Walker, 1999). Leopards have a catholic diet (Estes, 1991; Mills & Biggs, 1993; Bothma & Walker, 1999; Grimbeek, 1992; Hayward *et al.,* 2006) and have the ability to utilize habitats and food resources that are not favoured by most other predators (Bailey, 1993; Mills & Biggs, 1993; Hayward *et al*., 2006). Leopards will eat whatever food is the easiest to obtain (Estes, 1991; Bothma & Walker, 1999; Chauhan *et al.*, 2000), which is usually perceived as the most common prey item in the area (Carbone & Gittleman, 2002; Breuer, 2005; Hayward *et al.,* 2007). It was however suggested by Hayward *et al.* (2006) that leopards are not totally non-selective when it comes to selecting prey. Leopards feed predominantly on small to medium sized antelope (Kruuk & Turner, 1967; Grobler & Wilson, 1972; Smith, 1977; Bothma & Le Riche, 1984; Norton *et al.*, 1986; Le Roux & Skinner, 1989; Hes, 1991; Bailey, 1993; Mills & Hes, 1997; Ray *et al.*, 2005; Skinner & Chimimba, 2005; Schwarz & Fischer, 2006) of less than 70 kg and are highly adaptable in diet (Bailey, 1993; Hayward *et al.*, 2006). It also seems that the availability of prey tend to determine the home range size of leopards (Bothma *et al.,* 1997). Large ungulates can also be taken as an exception to the rule if the opportunity presents itself (Skinner & Chimimba, 2005).

Leopards are stalking and pouncing specialists (Hes, 1991; Bailey, 1993; Bothma & Walker, 1999; Ray *et al.*, 2005; Skinner & Chimimba, 2005, Hayward *et al.*, 2006; Balme *et al.*, 2007), and these masters of concealment use available cover and never-ending patience to get very close to prey before making the final charge (Bertram, 1975; Mills & Hes, 1997; Bothma & Walker, 1999; Sharma, 2004). Contrary to the findings of Hirst (1969), it was concluded by Bailey (2005), Hayward *et al.* (2006; 2007) and Balme *et al*. (2007) that leopards prefer to hunt in habitats where it was easier to catch prey rather than where prey was more common. Shultz *et al*. (2004) suggested that there exists no relationship between prey abundance and leopard predation rates. According to Skinner & Chimimba (2005), stalking distances vary substantially and depend on the type of cover and habitat. A leopard catches its prey with its front paws and kills it with a bite to the throat whereby it asphyxiates the prey (Hes, 1991; Bailey, 1993; Mills & Hes, 1997). Leopards usually start feeding at the soft underbelly between the hind legs and after feeding will cover scraps and stomach contents with grass and sand (Hes, 1991; Bailey, 1993; Mills & Hes, 1997; Hancock, 2000). According to Bailey (1993) and Mills & Hes (1997), leopards will readily scavenge if the opportunity presents itself. Ray *et al.* (2005) found that leopard densities are positively correlated with prey availability.

Balme *et al.* (2007) found the probability of a successful kill to be greater in areas with intermediate vegetative cover and that reduced detectability of prey in more dense vegetation is a principal factor determining hunting habitat types favored by leopards. Hes (1991) and Balme *et al.* (2007) found that leopards might use alternative hunting strategies when the situation calls for it. Hes (1991) suggested that leopards apparently favour an ambush-pounce technique in dense riverine woodland, whereas Balme *et al.* (2007) found that leopards tend to rely more on ambushing or flushing prey in thicker vegetation types, because prey detectability was markedly reduced in these areas. Leopards significantly avoided grassland vegetation types (Balme *et al.*, 2007) and the suggested reason for this was that predator detectability by prey would be enhanced by lack of available cover. In terms of the degree of sociality of potential prey species, leopard predation rates on terrestrial species living in smaller groups seem to be the highest (Shultz *et al*., 2004).

According to Mills & Biggs (1993) leopards rarely lose their kill to other predators as they display caching behaviour by hoisting their kills into trees or hiding it in underground holes and under dense bushes (Bailey, 1993; Mills & Hes, 1997; De Ruiter & Berger, 2001; Skinner & Chimimba, 2005; Hayward *et al.,* 2006; Balme *et al*., 2007). Leopards may kill more than they immediately require (Hes, 1991; Bothma & Walker, 1999; Hancock, 2000; Skinner & Chimimba, 2005, Al-Johany, 2007), a phenomenon known as surplus-killing. Bothma & Walker (1999) suggested that this would only happen in opportunistically unique circumstances when prey vigilance or reactions are impaired.

Some individuals may become habitual killers of a single type of prey (Hes, 1991; Bothma & Walker, 1999). Bothma & Walker (1999) suggested that leopards will readily adapt their diet to may make use of seasonally abundant food resources and diet might vary between individuals (Shultz *et al*., 2004). Leopards will selectively hunt for prey type, age, sex and body condition (Bothma & Walker, 1999), thus exercising energy maximization. It is, however, important to always keep in mind that predators such as leopards can display behavioural changes when they occur in habitats where they are not competing with larger carnivores (Eisenberg & Lockhart, 1972). In this regard, Chauhan *et al.* (2000) found that leopards display behavioural changes due to pressures of habitat destruction and loss of available prey species and became extremely audacious in the presence of humans.

6.4 Feeding Ecology of the Brown hyaena *Parahyaena brunnea* (Thunberg, 1820)

Brown hyaenas are nocturnal animals and have the most varied diet of all hyaenids (Estes, 1991; Mills, 1994; Bothma & Walker, 1999; Skinner & Chimimba, 2005). They hide in thick bushes or holes during the day, have a very secretive nature, rarely vocalize and are generally very difficult to detect (Mills, 1994). These animals usually live in association with other large carnivores and they benefit from their presence by scavenging on the kills made by their larger counterparts (Mills, 1982; Mills, 1994; Skinner & Chimimba, 2005). Carcasses abandoned by other predators therefore seem to constitute the most important part of brown hyaenas' diet (Owens & Owens, 1978). According to Skinner & Chimimba (2005) they are able to detect carcasses over vast distances. Brown hyaenas are predominantly opportunistic scavengers of vertebrate remains and will scavenge up to 96% of all the food items in their diet (Skinner, 1976; Mills & Mills, 1977; Skinner & van Aarde, 1981; Mills, 1982; Estes, 1991; Mills, 1994; Bothma & Walker, 1999; Lacruz & Maude, 2005; Maude, 2005; Maude & Mills, 2005; Skinner & Chimimba, 2005; Carnaby, 2006). When scavenging they tend to show a preference for fresh meat (Skinner & Chimimba, 2005) and the types of remains most commonly consumed depend on the type of prey species most commonly present in the area (Skinner *et al.,* 1992; Mills, 1994).

Brown hyaenas are considered to be inefficient hunters (Mills, 1994; Kuhn *et al.,* 2008; Maude, 2005) which will occasionally kill small animals such as rodents, reptiles, birds or insects while foraging (Mills, 1982; Mills, 1994; Bothma & Walker, 1999; Skinner & Chimimba, 2005). According to Maude (2005) they rarely obtain food by hunting. The hunting technique of brown hyaenas can be described as a poorly developed, unsophisticated, primitive 'chase and grab affair' (Mills, 1994; Bothma & Walker, 1999). Brown hyaenas lack agility and stealth and will primarily surprise sleeping prey animals rather than to run them down (Carnaby, 2006). When they do take the trouble to stalk prey, they make no effort to move quietly and will pursue prey for only a short distance (Estes, 1991; Skinner & Chimimba, 2005). Most of their food items, which are not shared with other individuals, consist of scavenged old limbs, small pieces of bone and even skull bones. (Bothma & Walker, 1999) and it was suggested by the same authors that they will only hunt when carrion is scarce. Some individual hyaenas are also known to show preference for a certain prey species and will exert extra effort to hunt such species (Mills, 1994; Bothma & Walker, 1999).

This predator forages solitarily and all individuals of a clan will use a network of extensive pathways throughout the clan's home range, which they patrol while foraging (Estes, 1991; Bothma & Walker, 1999; Skinner & Chimimba, 2005; Carnaby, 2006). Due to the fact that majority of the brown hyaena's food items encountered while foraging is so small, it can only provide enough nutrition for one hyaena at a time. Brown hyaenas forage by covering the ground in a punctuated, zig-zag course with the head held in a raised position, relying mainly on smell (Estes, 1991; Mills, 1994). They typically move from one food item to the next (Mills, 1994) and a single brown hyaena will forage up to 10-20 km per night in the wet season, with the distance increasing to 20-30 km per night during the drier times of the year (Mills, 1994; Bothma & Walker, 1999). Estes (1991) also stated that brown hyaenas show drastic changes in their diet between the wet and dry seasons. An overlap in diet does exist between brown hyaenas and leopards and both species gain and loose food items to each other (Mills, 1994).

Brown hyaenas display caching behaviour and will carry severed pieces of a carcass, such as limbs, up to 2 km away from the carcass to store it for later use or to the densite to feed the cubs (Estes, 1991; Mills, 1994; Bothma & Walker, 1999; Skinner & Chimimba, 2005). When a brown hyaena finds a large quantity of food, it will quickly eat some and then carry severed parts off to be stored. It will also sometimes return to the densite to fetch one or two more members to share in the spoils (Mills, 1994). Brown hyaenas will firstly feed on the entrails of a kill and they can effectively wedge the ball of a femur from its socket in order to remove the limb (Mills, 1994; Bothma & Walker, 1999). As many as six individuals will feed together at a carcass (Estes, 1991; Bothma & Walker, 1999), with only one animal feeding at a time as others are watching (Mills, 1994), while subadults will not feed in the presence of more dominant animals.

6.5 Leopards and Brown Hyaenas as Livestock Predators

Leopards have an amazing ability to persist in human-modified habitats where other large felids cannot (Norton *et al.,* 1986; Seidensticker, 1994; Ray *et al.*, 2005; Athreya & Belsare, 2007). Leopards and hyenas are globally considered to be the responsible predators in livestock predation (Skovlin, 1971; Butler, 2000; Grimbeek, 1992; Kolowski & Holekamp, 2006; Al-Johany, 2007; Holmern *et al.*, 2007; Sangay & Vernes, 2008; Rahalkar, 2008; Dar *et al.*, 2009; Maclennan *et al.*, 2009). Predation on livestock is further the main cause of conflict between humans and leopards (Patterson *et al.*, 2004).

Leopards do not necessarily take advantage of small domestic stock when other food is abundant (Mizutani, 1993; Schwartz & Fischer, 2006). Mizutani (1993) found that only 11% (1 out of 9) of leopards would show a preference for hunting livestock. Rabinowitz (1986) suggested that the removal of a so-called problem leopard only serves as a short-term solution to the loss of livestock, since the territorial vacancies left by this practice are likely to quickly fill with other leopards that may potentially also take to livestock depredation on the long run. Balme *et al.* (2009) found that territorial males that were removed could be replaced in the very short period of three months. Linnell *et al.* (1999) found no evidence for the notion that 'problem individuals' actually exist. In some extreme cases, some individual leopards may become habitual man-eaters (Santiapillai & Jayewardene, 2004; Chauhan *et al.*, 2000; Ray *et al.*, 2005).

Outside protected areas, brown hyaenas mainly occur on agricultural land which provides adequate nutritional resources in the form of carcasses of domestic animals that die of natural causes (Skinner, 1976; Mills, 1994). Brown hyenas clean up carcasses in the veld, minimizing the spread of disease (Hodkinson *et al.,* 2007). Skinner (1976) found that brown hyenas in the farming areas of Gauteng and Limpopo feed mainly on cattle and small to medium sized mammals. He suggested that livestock killing by brown hyenas is rare. Maude (2005) found that brown hyaenas living in areas with livestock have a different diet to those living in protected areas. According to Skinner (1976) and Skinner & Chimimba (2005), only some individual brown hyenas in a population are known to be responsible for livestock losses and become quite habitual and adept in this practice. In the areas where brown hyaenas are known to be livestock killers, they hunt for calves very inefficiently (Mills, 1982) and Bothma & Walker (1999) also suggested that brown hyaenas may learn to prey upon small to medium sized livestock or on the calves of larger livestock. Although Skinner (1976) found that the depredation of livestock is usually restricted to certain individual brown hyaenas, Hodkinson *et al.* (2007) suggested that individual brown hyenas rarely become habitual livestock killers. Kuhn *et al*. (2008) and Skinner (2006) suggested that they will prey on domestic livestock provided the livestock is held in enclosures overnight.

The study conducted by Maude (2005) in the Makgadigadi National Park and surrounding areas between July 2000 and March 2003 showed that livestock made up between 40 - 55% of the diet of brown hyenas on agricultural land and Maude (2005) suggested that the mortality of livestock provided brown hyena with a reliable abundant, permanently available food source, since livestock carcasses were the single most important food item eaten. Maude (2005) found that brown hyenas mainly scavenge on carcasses of livestock animals that were killed by larger predators such as lions. Livestock predation by leopards and brown hyenas is limited, restricted and highly localized to certain well-defined areas (Hodkinson *et al.,* 2007). Leopards are prone to taking small to medium sized livestock such as calves (Grimbeek, 1992; Sangay & Vernes, 2008). Maude (2005) suggested that it is highly unlikely for brown hyena to kill livestock and found no evidence that they do so. However, according to Bothma & Walker (1999), brown hyaenas will take to hunting in the absence of a regular supply of carrion.

Distinct physical signs can clarify the identity of the predator responsible for livestock predation. These signs include footprints (*vide* Fig. 3.2) and bite mark patterns (Fig. 6.1 and Fig. 6.2) as well as claw marks (Fig. 6.2). The position of bite marks as well as parts of prey consumed and damage to the stomach, intestines and bones of a carcass is also useful for identification of responsible predators (Table 6.1).

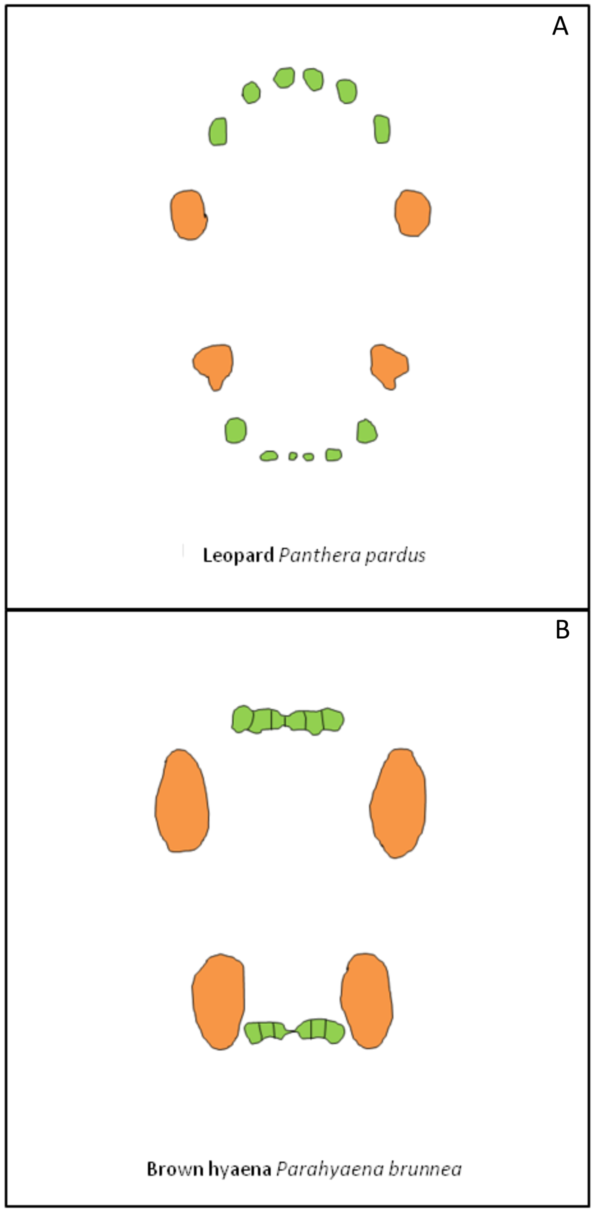

Figure 6.1 Bite mark pattern of **A,** leopard and **B,** brown hyaena redrawn from Athreya & Belsare (2007). Orange areas, markings left by canines; green areas, marks left by insisivi.

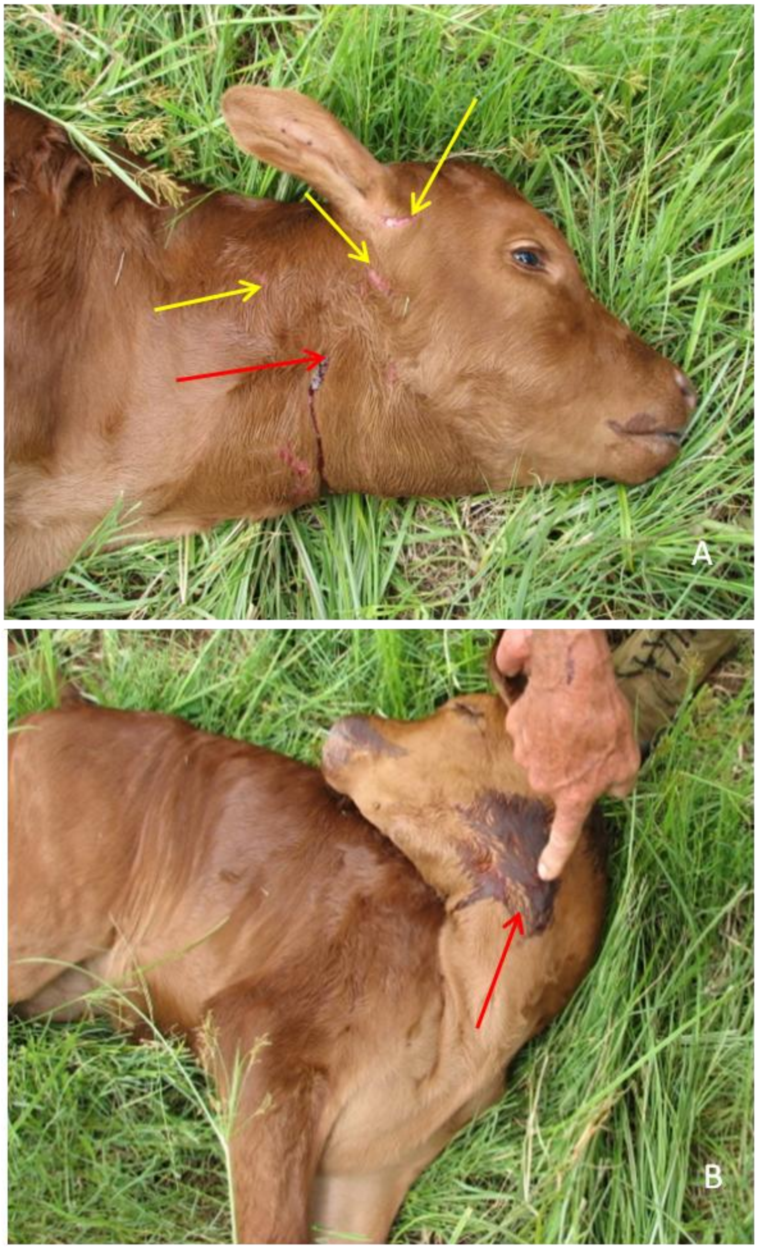

Figure 6.2 Characteristic injuries caused by leopard include bite wounds (red arrows, A & B) and claw marks (yellow arrows, A).

Table 6.1 Predator identification according to visual markings on livestock carcasses. Compiled from Hodkinson *et al*. (2007).

Predator	Claw marks	Location of bite marks	Width of bite marks (mm)	Parts of prey consumed	Damage to stomach/ intestines	Damage to bones of prey	Other evidence
Leopard	Grouped as 4 short marks.	Back of neck / throat	40 – 46	Lower hind quarters and lower forequarters.	Intact – prey disembowelled.	Ends of ribs chewed off.	Fur and wool pulled out and scattered. Do not feed on skin or guts.
Brown hyaena	None.	Huge bite marks at back of skull. Hind quarters of medium to larger prey.	47 – 58	Lower hind quarters and skull.	Partly eaten / ripped apart / strewn about.	Skull crushed.	Wool, fur, skin and remains scattered. Bites on rump. Ears torn or chewed off. Only crushed bones, wool, hooves, blood and guts remain.

6.6 Results

From the onset of January 2005 until mid-October 2010, 74 calves were lost to predation in the Roodewalshoek Conservancy (Table 6.2). Based on the average livestock prices over a six year period, this resulted in an economic loss of approximately R 240 000. Unfortunately no data was available for number of attacks on calves or responsible predators for calf losses during 2005. Since the beginning of 2006, 54 calves fell prey during 39 predator attacks, of which 17 attacks were known to be by leopards and brown hyaena. On these 17 occasions, 21 calves were killed. In 2007 the cattle breeding herd was moved to a farm outside the valley, which led to a rapid decrease in predation on these livestock. Calves were attacked regardless of their surrounding vegetation and it seemed that these large predators simply preyed on calves where the herd spent the night, even if it were in open areas covered only by medium-length grass (Fig. 6.3).

Figure 6.3 Cattle calves killed in **A,** open areas as well as **B,** densely vegetated areas in the Roodewalshoek Conservancy.

There was considerable variation in the number of calves lost annually to predation from January 2005 until October 2010. During 2005, when the livestock breeding herd was left in the conservancy, 20 calves were lost to predation. During January and July 2006, only four calves were killed. In 2007, when three calves were preyed upon in May, the decision was made to move the cattle breeding herd to a farm outside the conservancy and predation subsided. Thereafter, in 2008, the breeding herd was relocated to the conservancy, and as a result 17 calves were lost to predation. With the herd left to remain in the conservancy in the year of 2009, 18 calves were lost to predation. The cattle breeding herd was moved to a farm outside the conservancy during the latter half of October 2010, up until which 12 calves were lost to depredation by leopards and brown hyaenas (Table 6.2).

From January 2005 until October 2010, there was an overall increase in the number of calves lost to predation, with the most calves killed during 2008 and 2009 (Fig. 6.4 A). Over a five year period, between 2006 and 2010, there was a more punctuated trend in calf predation by leopards than by brown hyaena. During 2007 and 2008, the majority of calves were lost to brown hyaena and during 2009 leopards were responsible for more than twice as much calf losses than brown hyaena (Fig. 6.4 B).

Table 6.2 Annual calf losses in the Roodewalshoek Conservancy from January 2005 to October 2010. FQ – First quarter; FM – Full moon; LQ – Last quarter; NM – New moon

Date of attack	Moon phase	Light phase or dark phase	Number of calves	Predator
2005 No specific dates noted	Unknown	Unknown	**20**	Unknown
Total			**20**	
25-Jan-06	LQ3	Dark	1	Unknown
26-Jan-06	LQ4	Dark	1	Unknown
17-Jul-06	LQ0	Dark	2	Brown hyena
Total			**4**	
4-Feb-07	FM2	Light	1	Unknown
15-May-07	LQ5	Dark	2	Brown hyena & leopard
Total			**3**	
8-Jan-08	NM0	Dark	1	Unknown
6-May-08	NM1	Dark	1	Unknown
14-Jun-08	FQ4	Light	1	Unknown
10-Jul-08	FQ0	Light	1	Unknown
12-Jul-08	FQ2	Light	2	Unknown
1-Aug-08	NM0	Dark	1	Brown hyena
15-Aug-08	FQ7	Light	1	Brown hyena
4-Oct-08	NM5	Dark	1	Brown hyena
5-Oct-08	NM6	Dark	1	Unknown
31-Oct-08	NM3	Dark	2	Unknown
3-Nov-08	NM6	Dark	1	Unknown
22-Nov-08	LQ3	Dark	2	Unknown
23-Nov-08	LQ4	Dark	1	Unknown
12-Dec-08	FM0	Light	1	Unknown
Total			**17**	
3-Jan-09	NM7	Dark	2	Brown hyena & leopard

Table 6.2 Continued

4-Jan-09	FQ0	Light	2	Unknown
15-Jan-09	FM4	Light	1	Unknown
3-Apr-09	FQ1	Light	1	Leopard
7-Sep-09	FM3	Light	1	Brown hyena
14-Sep-09	LQ2	Dark	1	Leopard
21-Sep-09	NM3	Dark	1	Leopard
11-Oct-09	LQ0	Dark	1	Brown hyena
3-Dec-09	FM1	Light	2	Leopard
10-Dec-09	LQ1	Dark	1	Brown hyena
15-Dec-09	LQ6	Dark	2	Leopard
17-Dec-09	NM1	Dark	1	Unknown
22-Dec-09	NM6	Dark	2	Leopard
Total			**18**	
6-Jun-10	LQ2	Dark	1	Unknown
4-Aug-10	LQ1	Light	4	Unknown
12-Sep-10	NM4	Dark	1	Unknown
26-Sep-10	FM3	Light	1	Unknown
1-Oct-10	LQ0	Dark	1	Unknown
6-Oct-10	LQ5	Dark	3	Unknown
15-Oct-10	FQ1	Light	1	Unknown
Total			**12**	
TOTAL			**74**	

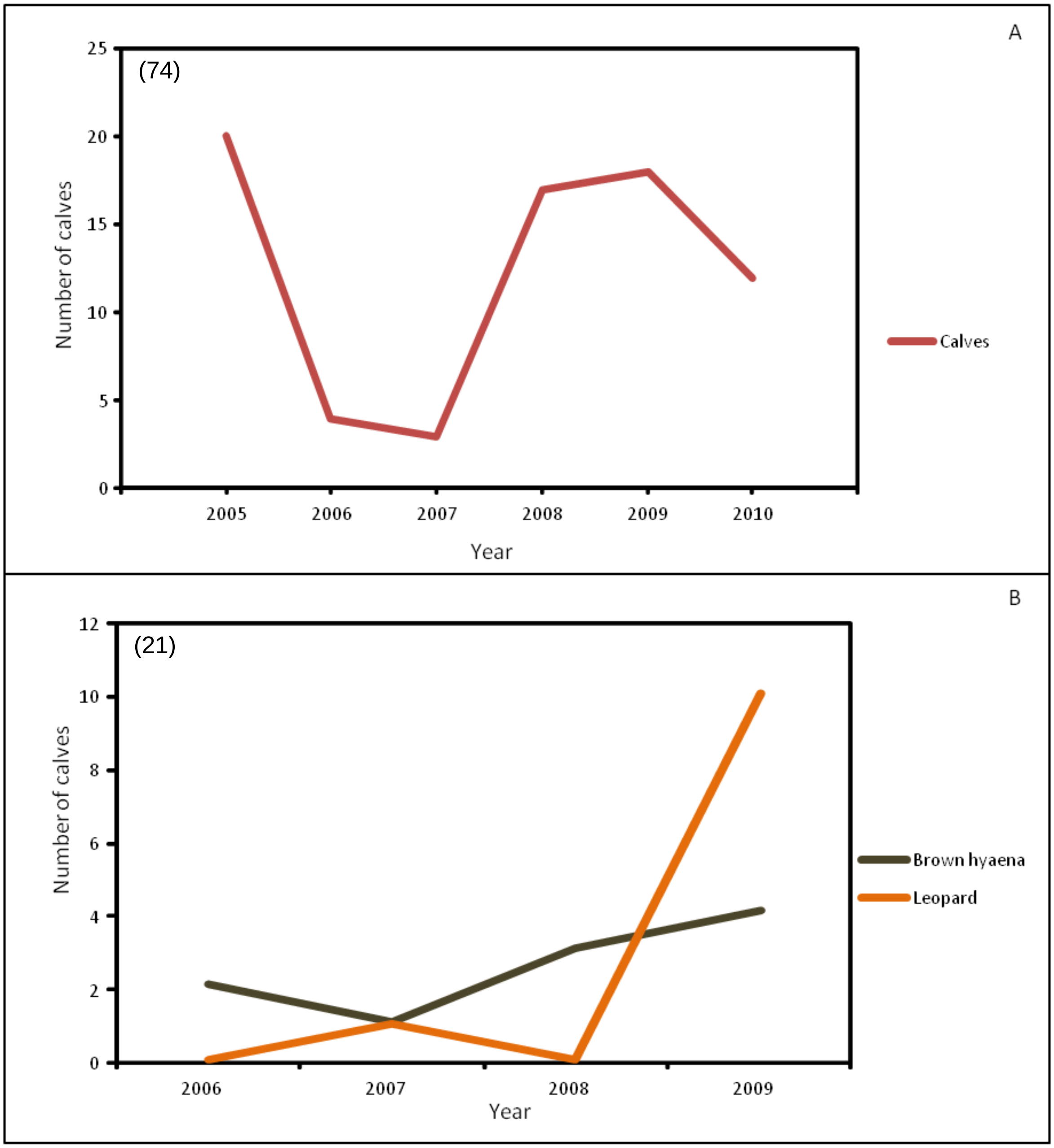

Figure 6.4 Annual number of calves lost to **A,** predation and **B,** killed by brown hyaena and leopards from January 2005 to October 2010 in the Roodewalshoek Conservancy. Numbers between brackets indicate number of calves.

Occasions of predation where the problem animal could be identified showed brown hyaenas were responsible for 48% and leopards for 52% of livestock losses (Fig. 6.5 A). When taking instances where the predator responsible remained unknown (61%) into account, brown hyaenas and leopards were merely responsible for 19% and 20% of all calf losses respectively. There were several instances where an unidentified predator preyed upon calves and either a brown hyaena or leopard was photographed with a camera trap on the same evening. This implicates that two more killings could be related to predation by brown hyaena and four more to predation by leopards. Over a five year period between 2006 and 2010, almost 78% of all calf losses occurred from the onset of spring until mid-summer. During spring and early summer, as well as during mid-summer, 39% of calf losses occurred, respectively. The smallest number of calves, 4%, was lost to predation during late summer and autumn, followed by an increase in calf predation during winter from May to July when 19% of calves were caught (Fig. 6.5). The majority of brown hyaena predation on calves occurred during mid-winter and early summer, while the majority of leopard predation took place during early and mid-summer periods (Fig. 6.5).

Overall, the monthly presence of large predators showed a weak positive correlation with the monthly number of calves lost to predation (R^2 = 0.0304; r = 0.1745). The presence of both large predators displayed a positive correlation with the number of calves lost to predation, however, the stronger correlation was found with the presence of leopards (R^2 = 0.0848; r = 0.2912). During mid-summer, a corresponding increase was observed in the presence of large predators and in calves lost to these predators (Fig. 6.6). A decrease in the number of calves lost to leopards and brown hyaenas and an increase in the presence of these predators were found during late summer and the onset of autumn. During winter months the presence of both predators initially decreased, but increase later in July. During this time, only sporadic instances of calf predation by brown hyaenas and leopards were reported. During the summer however, there was an increase in the presence of both brown

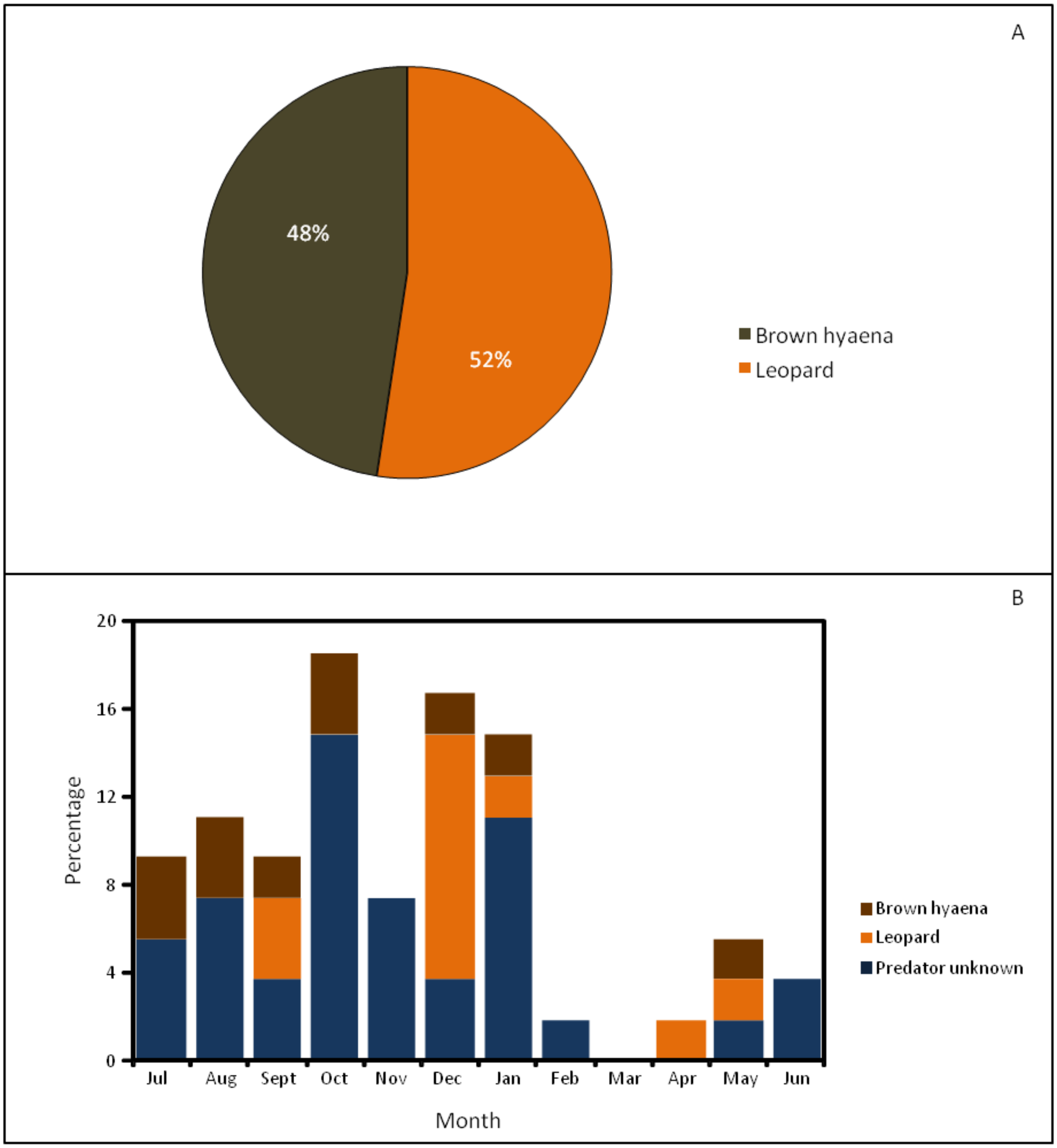

Figure 6.5 **A,** Predation on calves by brown hyaena and leopard and **B,** average monthly predation on calves by brown hyaenas, leopards and unidentified predators in the Roodewalshoek Conservancy between January 2006 to October 2010.

hyaenas and leopards with corresponding increases in the number of calves lost due to predation (Fig. 6.6).

No correlation was calculated between the monthly number of potential prey and the number of calf losses (R^2 = 0.009546; r = -0.0977). However, during mid-summer, a corresponding increase in the presence of prey and calf losses was observed (Fig. 6.7). This was followed by a sudden decrease in both calf losses and the presence of prey towards late summer in February. During late summer and autumn a corresponding increase in the presence of prey and the number of calves lost to was once more evident, however not as noteworthy as during mid-summer. The only period during which the number of prey decreased while calf losses increased, was during early summer in October. This was followed by a sudden decrease in predation in November when the number of prey animals increased slightly (Fig. 6.7). The majority of calf losses (59%) occurred during the wet summer months, with only 41% of losses recorded during winter months with low precipitation (Fig. 6.8). However, no correlation could be found between rainfall and the number of calves lost (R^2 = 0.0003; r = 0.0172).

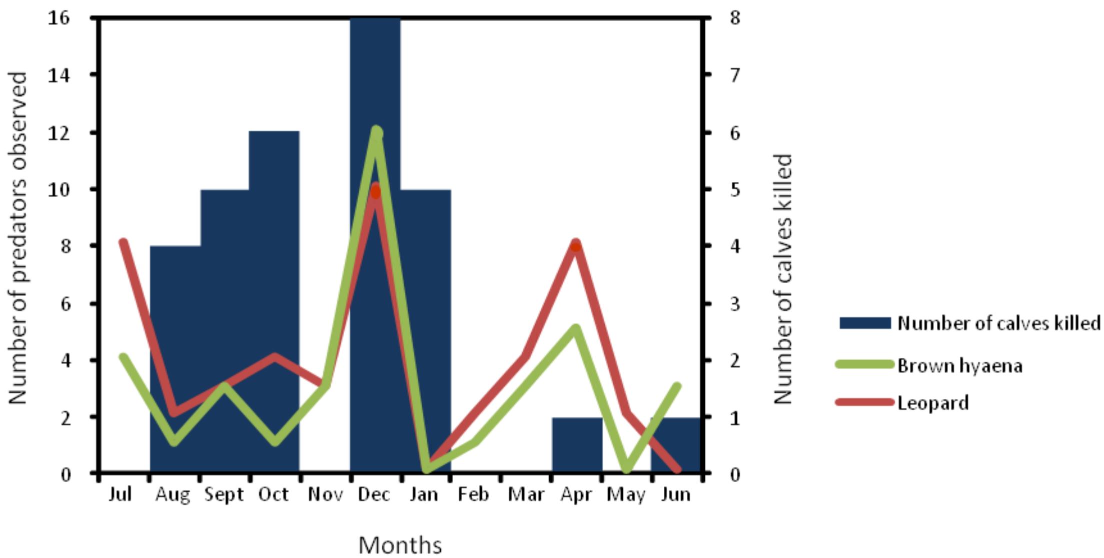

Figure 6.6 Number of observations of leopards and brown hyaena and calf predation in the Roodewalshoek Conservancy between 2006 and 2010.

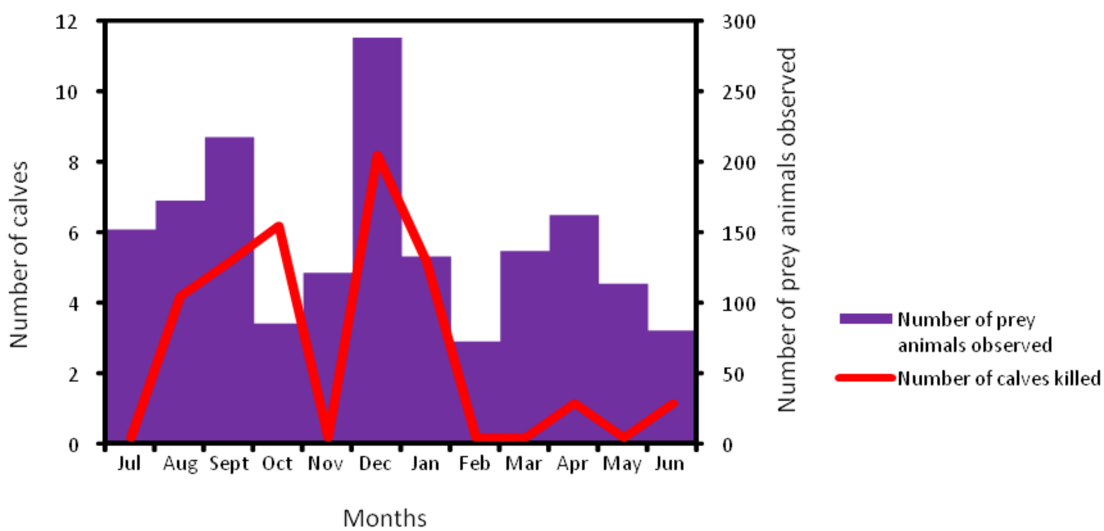

Figure 6.7 Observations of possible prey animals and total number of calves lost to predation in the Roodewalshoek Conservancy between 2006 and 2010.

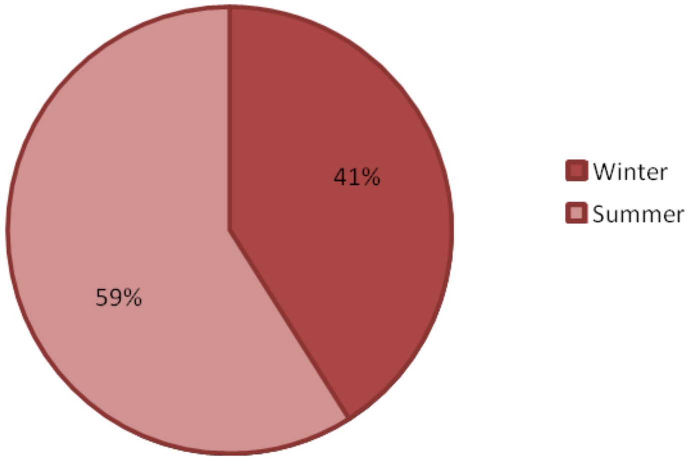

Figure 6.8 Loss of calves due to predation during different seasons in the Roodewalshoek Conservancy between January 2006 and October 2010.

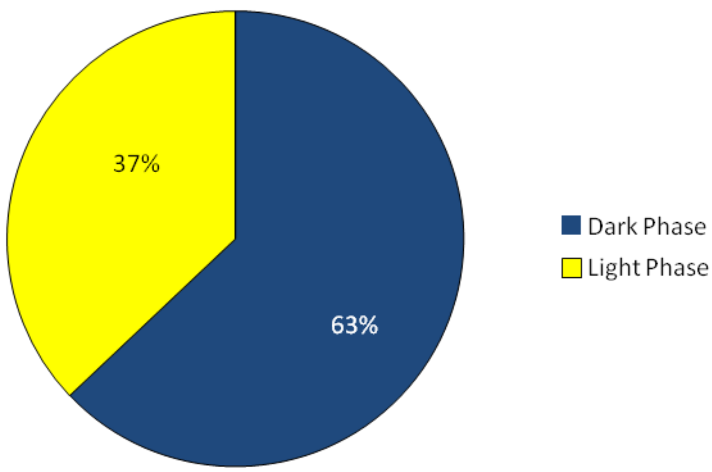

Figure 6.9 Loss of calves due to predation during different moonlight intensities in the Roodewalshoek Conservancy between January 2006 and October 2010.

Both brown hyaenas and leopards caught more calves during low moonlight intensity. Although a weak negative correlation was found between the intensity of moon light and the monthly number of calves lost (R^2 = 0.011571; r = -0.1076), the majority of calf predation (63%) took place during the dark phase of the moon when moonlight intensity is low (Fig. 6.9). Calf predation by leopards varied throughout the moon cycle and proved to be the highest (29%) during Full moon and lowest (11%) during First quarter. In contrast, calf predation by brown hyaenas show less variation during different moon phases and is at its highest (17%) during Last quarter and lowest during (11%) the First quarter (Fig. 6.10 B). Calf losses occur on a continuous basis during low and intermediate moonlight intensities preceding Full moon. During the following period of high moonlight intensity, calf losses decrease whereafter a sharp increase was observed during the following period of intermediate luminescence. With the onset of the low luminescent period in moonlight, a sharp decline in calf predation occurred (Fig. 6.11).

Two cases were recorded where both a leopard and a brown hyaena killed a calf each on the same night (*vide* Table 6.2). Both instances took place during low moonlight intensity and two calves were killed on each of these nights. All instances of calf depredation took place at night with the exception of one occasion in December 2009 when a leopard (LF02) killed two calves in the early morning hours, just after sunrise. Although leopards seemed more prone to surplus-killing, both leopards and brown hyaenas displayed this behaviour. Only one occasion of surplus-killing by brown hyaenas, during which two calves were attacked on the same night, was recorded. This incident happened while moonlight intensity was low. These calves were not killed instantly, however, but the sustained injuries proved fatal. Three occasions of surplus-killing by leopards were recorded. On each occasion a leopard killed two calves and removed one calf from the area, leaving the other behind only returned early the following evening to collect the remaining calf. Two of last mentioned surplus-killings by leopard occurred when moonlight intensity was dark, while another happened when moonlight intensity was low (*vide* Table. 6.2).

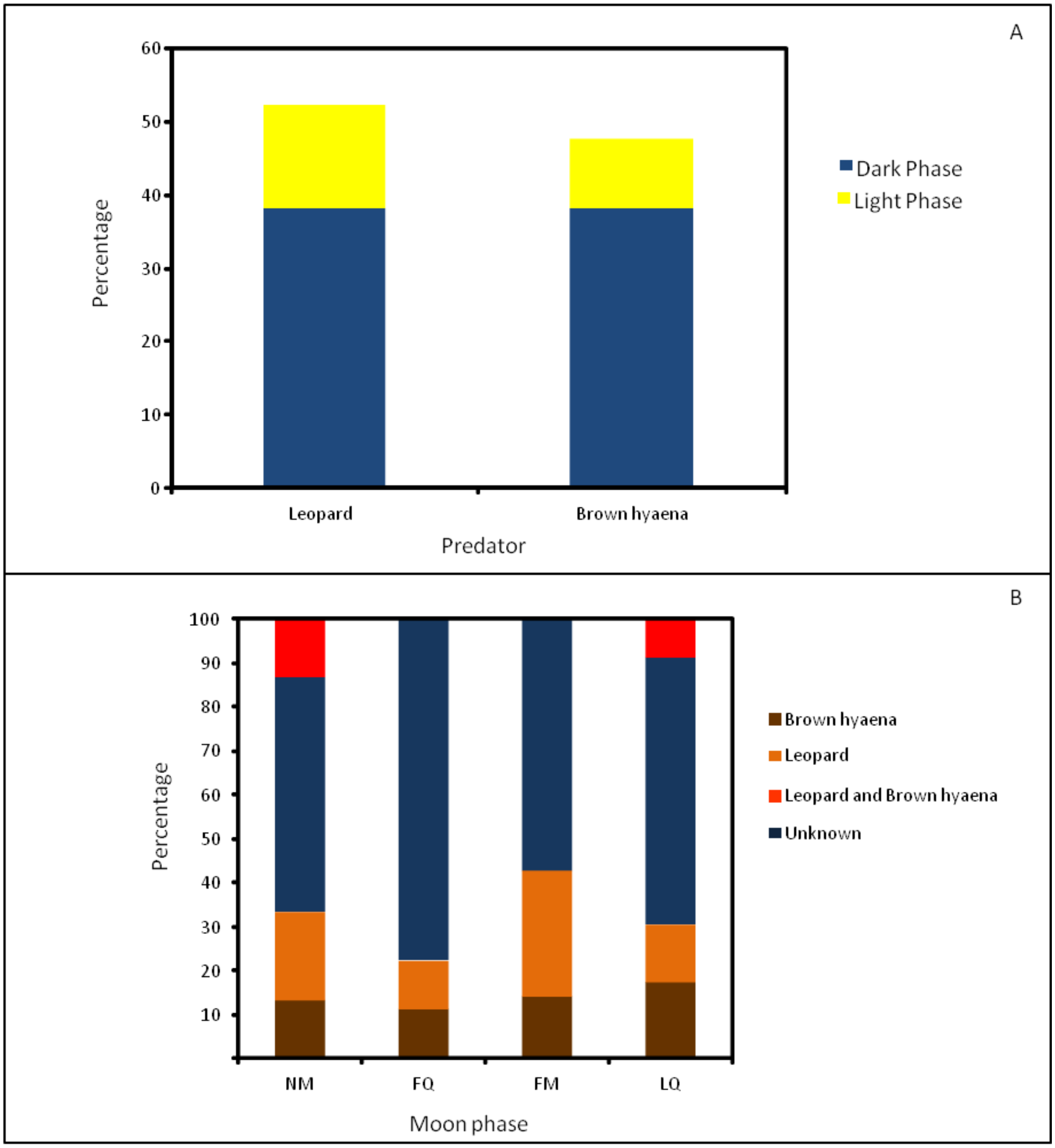

Figure 6.10 Calf predation by brown hyaenas and leopards during **A,** different moonlight intensities and **B,** different moon phases in the Roodewalshoek Conservancy between 2006 and 2010. NM, new moon; FQ, first quarter; FM, full moon; LQ, last quarter.

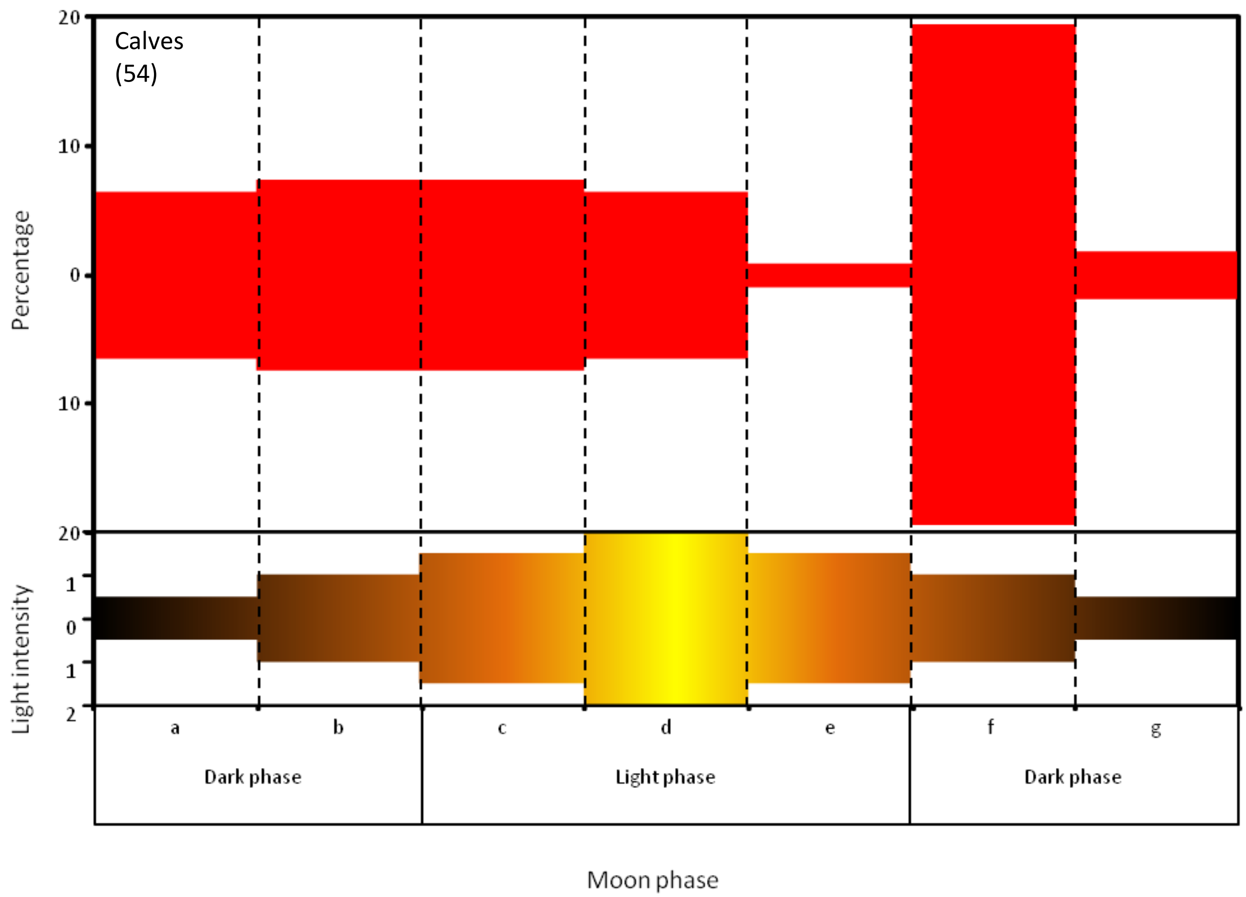

Figure 6.11 Calf losses during periods of lunar light in the Roodewalshoek Conservancy between January 2006 to October 2010. **a,** period from new moon to 3rd night after new moon; **b,** period from 4th night after new moon to night before first quarter; **c,** period from first quarter to 5th night after first quarter; **d,** period from 6th night after first quarter to 3rd night after full moon; **e,** period from 4th night after full moon to 7th night after full moon; **f,** period from last quarter to 5th night after last quarter; **g,** period from 6th night after last quarter to night before new moon. Numbers between brackets indicate number of calves.

6.7 Discussion

Leopards and brown hyaenas are rarely regarded as the most important predators of livestock in their distributional range (Butler, 2000; Maude, 2005; Kolowski & Holekamp, 2006; Holmern *et al.*, 2007; Sangay & Vernes, 2008; Dar *et al.*, 2009). The opposite seems to be true in the Roodewalshoek Conservancy. Although it was not always possible to determine the responsible predator for every instance of predation, leopards and brown hyaenas proved accountable for most calf losses. Due to the absence of other large carnivores and leopards being masters at caching their prey (Mills & Biggs, 1993; Bailey, 1993; Balme *et al.,* 2007), carrion is a scarce food source in the conservancy. Contrary to the findings of Maude (2005), brown hyaenas in the conservancy are very apt in hunting livestock of suitable size. This coincides with the statement by Bothma & Walker (1999) that brown hyaenas will take to hunting in the absence of a regular supply of carrion. No evidence of individual problem leopards or brown hyaenas could be found, suggesting that these predators simply catch livestock when this food source is obtainable.

The fairly large number of livestock lost to predation each year may be due to a combination of several factors. Firstly, the Roodewalshoek Conservancy is surrounded on all sides by game farms and other protected areas, while the farm outside the conservancy is situated in grassland, surrounded by similar livestock farms. It is clear that calves are more prone to depredation by these predators while the breeding herd is kept inside the conservancy during the calving season (*vide* Fig.6.4 A and Table 6.2). The reason for this may be that the areas surrounding the conservancy, where eradication of predators is non-existent, may be a constant source of leopards and brown hyaenas wandering into the conservancy. The farm located outside the conservancy is surrounded by other livestock farms where predator persecution is a more common practice, therefore the influx of predators to that specific farm is limited. Areas holding livestock which are situated close to protected areas will be more vulnerable to predation compared to areas located further away (Skinner *et al.*, 1992;

Butler, 2000; Holmern *et al*., 2007; Dar *et al.*, 2009). The tendency of livestock predation patterns in the Roodewalshoek Conservancy therefore seems to underscribe this view.

Secondly, livestock in the conservancy are held in an open, mostly unattended system in which, as suggested by Stahl *et al*. (2002), livestock is more prone to predation compared to livestock that are herded in bomas or kraals at night. Furthermore, the majority of medium sized prey that occurs in the conservancy is solitary animals that rely on well-developed anti-predator strategies preventing detection by predators. In contrast, cattle prefer sleeping in open, less dense vegetated areas, which increases detectability of the herd at night even when moonlight intensity is low. Calves were almost always attacked at night and were always in the near vicinity of cows, which concurs with the findings of Linnell *et al.* (1999) that domestic livestock lack the proper anti-predator behaviour to deter predators. Energy spent by a predator when hunting a calf would therefore be much less compared to hunting of natural prey. In general it seemed that calf predation increases slightly when prey species are more active in the area, except during early summer.

Recent increase in protected areas around the conservancy, as well as farming with livestock in the conservancy on a continual basis, provide easy obtainable prey on a year-round basis and resulted in increased predation over the last six years (*vide* Table 6.2). This steady supply of easily obtainable prey for resident predators might have reduced travel distances between food items, and in accordance with the findings of Maude (2005), more localized feeding behaviour by predators might have reduced the size of their home ranges. In turn, reduced home range sizes can result in an increase in the presence of predators in the conservancy, which will result in an increase in livestock predation. Even though ample occurrences of natural prey could be found in the Roodewalshoek Conservancy, predation on livestock persists during the calving season. During autumn, represented by the month of April, a high presence of bushbuck in the sampled areas with a corresponding increase in the activities of both brown hyaenas and leopards were observed in the area. Not only did the presence of preferred prey of common grey duikers and impalas peak in mid-summer (December), but there was also an increase in the number of calf losses, as well as peaks in the presence of both brown hyaena and leopards. This contradicts the findings of Ray *et al.* (2005) and supports the suggestions by Polisara *et al.* (2003) and Wang & Macdonald (2006), who found that where food items, in this case cattle calves, are abundant, predators will aggregate and predation losses will be high. Therefore it seems that predators in the Roodewalshoek Conservancy hunt calves selectively, in the presence of sufficient natural prey items.

The behaviour of surplus-killing by both predator species shows the ability to fully exploit all the available resources in their area. Data collected during this study suggests that leopards and brown hyaenas are worthy resource-competitors in the conservancy. However, surplus-killing leopards might indicate their predatory dominance by leaving a calf where it was caught only to collect it early the following evening. The possibility of a brown hyaena stealing such a carcass from a leopard killing site therefore seems slim. One occasion of such a leopard surplus-killing was recorded during Full moon. This suggests that the combination of their hunting strategy with the absence of sufficient anti-predator strategies of livestock, enabled leopards to kill two calves in the open and in the presences of the cows, while moonlight intensity was bright. Owing to their unsophisticated hunting strategy (Carnaby, 2006), it is not surprising that the only recorded occasion of surplus-killing by brown hyaenas took place while moonlight intensity was low. The resident leopard female, LF02, was with cubs during this study and several instances of leopard surplus-killings support the findings of Bothma & Coertze (2004) that a female with cubs will rely heavily on easier obtainable prey. This also adds to the above mentioned conclusion that these predators hunt for calves selectively in the Roodewalshoek Conservancy, rather than opportunistically.

During the study no ill or injured leopards or brown hyaenas were observed in the conservancy. This supports the findings of Aune (1991) and Riley *et al.* (1994) who found that mostly healthy, mature individuals are likely the most important predator on livestock in an area. According to calf-loss records over a period of five years (January 2006 to October 2010), no calves were ever killed during the end of summer (March). The reason for this may be that the calves, which are usually born during July, are already weanlings and fall outside the medium sized prey class of 15 to 60 kg. Calves seem to be most vulnerable to predation during mid-winter (July) until the end of spring (October) (*vide* Fig. 6.5 B). This time of year represents the height of the calving season and calves are still small and assembled in a relatively big herd, thus supporting the findings of Dar *et al.* (2009) who suggested that only small to medium sized livestock are prone to depredation.

Regarding the key predator of livestock in the conservancy, both leopards and brown hyaenas are almost equally accountable and display alternating periods of calf predation (*vide* Fig. 6.4 B). During times when brown hyaenas were responsible for the most calf losses (2008), predation caused by leopards was low. High incidences of leopard predation consequently resulted in lowered brown hyaena predation. This could be due to inter-predator competition for shared resources, which in the case of leopards and brown hyaenas could be fierce as these two carnivores are ranked equivalent on the carnivore dominance hierarchy (Bothma & Walker, 1999). Overall, the majority of calves were killed during the wet season (*vide* Fig. 6.8). Bothma & Coertze (2004) and Hayward & Kerley (2005) suggested that predators will select hunting habitats where energy expenditure is low and Maheshwari (2006) found that predators prefer habitat types harboring the easiest obtainable prey. During the wet rainy months in the Roodewalshoek Conservancy much denser vegetation can make the hunting of natural prey species more arduous. Therefore, leopards and brown hyaenas would resort to alternative prey, amply provided during these months in the form of calves.

The only corresponding peak in circadian rhythm between predator and prey was between that of bushbuck and both brown hyaena and leopard during the late night hours between eight o'clock and mid-night. Thus, corresponding daily activity, coupled with matching peaks in monthly presence during autumn, might indicate bushbuck to be the preferred prey of both predators in the Roodewalshoek Conservancy.

Lunar cycles seem to play a distinctive role in livestock depredation with almost two thirds of livestock losses occurring when moonlight intensity is low (*vide* Fig. 6.9). Even though they possess different hunting strategies, low intensity of moonlight may benefit both leopards and brown hyaenas and both predators will be able to stalk much closer to calves before making the final charge. Predators would also detect a raucous herd of cattle in the dark with much more ease compared to solitary, well camouflaged natural prey. When moonlight intensity is bright, leopards tend to catch more calves compared to brown hyaenas (Fig. 6.10 A) and this could be due to their widely different hunting strategies. The effective stalk-and-pounce approach will allow leopards to hunt more proficient in illuminated surroundings compared to brown hyaena, which hunt with an unsophisticated run-and-grab strategy.

The majority of prey and predator species in the Roodewalshoek Conservancy was active during periods of moderate moonlight intensity. The majority of bushbuck and common grey duiker presence occurred when moderate luminescence was increasing during the evenings prior to Full moon. A similar trend was also found for brown hyaenas and leopards, suggesting that both prey and predator prefer to be active when they have equal chances of detection and being detected. Most calves were killed when moonlight intensity was moderate to low, which coincide with the preferred moonlight intensity of leopards, brown hyaenas as well as favored prey species. This trend also confirms the findings of Polisara *et al.* (2003) and Wang & Macdonald (2006), suggesting the Roodewalshoek Conservancy to be a livestock predation hotspot.

6.8 Conflicts of Cohabitation in the Roodewalshoek Conservancy

The Roodewalshoek Conservancy and the surrounding protected areas house an abundant supply of natural prey species. The absence of predator-control practices in this area with a natural supply of prey species, results in an aggregation of predators and consequently increased chances of livestock predation. The presence of the surrounding wildlife conservation areas, and persistent livestock-farming, the conservancy provides ample opportunity for incidences of conflict between livestock farmers and predators. It is to be expected that this area would be a hotspot of conflict between such farmers and the two large predators roaming the area, especially if preventive measures are not taken where cattle are held in open, mostly unattended systems. Due to the topographical nature of the area, as well as the absence of general infrastructure such as accessible roads, management of livestock in the area poses several problems. It would be unfeasible to herd cattle in pens and therefore the adoption of livestock guarding dogs should prove worthwhile.

In terms of monthly presence and absence from the sampled area, both brown hyaenas and leopards seemed to utilize the area in a similar fashion (*vide* Fig. 5.3). Ecologically, leopards and brown hyaenas share many behavioural traits (*vide* Table 5.2), which suggests that these predators rank almost equally on the carnivore dominance hierarchy (Bothma & Walker, 1999; Carnaby, 2006). Therefore, due to their ecological similarities and similar seasonal movements in the conservancy, it is expected that marked competition exists between these two carnivores. Inter-predator competition between leopards and brown hyaenas is evident in the alternating periods of livestock predation by these two species. High incidences of leopard predation resulted in lowered brown hyaena predation and the successful conservation of leopards, especially conservation of large territorial males, may control the number of brown hyaenas in the area, which in turn may result in an overall decrease in cattle depredation. Although several authors found that brown hyaenas cannot be regarded as efficient livestock predators (Skinner, 1976; Mills, 1982; Maude, 2005), this study implicated brown hyaenas to be as important livestock predators as leopards, which may be unique to this conservancy. Thus this study waylaid the conventional idea that leopards are usually responsible for more livestock losses than brown hyaenas.

7

Summary

CHAPTER 7
SUMMARY

Conflict between livestock farmers and predators has been an ongoing battle since the breeding of domestic animals were first attempted by man. Insufficient data on the dynamics of predators, especially in regions outside formal protected areas where they are perceived as problem animals, make control methods almost impossible. Due to complaints of predation by cattle farmers in the unspoiled Roodewalshoek Conservancy, the dynamics of livestock predation was investigated. Specific emphasis was placed on the relationship between the ecological traits of leopard, brown hyaena and natural prey species and the consequences thereof on livestock losses. Investigations were carried out by means of motion-sensing camera traps, combined with seasonal field observations of all physical signs of animals.

The presence of recorded prey species showed a monthly variation, with some prey species present all year round while others showed definite periods of occurrence. Rainfall seemed to have some influence on the occurrence of such species. Most small potential prey species was observed continuously during the winter months and only sporadically during the summer. Medium sized potential prey species that occurred on a constant basis throughout the year in the study area included bushbuck, Chacma baboons and common grey duikers. Sporadic occurrence of impala and mountain reedbuck were encountered mostly during the mid-summer months, especially during December. All species classified as large prey were continuously present throughout the year, except for the aardvark which showed a sporadic presence and were mostly observed during mid-summer.

Large predators were continually observed in the conservancy except in late summer during the month of January and reached highest numbers during early autumn, mid-winter and in the height of summer. All the other predators, including small and medium-sized predators, were present on a frequent basis except during late summer and only reached a high in mid-winter and early spring. It was also evident that, when the presence of large predators in the study area increased, the presence of other predators diminished. The majority of calves (59%) were killed by predators during the wet summer months, while only 41% of calves were predated upon during winter months with low precipitation. Lunar cycles seem to play a distinctive role in livestock predation with almost two thirds of calves lost to predators when moonlight intensity was low. Even though sufficient occurrences of natural prey could be found in the Roodewalshoek Conservancy, predation on livestock persists during the calving season.

Regarding the key predator of livestock in the conservancy, both leopards and brown hyaenas were almost equally accountable and displayed alternating periods of calf predation. Instances of predation where the problem animal could be identified, implicated brown hyaenas in 48% and leopards in 52% of livestock losses. During times when brown hyaenas were responsible for the most calf losses, predation caused by leopards was low. High incidences of leopard predation consequently resulted in lowered brown hyaena predation. This could be due to inter-predator competition for shared resources. The behaviour of surplus-killing by both predator species is indicative of the ability to fully exploit all the available resources in their area.

The relatively large number of livestock lost to predation each year may be due to a combination of several factors. These include the lack of predator control in adjacent game farms and other protected areas, continuous presence of livestock, leopards and brown hyaenas as well as the open, unattended system in which livestock is kept in the Roodewalshoek Conservancy.

8

Opsomming

CHAPTER 8
OPSOMMING

Die situasie van konflik tussen vee-boere en predatore bestaan sedert die onstaan van die mak-maak van huisdiere en vee. Onvoldoende inligting aangaande die dinamika van predatore, veral dié buite die grense van bewaarde gebiede, bemoeilik die beheer-metodes van hierdie diere in areas van konflik. As gevolg van gereelde klagtes deur vleisbees-boere in die Roodewalshoek Bewarea, is die dinamika van vee-predasie in hierdie area ondersoek. Spesifieke klem is geplaas op die verwantskap tussen die ekologiese eienskappe van luiperds, bruin hiënas en natuurlike prooi-spesies, en die invloed hiervan op vee-verliese is ondersoek. Data-insameling is met behulp van beweging-sensitiewe kamera lokvalle, tesame met seisoenale veld observasies uitgevoer, ten einde alle fisiese teenwoordigheid van hierdie diere aan te teken.

Die maandelikse teenwoordigheid van aangetekende prooi-spesies het variasie getoon, met sommige prooi-spesies aaneenlopend deur die hele jaar teenwoording terwyl ander opvallende periodes van afwesigheid getoon het. Dit blyk asof reënval ‘n invloed op die verspreiding van hierdie spesies het en die meerderheid van potensiële prooi-spesies is aaneenlopend tydens winter-maande en sporadies gedurende die somer waargeneem. Potensiële prooi-spesies van medium-grootte wat deurlopend in die studie-area teenwoordig was sluit die bosbok, bobbejaan en gewone duiker in. Sporadiese teenwordigheid van rooibokke en rooiribbokke is gedurende hoog-somer, veral tydens Desember, waargeneem. Alle spesies geklassifiseerd as groot prooi was heel-jaar teenwoordig, uitsluitend die erdvark wat sporadies in mid-somer teenwoordig was.

Groot roofdiere was deurlopend oor die hele jaar, uitsluitend laat-somer in Januarie, in die bewarea teenwoordig. Die meerderheid waarnemings was egter tydens vroeg-herfs, mid-winter en hoog-somer. Alle ander predatore, dié van klein en medium-grootte, was aaneenlopend teenwoordig, behalwe tydens laat-somer. Die meerderheid van hierdie predatore is gedurende die middel van die winter asook vroeg in die lente waargeneem. Dit was ook duidelik dat, soos die teenwoordigheid van groot predatore in die studie-area toeneem, die teenwoordigheid van alle ander predatore afneem. Die meerderheid kalwers (59%) is tydens die nat somer-maande gevang, terwyl slegs 41% van kalf-verliese tydens droë winter-maande plaasgevind het. Die maan-siklus blyk 'n bepalende rol in die predasie op vee te speel, met ongeveer twee-derdes van kalwers gevang tydens lae maanlig-intensiteit. Alhoewel genoegsame natuurlike prooi-diere in die Roodewalshoek Bewarea gevind kan word, duur predasie op kalwers gedurende die kalf-seisoen voort.

Beide luiperds en bruin hiënas is ewe veel te blameer vir vee-verliese in die bewarea en dié roofdiere het afwisselende tydperke van predasie getoon. Gevalle waartydens die probleem-dier wel geïdentifiseer kon word, het getoon dat bruin hiënas vir 48% en luiperds vir 52% van vee-verliese verantwoordelik was. Periodes waartydens bruin hiënas vir die meerderheid verliese verantwoordelik was, het kalf-predasie deur luiperds afgeneem. Daarteenoor het hoë vlakke van kalf-predasie deur luiperds tot 'n verlaging in kalf-predasie deur bruin hiënas gelei. Die rede hiervoor kan inter-predator kompetisie om dieselfde hulpbronne tussen hierdie diere wees. Veelvuldige doodmaak van prooi deur beide groot roofdiere dui op 'n vermoë tot die volledige benutting van om alle beskikbare hulpbronne in hul area.

Die substansiële jaarlikse vee-verliese as gevolg van predasie mag die resultaat wees van verskeie faktore. Hierdie faktore sluit in die tekort aan predator-beheer in die omliggende bewaarde gebiede, asook die aaneenlopende teenwoordigheid van beeste en luiperds en bruin hiënas. Tesame met die oop, onbewaakte sisteem waarin beeste in die Roodewalshoek Bewarea gehou word is dit nie verbasend dat 'n konflik-situasie in hierdie area ontstaan het nie.

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*Original article not seen.

Acknowledgements

ACKNOWLEDGEMENTS

The author would like to acknowledge and express her heartfelt appreciation to the following persons and institutions:

My supervisor, Mnr. Hennie Butler. His guidance, support, encouragement and patience during this study and the writing up of this thesis is much valued and appreciated.

Oom Gert and Tannie Liesbeth Stoltz, for their enthusiasm, interest, love and support during the whole process of doing fieldwork and writing up.

The land-owners in the Roodewalshoek Conservancy, the Kuit-, De Klerk-, van Der Nest- and Stoltz-family on who's farms data-collection was conducted. Their interest and keenness in conservation was inspiring and it was a privilege to collaborate with such an involved community.

The Research Committee of the University of the Free State, Qwa-qwa Campus, for financial support in this study.

My husband Johann van As, for his love, patience and guidance during fieldwork and the final write up of this thesis. I am privileged to share a love for nature, conservation and a career in zoology with him and his support during this experience was incomparable.

My loving parents and brother. Their interest, financial and emotional support throughout my entire undergraduate and postgraduate years of study is cherished and treasured.

My in-laws, Prof. Jo van As and Prof. Liesl van As. Their willingness to provide guidance, encouragement, interest and support for this study, especially during the write up of this thesis is much appreciated.

Ben Lee and Danielle Ray-Spitzer, for their help, support and encouragement during the first part of this study.

The Department of Zoology and Entomology, University of the Free State, Qwa-qwa campus for the opportunity to conduct my study, their encouragement and for the use of departmental facilities.

The Ingwe Leopard project, especially Mnr. Gerrie Camacho, for their help and support during the initial phase of this study.