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MASTER OF SCIENCE

Untersuchung der Nahrungsökologie von Leoparden (Panthera pardus)
mit Hilfe von Aktivitäts- und Ortungsdaten: eine Pilotstudie

Studying the foraging ecology of leopards (Panthera pardus) using activity and
location data: an exploratory attempt

vorgelegt von

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I. Table of Contents

II.   List of Tables

II.   List of Figures

Abstract

Leopards (*Panthera pardus*) are considered to have the most wide ranging distribution of all felids, but outside savanna habitats their ecology is poorly understood. To improve our knowledge on feeding habits of these elusive carnivores, we used telemetric data obtained by GPS-Plus collars of Vectronic Aerospace GmbH with included dual-axis accelerometers in the Cederberg Mountains of the Western Cape, South Africa. Apart from spatial use and activity pattern, hunting activity of a single female leopard was examined using a novel approach of combining both GPS cluster analysis and activity data obtained by acceleration measurement during June 2008 - July 2009. In total, 2588 GPS positions with a fix success of 87% were obtained. The leopard avoided open flats and spent most time on rocky slopes of the Cederberg's Fynbos section. During summer, tendencies of a crepuscular activity pattern were found, but shifted towards diurnality in winter. Within the GPS cluster investigation period of 254 days, 78 potential kill sites from GPS data records were identified. Fifty-four of these sites were investigated 171 ± 91 days (mean ± sd) after the potential predation event which resulted in the detection of prey remains at 31 sites and thus a success rate of 57.4 %. The majority (76%) of prey consisted of rock hyraxes *Procavia capensis* and klipspringers *Oreotragus oreotragus*, diurnal species that live in rugged terrain. We were not able to distinguish confirmed kill clusters from non-kill clusters using Generalized additive modeling (GAM) of activity data. However, there was a significant difference between the activity pattern at small-kill (rock hyrax, rock rabbit) sites and large-kill (antelope) sites. Furthermore, results of frequency analyses of activity data allowed the differentiation between feeding cluster and non-feeding activity outside clusters. The combination of different methods such as GPS telemetry and acceleration data provides a valuable means in regions like the rugged and largely inaccessible Cederberg Mountains, where direct observation and scat collection are difficult. However, future studies on the foraging ecology of leopards will require a larger sample size, shorter fix intervals and earlier field investigations.

Zusammenfassung

Leoparden (*Panthera pardus*) haben das größte Verbreitungsgebiet aller Großkatzen, ihre Ökologie außerhalb von Savannenregionen ist jedoch weitgehend unbekannt. Um das Verständnis über die Nahrungsökologie dieser scheuen Raubtiere zu verbessern, wurden telemetrische Daten aus GPS-Plus-Halsbändern (Vectronic Aerospace GmbH) mit integrierten zweiaxialen Beschleunigungssensoren an Leoparden in den Cederbergen des Westkaps, Südafrika, genutzt. Neben Raumnutzung und Aktivitätsmuster wurde das Jagdverhalten einer einzelnen Leopardin im Zeitraum Juni 2008 - Juli 2009 mit Hilfe einer neuartigen Methode untersucht, die GPS-Cluster- und Aktivitätsdaten kombiniert. Insgesamt wurden 2588 GPS-Positionen gewonnen, was einem Ortungserfolg von 87% entsprach. Die Leopardin vermied offene Ebenen und hielt sich die meiste Zeit auf den felsigen Hängen der Fynbos-Region in den Cederbergen auf. Während der Sommermonate wurde eine tendenzielle Dämmerungsaktivität festgestellt, im Winter war die Leopardin jedoch eher tagaktiv. Innerhalb der GPS-Cluster-Untersuchungsperiode von 254 Tagen wurden 78 potentielle Rissstellen mit Hilfe von GPS-Daten identifiziert. 54 dieser Stellen wurden 171 ± 91 Tage (Mittelw. ± SD) nach dem potentiellen Riss erkundet, was in der Entdeckung von Beuteresten an 31 Stellen resultierte und somit einem Sucherfolg von 57.4 % entsprach. Der Großteil der Beutetiere (76%) bestand aus Klippschliefern *Procavia capensis* und Klippspringern *Oreotragus oreotragus*, tagaktive Säugetiere, die in felsigem Terrain leben. Mit Hilfe von Generalisierten Additiven Modellen (GAM) von Aktivitätsdaten konnte nicht zwischen bestätigten Risstellen und Nicht-Riss-Clustern unterschieden werden. Es gab jedoch einen signifikanten Unterschied zwischen dem Aktivitätsmuster von Rissen kleiner (Klippschliefer, Rotkaninchen) und großer (Antilopen) Beutetiere. Außerdem erlaubten Ergebnisse der Frequenzanalysen von Aktivitätsdaten die Unterscheidung zwischen Fressaktivität in Clustern und Aktivität außerhalb von Clustern. Die Kombination verschiedener Methoden wie GPS-Telemetrie und Beschleunigungs-sensorik bietet ein wertvolles Hilfsmittel in zerklüfteten und größtenteils unzugänglichen Gebieten wie den Cederbergen, in denen direkte Beobachtungen und Kotsammlungen schwierig zu bewerkstelligen sind. Für zukünftige Studien ist jedoch wichtig, mehr Individuen, kürzere Ortungsintervalle und frühere Felderkundungen einzubeziehen.

1   INTRODUCTION

1.1   Investigating feeding habits of large carnivores with GPS telemetry

Successful conservation of large carnivores does not only require knowledge of their home range and movement patterns, but also their feeding habits and prey–predator interactions (Tambling *et al.,* 2010). Effective management of predator–prey systems depends on reliable estimates of the components of predation such as kill rate and prey composition, and knowledge of the ecological factors causing these to vary (Knopff *et al.,* 2010). Obtaining necessary data for wide-ranging and elusive large carnivores can be difficult, resulting in gaps in our understanding of predation. For example, continuous observation is considered to be the best method to obtain data regarding hunting habits, prey selection and range use of large African carnivores (Mills 1992), but feasibility is low in mountainous and inaccessible terrain such as the Cederberg Wilderness of the Western Cape, South Africa. Even though there are possibilities of behavioural observations of hunting and feeding habits, such methods are time-consuming, labour-intensive, or logistically unrealistic (Tambling *et al.*, 2010). Also, the success of VHF telemetry for studying leopard ecology has been found to be limited (Norton *et al.,* 1986; Bailey, 1993), for example because it is often restricted to primarily daytime locations (Ruth *et al.*, 2010). Compared to traditional VHF telemetry, global positioning system (GPS) technology enables collection of high-resolution spatio-temporal movement data, and large amounts of data can be sampled with low manpower input (Hulbert and French, 2001). In particular, high precision and intensity of animal positions should allow detailed analyses of habitat use, movement pattern, territory size, space use, social behaviour, and predation (Hulbert and French 2001, Zimmermann *et al.*, 2001).

In the past decade, the application of GPS telemetry has turned out to be a powerful method to investigate diet and prey selection of carnivores in remote areas through retrospective analysis of GPS location data (Anderson and Lindzey, 2003; Sand *et al.*, 2005; Knopff *et al.*, 2009). GPS collars have been used to obtain home locate kill sites, identify prey species, and thereby determine species-specific kill rates of large carnivores such as

3

wolves *Canis lupus* (Sand *et al.*, 2005), cougars *Felis concolor* (Anderson and Lindzey, 2003; Knopff *et al.*, 2009), lions *Panthera leo* (Tambling *et al.,* 2010) and, very recently, leopards *Panthera pardus* of the Cederberg Mountains of South Africa (Martins *et al.*, 2011). GPS positions and kill site detection are associated with the analysis of the predator movement pattern: while the predator is handling the kill, it will stay at the same place over a longer time period than for most non-foraging movements (Merrill *et al.*, 2010). Given that sampling frequency is high, consecutive, single positions will indicate movement, while 'clusters' of positions will indicate non-movement (Merrill *et al.*, 2010). As it is believed that leopards stay close to carcasses until they are completely consumed (Bailey, 1993; Jenny and Zuberbühler, 2005), a kill made by leopards fitted with GPS collars will be thus represented by a cluster of GPS locations, provided that the fixing schedule is set at an appropriate interval (Swanepoel, 2008). Therefore, a GPS location cluster is defined as consecutive GPS fixes in close proximity to each other over a period of several hours or days, and by investigating these GPS clusters, prey killed can be identified to aid in feeding ecology studies (Anderson and Lindzey, 2003; Sand *et al.,* 2005). For example, Anderson and Lindzey (2003) used a rule of greater than two locations within 200 m within 6 days for cougars feeding on multiple prey types. Based on the Holling's disk equation for type II functional response (Holling, 1959), the total time measured in estimating kill rates can be viewed as two key behaviours that potentially can be distinguished in movement patterns (Merrill *et al.*, 2010): (i) time allocated to searching, capturing and killing prey (T_k); and (ii) time devoted to handling prey (T_h) at a kill site (Fig. 1).
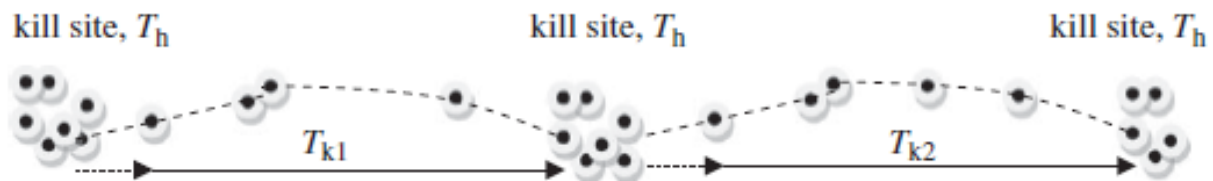
Figure 1. Potential kill sites derived from GPS location data. Clusters indicate time spent at a kill site (handling time, T_h), dashed line is the path of the animal between kills, killing time T_k is the time between first location after leaving a kill site and the first location at the kill site. From: Merrill *et al.*, 2010.

Several studies have shown that the majority of predation events occur during the night (Anderson and Lindzey 2003; Sand *et al.*, 2005; Zimmerman *et al.*, 2007), and this type of information can be extracted from GPS positions given that they are sampled with adequate frequency. In rugged mountain areas where prey is small, predator kills are hard to locate without the assistance of GPS technology (Martins *et al.*, 2011). Due to the relatively high energy demands of GPS fixes high intervals between locations are usually used (Krop-Benesch *et al.*, 2010). Thus, generally larger kills are located, and the value of GPS locations for identifying sites of smaller kills remains unclear (Knopff et al., 2009). However, Martins *et al.* (2011) have shown that GPS location clusters can also be used to locate kills of a range of smaller prey items such as rock hyrax *Procavia capensis* generally weighing < 5 kg (Skinners and Smithers, 1990)

1.2   Measuring activity patterns

Daily and seasonal changes in the environment limit windows of opportunity in time for animal activities, varying activity patterns of a species are therefore important components of its behavioural ecology (Krop-Benesch *et al.,* 2010). In order to understand the behaviour of animals that are difficult to observe, there is a crucial need to quantify activity budgets. Measuring activity levels in animals is essential to improve our understanding about their foraging behaviour and may be a relevant factor in management and conservation (Coulombe *et al.*, 2006). The most unambiguous way to study animal behaviour is by direct observations of focal animals, but this method bears several problems. On one hand, animals might be disturbed by the approaching observer and might flee (Löttker *et al.*, 2009). On the other hand, direct observations depend much on the territory and are biased against nocturnal activity or activities that occur in areas with a low visibility (Gervasi *et al.*, 2006). Elusive species, like the leopard, which move great distances in a largely inaccessible area in the mountains of the Western Cape, require other, indirect methods. For a long time researchers have used VHF-telemetry to study activity patterns (Löttker *et al.*, 2009, Krop-Benesch *et al.*, 2010). As it is believed that animal movement can influence the transmission of radio signals, signal changes in tone or strength during a fixed time interval were interpreted as active behaviour (Gervasi *et al.*, 2006). However, this method is consi-

dered to be an unreliable index of activity, mainly because it requires a subjective interpretation of radio signal quality and covers only a fraction of the actual locomotor activity (Coulombe *et al*., 2006). Moreover, activity not related to locomotion, but to feeding, comfort or social behaviour is not recorded (Krop-Benesch *et al*., 2010).

In the past decade, a new generation of GPS-collars has been equipped with dual-axis acceleration sensors sensitive to vertical and horizontal head and neck movements, which means that all kinds of activity are included and the intensity of activity is taken into account (GPS collars from VECTRONIC Aerospace; e.g. Gervasi *et al*. 2006; Löttker *et al*., 2009). Behaviour is often expressed through movement or non-movement, and recorded data are a direct consequence of the movements of the collared animal. Hence, there is the possibility to study behaviour using accelerometers (Heckmann, 2007). Crucial for this purpose is the way of recording and the acquired parameters (temporal resolution, spatial orientation and number of axes, conditions like head down/up). However, initially there is the persisting necessity to match the data recordings with actual observations in order to interpret the measured data accurately (Löttker *et al*., 2009). The possibility of recording activity using GPS-collars with integrated electronic measuring systems is accompanied by significant advantages in terms of wildlife research. Firstly, the focus animal is not influenced by the presence of human observers. Secondly, data recording is not interrupted when the animal is out of sight due to field or light conditions. However, a dense forest canopy can be an interference factor for GPS telemetry (Swanepoel, 2010). And lastly, the duration of data recording is only limited by battery life or storage capacity and can amount to weeks and years. Providing the relative level of movement – acceleration - the sensor has experienced within the sampling interval, these activity measurements need little energy, thus allowing a virtually continuous monitoring of an animal for a long time without exploiting the battery (Krop-Benesch *et al*., 2010). Although the sensor-measured values provided information on the degree of activity only at a broader scale (Gervasi *et al.,* 2006), using parallel observations of the species-specific behaviour motions and durations and coupling activity to GPS positionings one can distinguish between different behavioural categories (Krop-Benesch *et al*., 2010). For example, Löttker *et al.* (2009) were able to discriminate resting from slow locomotion / feeding in red deer based on the acceleration

measurements. Therefore, dual-axis GPS motion sensors can be used to reliably record activity data (Coulombe *et al.*, 2006, Gervasi *et al.*, 2006) and clearly bear the advantage of simultaneously collecting behavioural and position data. In combination, these data can provide new information on animal behaviour in terms of habitat use and the temporal distribution of behavioural categories (Löttker *et al.*, 2009).

1.3   Detection of biological rhythms in telemetric data

Activity and rest are the two basically different behavioural states that divide the life of most animals (Halle and Stenseth, 2000). Repeated alternations between the two states result in an explicit temporal pattern of one or several activity cycles during the 24-h daily cycle. Although some animal species display regular activity periods during the complete 24 hours of a day, we commonly classify animals as diurnal or nocturnal, and in some cases as crepuscular (Krop-Benesch *et al.*, 2010). Crepuscular activity rhythms are characterised by a bi-modal distribution of activities occurring around the light/dark transitions zones, namely dawn and dusk (Halle and Stenseth, 2000). Rhythms with a period length less than 24 hours are termed 'ultradian'. Activity rhythms of this type are well exemplified by the 2-3 hours feeding rhythm of Common voles *Microtus arvalis* that has been observed in both field and laboratory studies (Gerkema *et al.*, 1993). When analysing biological time-series, the major aim is the isolation of components which are driven by regular biological oscillations from those due to random fluctuations (Halle and Weinert, 2000). The most important measure is the period length of rhythm, which is defined as the duration of one complete cycle or as the interval between points at the same phase in consecutive cycles (Halle and Weinert, 2000). Special statistical procedures are necessary to test for the presence or absence of rhythmic components and to determine the period length of rhythms (Ruf, 1999). In telemetric and observational data from free-living animals we often find unevenly spaced time-series, which is mostly due to animal movements, weak transmitter reception or poor weather and lighting conditions that hinder observations (e.g. Arnold, 1995). Periodogram methods for evenly spaced data can still be employed in many of those cases after placing of data on an even-spaced grid, and interpolation or simply 'clamping' of missing values at the last valid point (Ruf, 1999). However, at least in certain cases of long and pos-

sibly regularly spaced data gaps these interpolation techniques can perform poorly and may produce false periodogram peaks (Press and Rybicki, 1989). The algorithm of the Lomb-Scargle periodogram (Lomb, 1976; Scargle, 1982), which is derived from the classical Fourier spectrum analysis, was originally developed to detect weak rhythms in noisy data from astronomical observations and to overcome the problems caused by missing data and uneven sampling (Ruf, 1999). It is known to be particularly suited to detect periodic components in unequally sampled time-series and data sets with missing values while restricting all calculations to actually measured values (Van Dongen, 1999). According to authors like Ruf (1999) and Van Dongen (1999), the Lomb–Scargle periodogram may serve as a useful method for the study of biological rhythms, especially when applied to telemetrical or observational time-series obtained from free-living animals which notoriously lack points.

1.4 Ecology and behaviour of the African leopard (*P. p. pardus*)

1.4.1 Introduction

Leopards have the widest distribution of all large felids and are adapted to life in more diverse habitats than any other mammal except humans and some rodents (Bothma and Walker, 1999). The African leopard (*Panthera pardus pardus*) occurring across most of sub-Saharan Africa is usually associated with areas of rocky outcrops, mountains, arid savannas and tropical rain forests (Skinners and Smithers, 1990). It is the most common large predator found in Southern Africa and fossil deposits there date back to 1.8 to 1 million years. In 2008, the leopard was classified as *Near Threatened* by the IUCN. However, due to habitat loss and fragmentation populations are decreasing and the species may soon qualify for the *Vulnerable* status (Henschel *et al.,* 2008).

1.4.2 Spatial use and activity pattern

Both male and female leopards are territorial and protect their territories against conspecifics of the same sex, e.g. through scent marking by spraying urine (Skinner and Smithers, 1990). Home range size depends on habitat quality, sex, age and reproductive status (Bai-

ley, 1993) and varies from 8 to 10 km² in moist, tropical areas (Hamilton, 1976) to 1137 km² in the Southern Kalahari (Bothma *et al.*, 1997). Leopard ranges are thought to have a high degree of stability with core areas being used more intensively (Hamilton, 1976). Territories of males are generally larger than those of females, while the territories of several females may overlap that of one male (Skinner and Smithers, 1990). Because they require larger home ranges, males will usually disperse at roughly 13-18 months of age to set up their permanent residence elsewhere, while females stay close to their natal areas through life (Bothma and Walker, 1999). Leopard density varies from region to region depending on prey abundance and its influence on range size. In sub-saharan Africa there seems to be a significant positive correlation between leopard density and prey biomass (Marker and Dickman, 2005). However, the elusive and solitary nature of leopards makes demographic studies of populations virtually impossible. Populations in sub-Saharan Africa can vary drastically in ecological characteristics, depending on food availability and terrain (Skinners and Smithers, 1990). Although there have been many studies using camera traps or GPS telemetry, these methods are costly and generally only assess one particular population (Martins, 2006).

Prior to the employment of acceleration sensors, activity patterns of leopards were predominantly determined by distances that had been covered during the day (e.g. Bailey, 1993; Bothma and Walker, 1999). Bothma and Walker (1999) concluded that daily movements are largely influenced by success or failure at satisfying nutritional or mating needs. Contrary to traditional believe of nocturnality, leopards can also be quite active during the day, when they will even hunt (Bailey, 1993; Jenny and Zuberbühler, 2005). However, in desert regions like the Southern Kalahari they usually rest during the hotter parts of the day (Bothma and Le Riche, 1984). Prey abundance seems to have an important influence on the daily movements of leopards. In prey-rich areas the range size and therefore the extent of leopards daily movements are small (Bailey, 1993). For example, in Tsavo National Park, Kenya, a daily distance of 2-5 km was reported (Hamilton, 1976), in Kruger National Park adult male leopards traveled nearly twice the distance (2.8 km) between days as adult females (1.5 km). Contrary, Bothma and Le Riche (1990) found in leopards of the Southern Kalahari that the state of hunger significantly influenced the daily distances moved, as the

daily distances that have been covered were a function of the number of days that the leopard was not feeding.

1.4.3 Feeding ecology

Leopards are known to be opportunistic predators and take prey usually in proportion to their availability in a given area (Bailey 1993, Martins *et al.*, 2011). In arid areas with limited resources such as the Southern Kalahari, adaptive hunting behaviour has important survival value for large predators as they have to hunt every possible, available prey ("number maximization"; Bothma and Le Riche, 1989). However, when potential prey species are abundant, leopards will hunt selectively for prey type, age, sex and even body condition in order to gain the best possible energy out of their food while expending the least possible energy ("energy maximization", Bothma and Walker, 1999).

Their adaptable diet has allowed leopard populations to extend their range, occupy diverse habitats, and so become one of the most widespread cat species in the world (Skinners and Smithers, 1990). Generally, mean leopard body mass is larger than that of their preferred prey and may be a reflection of their solitary hunting strategy (Hayward, 2006). In savanna habitat, leopards preferentially prey upon small to medium-sized ungulates within a weight range of 10–40 kg (Skinners and Smithers, 1990; Bailey, 1993). Where larger animals are not available, leopards commonly feed on small prey < 20 kg (Bothma and Le Riche, 1984; Norton *et al.*, 1986; see also 1.4.). Leopards also occur in some agricultural regions, where they are occasionally responsible for depredation of livestock such as sheep, goats or cattle. Such 'leopard-farmer' conflict often results in the local extermination of the species (Stuart, 1981; Martins and Martins, 2006).

In open habitat leopards preferably hunt at night under the cover of darkness, where their camouflage allows them to stalk exceedingly close to their quarry (Bailey, 1993). Conversely, in rainforest they are known to hunt diurnally with crepuscular peaks (Jenny and Zuberbühler, 2005). Leopards usually ambush their prey infrequently because this can only happen when there are places in the environment which prey animals will visit in a pre-

dictable way, like in Kruger National Park (Bailey, 1993). In more arid areas most prey is water-independent and therefore ambushes are rare there (Bothma and Le Riche, 1986). Following an optional short sprint at up to 60 km h^{-1} (Bertram, 1979) of variable distance depending upon the vulnerability of prey, leopards either suffocate the prey with grip on the throat, or kill it outright by a bite to the neck or base of the skull (Bothma and Walker, 1999). Although the leopard is a powerful hunter, there might be many unsuccessful hunting attempts during life time. Attempts only end in kills in 5% of hunts in the Serengeti (Bertram, 1979), and 16% of hunts in Kruger NP (Bailey, 1993). Hunting success depends on cover, prey that favor dense cover are more likely to be captured by leopards than prey using open habitats (Bothma and Walker, 1999). Balme *et al.* (2007) found that leopards in woodland savanna prefer hunting in habitats where prey was easier to catch rather then where prey was more abundant. In prey-poor areas like the southern Kalahari Savanna leopards have a hunting success as high as 23 % (Bothma and Le Riche, 1986). High demands of survival in a prey-poor environment make these leopards more successful or determined hunters (Bothma and Walker, 1999).

1.5   The Cape leopard

This study is based on research on the ecology of leopards in the Cederberg Mountains of the Western Cape, South Africa. From 2004, Cape leopards have been investigated using remote infra-red camera traps and GPS radio-collars focusing mainly on home ranges, population density, movements, activity, diet and future status (Martins, 2010). Leopards here form part of a population extending continuously throughout the Cape folded mountains (Norton *et al.*, 1986) and differ in many ways from leopards elsewhere in Africa. When *Panthera pardus* was first recorded in this region 400 years ago, they were sympatric with other large predators such as spotted hyena *Crocuta crocuta* and lion *Panthera leo* (Skead, 1980). Nowadays the species fills the role as apex predator in the Western Cape, as other large competing carnivores have been wiped out (Martins and Martins, 2006). Major threats for leopards in this area has been the persecution by farmers due to depredation of life stock and the increasing loss of wilderness areas through farming and human habitation (Norton *et al.*, 1986, Martins and Martins, 2006). Current research revealed that home

ranges in the Cederberg Mountains are exceptionally large with up to 910 km^2 (Lindsay, 2008; Martins, 2010), illustrating that population sizes are far smaller than previously estimated (Martins and Martins, 2006). Furthermore, it has been reported that leopards in the Cape region differ morphologically as well as genetically from leopards elsewhere in Southern Africa (Martins, 2006). "Bushveld" leopards of the savanna regions have an average weight of 50-60 kg for males and 30-40 kg for females, but leopards in the Cape are only half the mass (Stuart, 1981; Skinner and Smithers, 1990). In this region, small- to medium-sized mammals weighing < 20 kg, such as rock hyrax *Procavia capensis* and klipspringer *Oreotragus oreatragus* are known to form the majority of the leopard's diet (Norton *et al.*, 1986; Martins *et al.*, 2011), while feeding mainly on medium sized mammals and antelope species in the Kalahari (Bothma and Le Riche, 1984). However, nutrition has never shown to cause the differences in size of leopards (Martins, 2006).

1.6 Study objectives

The feeding ecology and activity pattern of leopards has been studied intensively in savanna and forest habitats (e.g., Bailey, 1993; Jenny and Zuberbühler, 2005), but there is little information from the isolated population in the Cederberg Mountains of the Western Cape, South Africa, where other large predators are absent (Norton *et al.*, 1986; Martins *et al.*, 2011). Most leopard diet studies have used faecal analysis or direct observations (Bothma and Le Riche, 1984; Norton *et al.*, 1986; Le Roux and Skinner, 1989; Bailey, 1993). However, direct observation and scat location of large carnivores in remote and mountainous regions are difficult, making studies of their feeding habits challenging (Tambling *et al.*, 2010). Nevertheless, the study area of the Cederberg Mountains has the magnificent advantage to lack sources of bias like potential scavengers or displacements by competing carnivores (Martins *et al.*, 2011), which would introduce error into kill rate estimates if not accurately detected.

In the past decade, the use of GPS location data has provided valuable insight into the diet and prey selection of elusive predators like cougars (Anderson and Lindzey, 2003; Knopff *et al.*, 2010) and wolves (Sand *et al.*, 2005, Demma *et al.*, 2007). Recent studies in Subsaha-

ran Africa were focusing on lions (Tambling *et al.*, 2010) and leopards (Martins *et al.*, 2011). However, distinguishing non-kill sites from kill sites of small prey remains an acknowledged challenge (Merrill *et al.*, 2010). Although GPS cluster analysis as well as the use of acceleration data from GPS collars are well established in behavioural and ecological studies (e.g., Anderson and Lindzey, 2003; Gervasi *et al.*, 2006, Löttker *et al.*, 2009; Merrill *et al.*, 2010), both methods have never been combined in order to gain more detailed information on feeding behaviour of large predators. This fact seems surprising if one considers that both kinds of data are recorded simultaneously in modern collars (GPS collars from Lotek Engineering; e.g. Coulombe *et al.*, 2006; GPS collars from Vectronic Aerospace, e.g. Löttker *et al.,* 2009).

Within the scope of the Cape Leopard project (www.capeleopard.org.za) this study explores the possibilities of a single and combined use of both GPS and activity data in order to get insight into the behavioural ecology and feeding habits of the leopard in the Cederberg Mountains. My aims were (i) to get insight both into spatial use and seasonal activity pattern of a female leopard using GPS location and acceleration data, respectively, (ii) to describe its feeding habits using the analysis of clusters of GPS locations, and (iii) to determine feeding patterns from the activity data that could correlate to the GPS cluster analysis that have been used to find kills.

2 METHODS

2.1 Study Area

This study is based on research conducted in the Cederberg Mountains, Western Cape, South Africa, at about 32° 27′ S; 19° 25′ E. The rugged mountainous terrain is situated about 200 km north of Cape Town and encompasses approximately 2000 km², stretching from the Pakhuis Pass in the north to Grootrivier in the south, and including the Cederberg Wilderness area and the Matjiesrivier Nature Reserve. The Cederberg occurs entirely within the Cape Floral Kingdom, the smallest of the six Floral Kingdoms in the world. The Cederberg Mountains fall within both the Sukkulent Karoo and Fynbos biomes in equal parts. Fynbos vegetation consisted of small shrubs, grass-like 'restios' interspersed with small trees (*Protea* species) and remnant populations of the endemic Clanwilliam Cedar *Widdringtonia cedarbergensis*, whereas Karoo vegetation was dominated by small shrubs and succulents (Mucina and Rutherford, 2006).
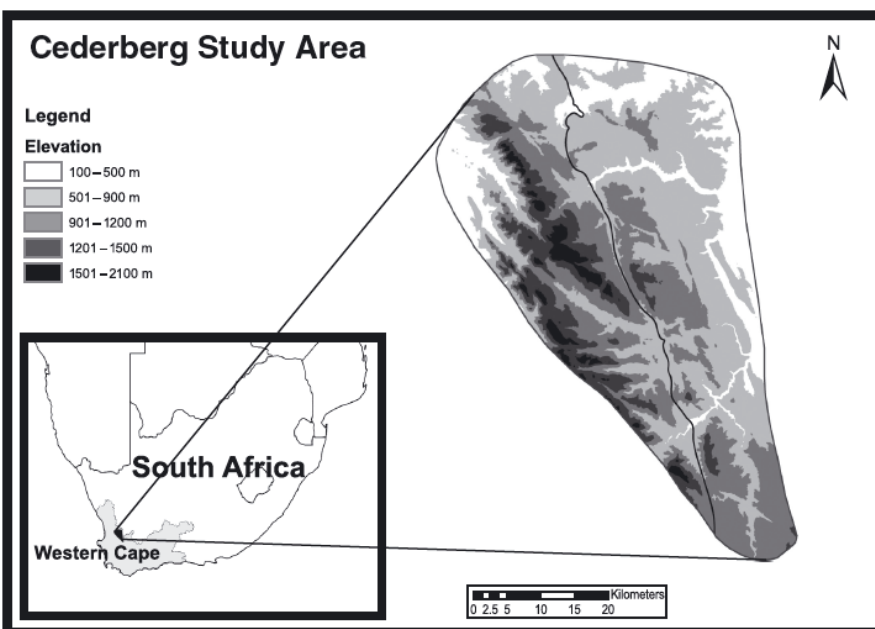
Figure 2. Location of the study area with key geographical features; dividing line separates Fynbos biome to the west and the Karoo biome to the east. From: Martins *et al*., 2011

The topography in both Fynbos and Karoo biomes consisted of rugged sandstone and shale mountains interspersed with open valleys and ravines (so calles 'kloofs'); the altitude varied from 200 to 2026 m. The climate of the Cederberg was subject to a relatively extreme seasonal temperature variation. Summer temperatures (recorded in January), range between 22.6 °C and 25 °C but may reach up to 40 °C (Walton *et al.,* 1984; Taylor 1996). Winter temperatures range between 10 °C and 15 °C (Walton *et al.,* 1984), with brief periods of snowfall in the upper regions (Taylor, 1996). Annual rainfall varied from 200mm in the Karoo to 1270 mm in the Fynbos biome (van Rooyen *et al.*, 1999). The austral summer extends from September to March and winter from April to August (Norton *et al.*, 1986). Most mammals in the study area were cryptic and/or nocturnal, and rarely observed. Chacma baboons *Papio ursinus*, rock hyraxes *Procavia capensis* and five small antelopes with a mass < 25 kg are fairly common in the Cederberg (Martins *et al.*, 2011). Of these, grey rhebuck *Pelea capreolus* was the largest, averaging 21 kg, and Cape grysbok *Raphicerus melanotis* the smallest, averaging 10 kg (Skinner and Smithers, 1990). Porcupine *Hystrix africaeaustralis*, honeybadger *Mellivora capensis*, Cape clawless otter *Aonyx capensis* and aardvark *Orycteropus afer* also occur although they are seldom seen (Rautenbach, 2009). The leopard is the Cederberg's largest predator; smaller predators include African wild cat *Felis silvestris lybica*, caracal *Caracal caracal*, bat-eared fox *Otocyon megalotis*, aardwolf *Proteles cristata* and Cape fox *Vulpes chama*. (Rautenbach, 2009)

2.2   Capturing and collaring of leopard F10

The female leopard F10 was trapped and radio-collared by the Cape Leopard Trust research team on 18.06.2008 using a double-door walk-through box trap measuring 2.0 x 0.80 x 0.75 m. She was anaesthetized by a veterinarian and subsequently examined for general health and breeding condition, weighed, measured and aged by tooth colouration and wear (Tab. 1). Subsequently, one GPS radio-collar by Vectronic Aerospace GmbH (Berlin, Germany), weighing < 2 % of body weight, was fitted to the healthy adult female. According to Martins (2010), capturing and collaring conformed to Western Cape Provincial Government's and American Society of Mammalogists' (Gannon *et al.*, 2007) guidelines.

Ethical approval was provided by the provincial nature conservation authority "Cape Nature".

Table 1. Summary characteristics and observation period of the study animal

Unique ID	**F10**
Date of Collaring	**18.06.2008**
Total monitoring period	**June 2008 – March 2010**
Sex	female
Age group	adult (≥ 3 years)
Weight	24 kg
Body length	102 cm
Head-tail	172 cm
Tail length	70 cm
Chest girth	54 cm
Neck circumference	33 cm
Head circumference	37 cm
Head length	24 cm

2.3 GPS collar measuring

Within the relevant period of cluster investigations, the collar recorded GPS locations on 3 schedules: 1) 6 locations per day at 02:00, 05:00, 08:00, 12:00, 18:00 and 22:00 from 18.06.2008 to 03.08.2008, 2) alternately 6, 12 or 24 locations per day from 03.08.2008 to 01.10.2008, and 3) 6 locations per day at 00:00, 02:00, 04:00, 08:00, 14:00 and 22:00 from 01.10.2008 to 30.03.2009 (see Tab. 3, Appendix I, for detailed fix schedule). It was managed to obtain uninterrupted data from F10 for 390 days. However, collar schedules relied on collar performance. Because leopards in this region are thought to be predominantly nocturnal (Martins, 2010), F10's collar was programmed to capture at least four night-time locations (18:00–06:00). According to project leader Q. Martins (pers. comm.), it was necessary first to track an animal using the VHF function of the collar in order to get the rough location, and then use the Handheld UHF remote-download unit to access GPS information.
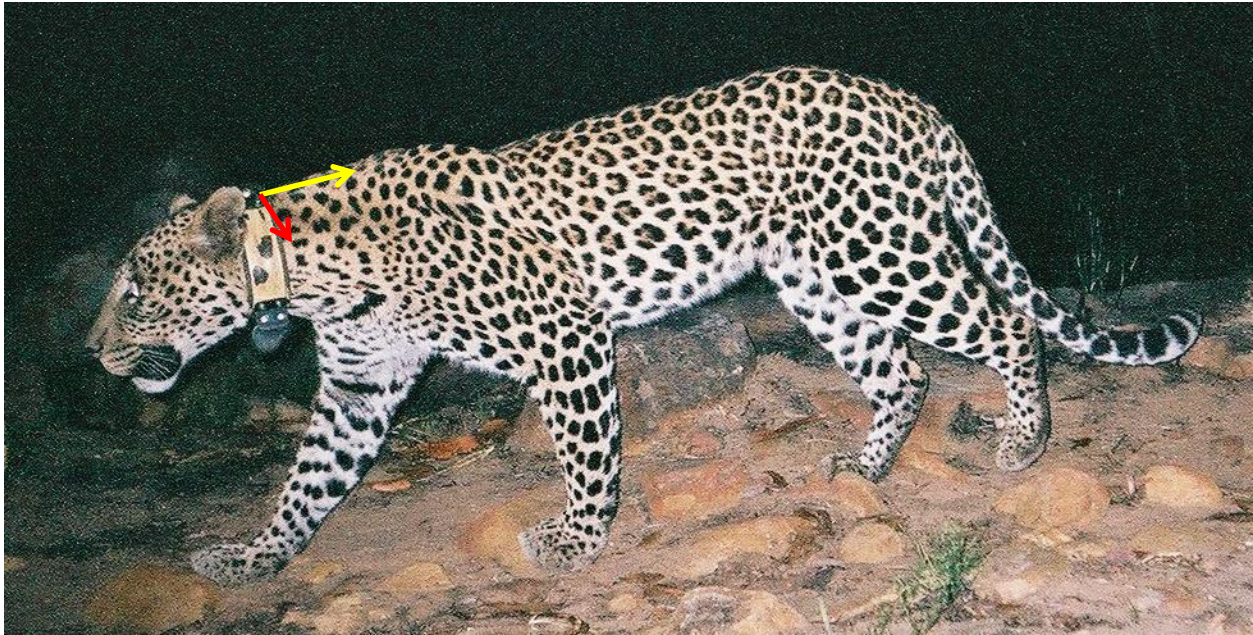
Figure 3. Collared female F10 with the two axes (x-axis red, y-axis yellow) used for activity measurement. The Cape Leopard Trust, 2010.

Besides the GPS function, collars are equipped with an acceleration sensor which records activity by measuring the acceleration on two axes. The horizontal sensor is oriented perpendicular and the vertical sensor being oriented parallel to the spine of the leopard (Fig. 2). Consequently, left-right and back-forth movements generate x- and y- values, respectively. Despite the orthogonal arrangement of the measuring axes, x- and y-values strongly correlated (r = 0.98). For that reason only x-values were included into statistical analyses. Data are recorded continuously 6-8 times per second, and the resulting values are accumulated and averaged in the time interval between two successive activity fixes, here in 5-minute intervals. The mean activity values are arranged on a linear numerical scale and range from 0 to 255 and are stored with the associated date, time and temperature. Although the sensor for the temperature measuring is located outside of the collar, the measuring is probably influenced by the body temperature of the animals and so the results are a mixture of the body temperature, environmental temperature and the sun radiation (Bucken, 2010). However, the influence of the animal's body heat is thought to be less than

5° C (A. Berger, pers. comm.). Because the amount of saved activity data in the collar is very large, it was downloaded remotely via a Handheld UHF Terminal only once per year.

2.4 GPS cluster analysis and field investigation

Because prey takes time to consume ("handling time"), large carnivores wearing GPS radio-collars set to an appropriate location-fix interval should produce multiple location fixes in places where prey are handled (Knopff *et al*., 2009). Initially, location data were plotted in ArcGIS 9.2 and sequentially inspected to identify location clusters. Herewith GPS location clusters that could signify potential feeding sites were defined as ≥ 2 locations within 100 m of each other over a minimum 4-h period. GPS location clusters provided the minimum time at a kill, and time spent in a GPS location cluster was hypothesized to be the best pre-dictor for a possible kill (Martins *et al.,* 2011). Only clusters that were identified within the period June 2008 – February 2009 were investigated. One GPS location from the cluster was loaded into a hand-held GPS to navigate to the kills and the central point in the tightest cluster was examined on foot between August 2008 and April 2009. Because GPS locations are somewhat inaccurate (Webb *et al.*, 2008), and because kill remains may be scattered around actual positions, a radius of 100 m within the selected positions was searched thoroughly for prey remains. Bones, hair, horns, feet and hooves were collected and used to identify prey species. If no prey remains were found after intensive search, a cluster was termed as non-kill cluster.

2.5 Location, activity and kill data analysis

With the GPS-Clusters that were confirmed as kill or non-kill sites after field surveys, further analysis was done. Statistical analyses were performed using R 2.11.1 (R Development Core Team, 2010), ArcGIS 9.2 (ESRI, 2010) and Activity Pattern 1.2.3 (Krop-Benesch *et al.*, 2010).

2.5.1 Home range calculation

GPS locations of F10, which are stored by the collar as Cartesian coordinates, were first converted to Gauss-Krueger coordinates using for further analyses using ArcGIS 9.2 and the extension Hawth's Tools (Beyer, 2004). Both Minimum Convex Polygon (MCP) and 95% Fixed Kernel were used to estimate the home range size of F10, including all available GPS data from 18 June, 2008 to 13 July, 2009. For 100% MCP, all data points are enclosed by connecting the outer locations in such a way as to create a convex polygon (Mohr, 1947). The area of an MCP was calculated by ArcGIS 9.2 ("Hawth's Tools"; Beyer, 2004). Although this is the most common and simple method for home range estimation, is has many disadvantages like the low information content (areas of high utilization have same value as areas of low utilization) and the sensitivity to sample size and outliers. Therefore also the Kernel method (Worton 1987) has been applied, which is particularly suited to the presentation and quantitative determination of activity densities within the ranges. This method mathematically converts the position coordinates into lines or areas with varying probabilities of use and presents these graphically. Longitude and Latitude of the GPS coordinates needed to be converted in UTM-format in ArcCIS 9.2 , 95 % Fixed Kernel was eventually calculated with R using functions (kernelUD) from packages ade4 and adehabitat (R Development Core Team, 2008).

2.5.2 Movement properties and turning angles

Initially, Euclidean distances between each two consecutive GPS locations were calculated in order to describe movement properties. To investigate how recorded acceleration correlates to distance traveled between consecutive locations, only data from the hourly fix schedule (Tab. 3, Appendix I) were included into analysis. Rayleigh's Test for Circular Uniformity (Zar, 1999) was used to look for any departure from uniformity in turning angles. Turning angles are defined as the change in direction between two consecutive movement vectors l_n and l_{n+1} (Fig. 4), i.e. three consecutive GPS locations define one turning angle (Revilla *et al.*, 2004). For each movement, the angle (θ) yields an (x, y) coordinate vector, or, equivalently (because angles have unit length), a ($\cos\theta$, $\sin\theta$) coordinate vector (Cain, 1989). It was hypothesized that turning angles within kill clusters are not uniformly distri-

buted, but have a certain mean angle, because the leopards usually show a high fidelity to kill sites and return frequently (Bailey, 1993). If this hypothesis turns out to be true, one would possibly be able to distinguish kill from non-kill clusters just by examining turning angles between the regarding movement vectors. In order to increase precision, only angles of kill clusters that consisted of more than 3 fixes were included and clusters with fix losses were left out. In order to compare with "normal" or non-feeding movements, the same analysis was done for turning angles outside GPS location clusters. Subsequently, 80 turning angles from kill clusters and 875 turning angles outside location clusters were included in the analysis.
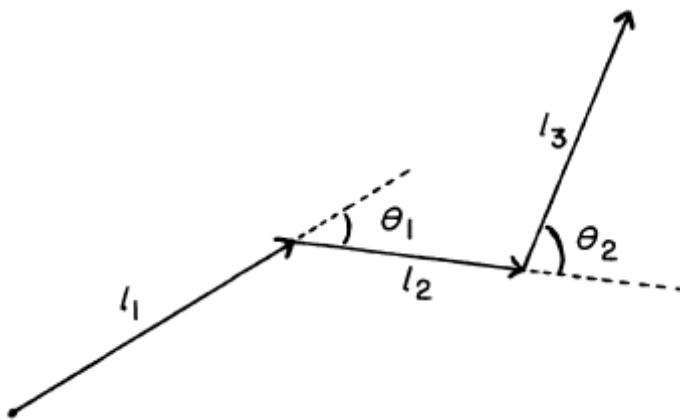
Figure 4. Turning angles and straight-line approximations to actual movement paths. Move lengths (l_i) are recorded as the net distance between the leopards successive GPS locations. From: Cain, 1989.

2.5.3 Analysis of activity data

Analytical methods for activity data using Activity pattern 1.2 are herein described according to Krop-Benesch *et al.* (2010). There are three major tools that were used in this study:

i.   *Actogram*

To give a first overview of the collected data, a graphical display of a time series with time of day on the x-axes and date on the y-axes is shown. To plot the processes at night continuously, successive days are plotted on a line (double-plot). The time is plotted on axis x (starting at 00:00 and ending 48 hours later), whereas the dates of the measurements are

plotted on the y-axis. The dates follow each other from top till bottom. Each data point is displayed as a coloured box whose colour corresponds to the intensity of activity.

ii. *Statistical chart by time*

This tool was used to calculate the mean activity values for one animal within the defined sampling interval of one hour and was chosen in order to investigate seasonal differences in F10's daily activity pattern. Although the austral summer extends from September to March and winter from April to August (Norton *et al.*, 1986), data from 20.12.08 to 20.01.09 (mid-summer) were used for "summer" activity and 20.06.08 to 20.07.08 (mid-winter) for "winter activity" in order to reveal potential temperature effects. Plotting these mean activity values as a function of the time establishes curves, which present the activity and activity peaks of the animals over the course of a day.

iii. *Time Budget*

The calculations in *Time budget* are based on an equation introduced by Hoogenboom *et al.* (1984). This equation takes account of seasonal and geographical changes of day length and requires longitude and latitude of the study area for the calculation. The Diurnality Index (DI) calculates the relation of activity between day and night for each day, which means it gives the ratio of diurnal and nocturnal activity and always lies in a range between -1 and +1. A DI of -1 means exclusive nocturnal activity, whereas animals with an index of +1 are only active during the day. The program uses sunrise and sunset as boundaries between day and night. Plotting against the course of a year shows long termed modification in the activity pattern. The Peak Analysis algorithm was used to calculate the number and the duration of activity bursts per day based on an activity threshold. Since the GPS Plus collar does not discriminate between active and inactive, but gives a quantitative measure on the intensity of activity, a meaningful activity threshold needs to be determined. The burst threshold is the mean activity value stored by the collar for one interval, minimum burst length was set to be 10 minutes. Subsequently the program counts the number of successive intervals in which this condition is fulfilled. Changes in activity state shorter than 10 minutes are ignored in this calculation.

2.5.4 Generalized additive modeling: Activity within GPS location clusters

Initially, activity data were used to validate cluster initiation in order to determine the correct time of kill and to adjust cluster duration as accurately as possible. Because activity data were broadly scattered, activity data were pooled in several measures of location and dispersion (mean, median, standard deviation, variance, maximum and minimum) for the first, the second and the third hour before and after cluster onset for both cluster types (kill and non-kill). For confirmed kill clusters, kill sites were distinguished for small prey size (< 5 kg, namely *P. capensis* and *P. rupestris*) and large prey size (> 5 kg, namely *O. oreotragus, S. grimmia, R. melanotis* and *H. africaeaustralis*). Additionally, the activity values for the fourth, fifth, sixth and seventh hour after cluster onset were pooled in the above mentioned measures. Generalized additive models (GAM) were used to investigate variables related to probability of a binary response (kill = 1, no kill = 0 and small kill = 0, large kill = 1) occurring at a GPS cluster. GAMs are a nonparametric extension of Generalized linear models (GLMs) in which the linear predictor is given by a user specified sum of smoothing functions of the covariates plus a conventional parametric component of the linear predictor (R Core Team, 2010). The simplified formula is:

$$g(\mu) = \alpha + \sum_{y=1}^{p} f_j(x_j)$$

where the f_j are unspecified smoothing functions. The strength of GAMs is their ability to deal with highly non-linear and non-monotonic relationships between the response and the set of explanatory variables by exploring data sectionally (Guisan *et al.*, 2002). Thus, the data determine the nature of the relationship between the response and the set of explanatory variables rather than assuming some form of parametric relationship (Hastie and Tibshirani, 1987). Features such as bimodality and pronounced asymmetry in the data can be easily detected; therefore GAMs provide a better tool for data exploration in this study than GLMs (S. Kramer-Schadt, pers. comm.). Using GAM functions of the R-package mgcv, binomial data were included and the models KillvsNonkill (binary response variable) ~ Activity (explanatory variable) and LargevsSmall ~ Activity were tested. We used a smoothing factor k of 7 for both models and tested if activity differs significantly over time for kills or prey size. In this study, p-values below 0.1 were read as significant.

2.5.5 Lomb-Scargle periodogram: Detection of periodic components

The fast Lomb-Scargle algorithm developed by Press and Rybicki (1989) was used to examine activity data for periodic components within each eight confirmed kill clusters and eight "normal activity" periods of at least 45 hours. Intervals of "normal activity" were chosen as periods in which distances between consecutive GPS locations did not come below 200 m. For each time-series of N data points $Y_j = Y(t_j)$ collected at times t_j where $j = 1,2...N$, with a mean of Y, the Lomb-Scargle periodogram was computed from (Ruf, 1999):

$$PN(\omega) = \frac{1}{2\sigma^2} \left\{ \frac{\left[\sum_j (Y_j - \bar{Y}) \cos \omega(t_j - \tau)\right]^2}{\sum_j \cos^2 \omega(t_j - \tau)} + \frac{\left[\sum_j (Y_j - \bar{Y}) \sin \omega(t_j - \tau)\right]^2}{\sum_j \sin^2 \omega(t_j - \tau)} \right\}$$

Where τ is defined by:

$$\tau = \left(\frac{1}{2\omega}\right) \tan^{-1}\left[\frac{\sum_j \sin 2\,\omega\,t_j}{\sum_j \cos 2\,\omega\,t_j}\right]$$

PN gives the normalized power as a function of angular frequency ($\omega = 2\pi/P$) for all periods (P) tested (Lomb, 1976; Scargle, 1982; Press and Rybicki, 1989). The term 'normalized' refers to σ^2, the total variance of the data $Y(t_j)$, in the denominator which allows to determine the statistical significance of peaks in the periodogram (Scargle, 1982). The term τ was introduced by Lomb (1976) to adjust for phase-shifts caused by unequally spaced data. The basic principle underlying this equation is that the maximum in the Lomb–Scargle periodogram occurs at the same period that minimizes the sum of squares in a fit of a sine wave to the data (Lomb, 1976; Scargle, 1982). Sinusoidal components of activity data are uncovered by the algorithm and reflected as amplitudes. Consequently the Lomb-Scargle method calculates levels of statistical significance of peaks in the periodogram (Scargle, 1982). For the frequency analyses a source period of 24 hours was used. This means, the detection of a significant signal at frequency 1 corresponds to a significant 24 hours rhythm, at frequency 2 to a 12 hours rhythm, etc. Periodic components of both kinds of activity data were compared after pooling frequencies in intervals of 0.5.

3 RESULTS

3.1 General analysis of GPS and activity data

3.1.1 GPS and kill locations of leopard F10

GPS location data used in this study was collected from a female adult leopard referred to as F10, for a period of 390 days with 2980 GPS fix attempts. The fix success rate was 87 %, resulting in 2588 obtained GPS locations. However, the proportion of 3D positions (including latitude, longitude and altitude data) obtained was only 73 %. Altitude used by F10 ranged from 498 to 1874 m, with an average of 1217 m.
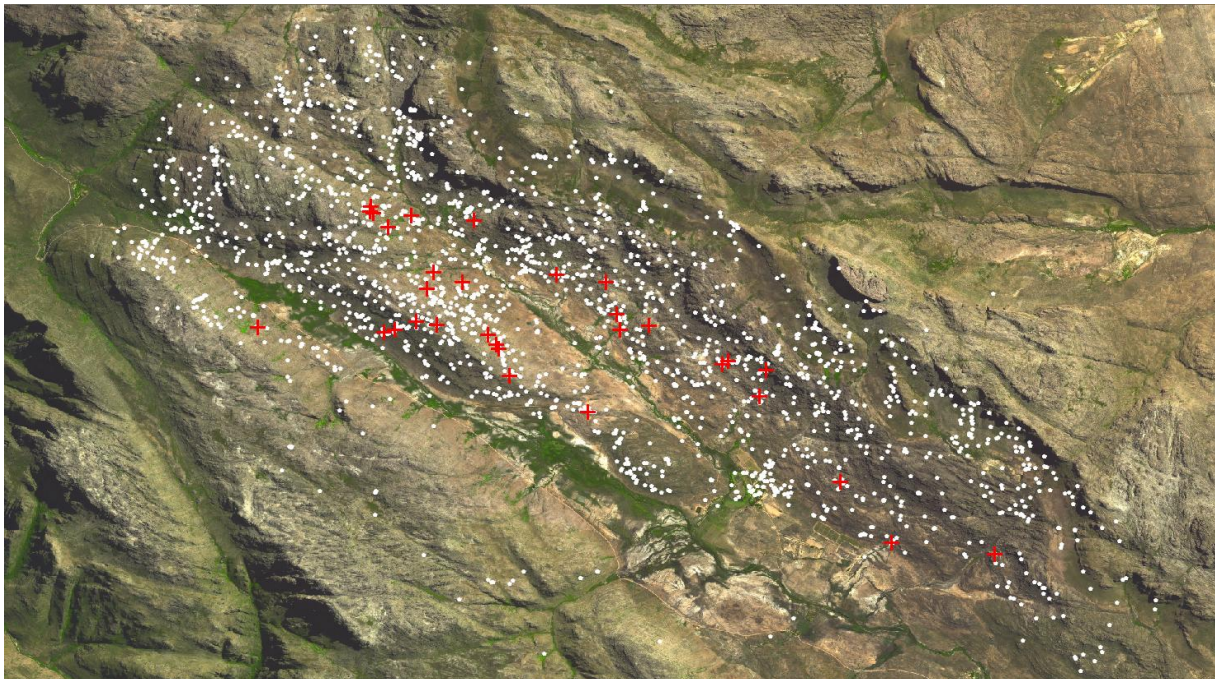
Figure 5. GPS locations (white points) and confirmed kill sites (red crosses) of F10. Period GPS locations: 18.06.08 – 13.07.09 (n = 2588), confirmed kills: 22.06.08 – 27.02.10 (n = 31).

Home range size estimated by Minimum Convex Polygon method (100 % MCP) was 178.9 km^2, so more than twice the calculated 95 % Fixed Kernel size of 84.7 km². The female's range was exclusively situated in the Fynbos region of the Cederberg Mountains. Kills occurred mostly on rocky slopes and flats of the Cederberg Wilderness. Open flats and river

beds of Driehoek and Welbedacht that are well-frequented by humans were generally avoided (Fig. 5, habitat classification by Martins, 2010).

3.1.2 Activity pattern of F10

The activity pattern of F10 tended to be crepuscular and nocturnal during the summer months from October to March, with the highest recorded activity around sunset/sunrise and night-time. The white gaps in Figure 6 demonstrate a considerably reduced activity level, but not a total cessation of movement, during the daylight hours. This pattern changed in autumn insofar as diurnal activity apparently increased and night-time activity declined. The daylight reduction of the activity level of this female leopard seemed therefore to be less pronounced in the cold season than in the hot season.
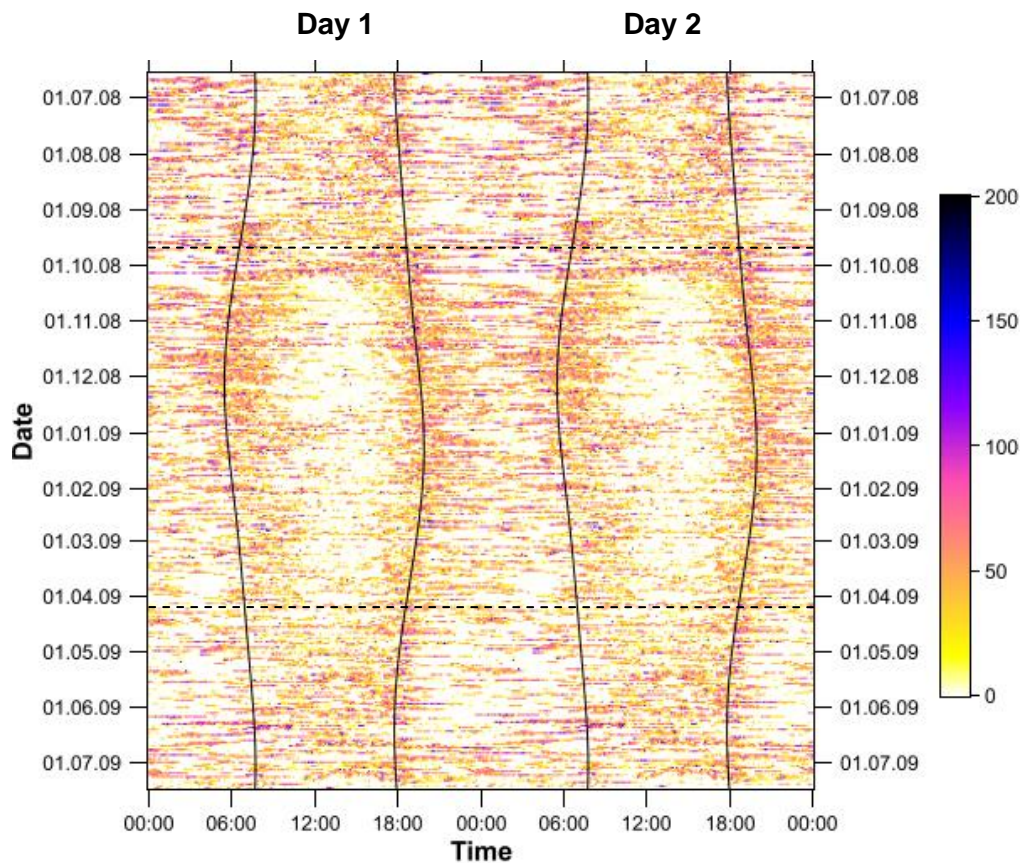
Figure 6. Doubleplot-Actogram of female leopard F10 over 390 days. Solid lines mark sunrise and sunset, respectively. Dashed lines roughly separate summer and winter time.
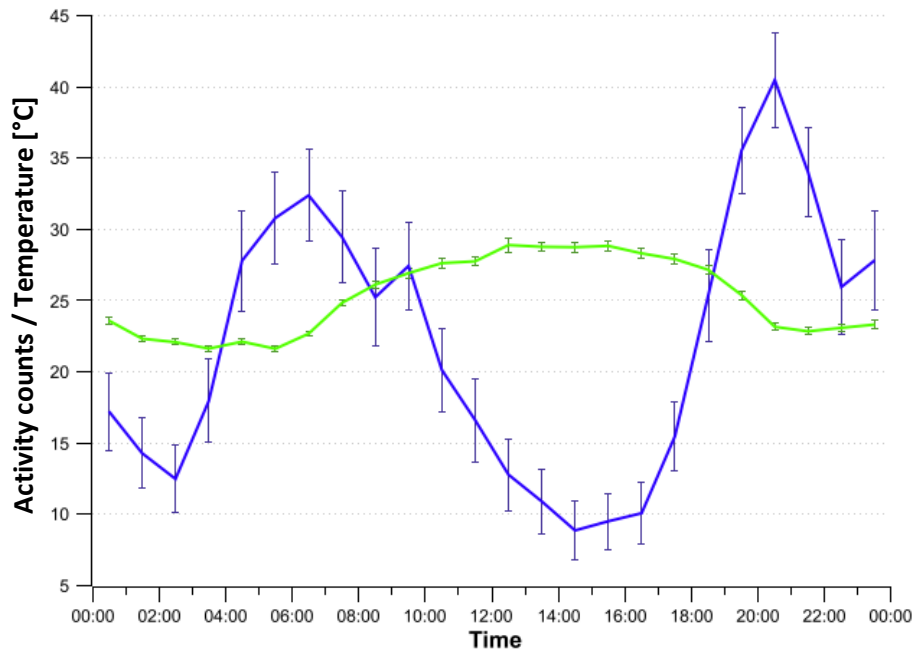
Figure 7. Activity of F10 over time of day during "summer". Activity blue, Temperature green (Mean ± 95 % confidence intervals).
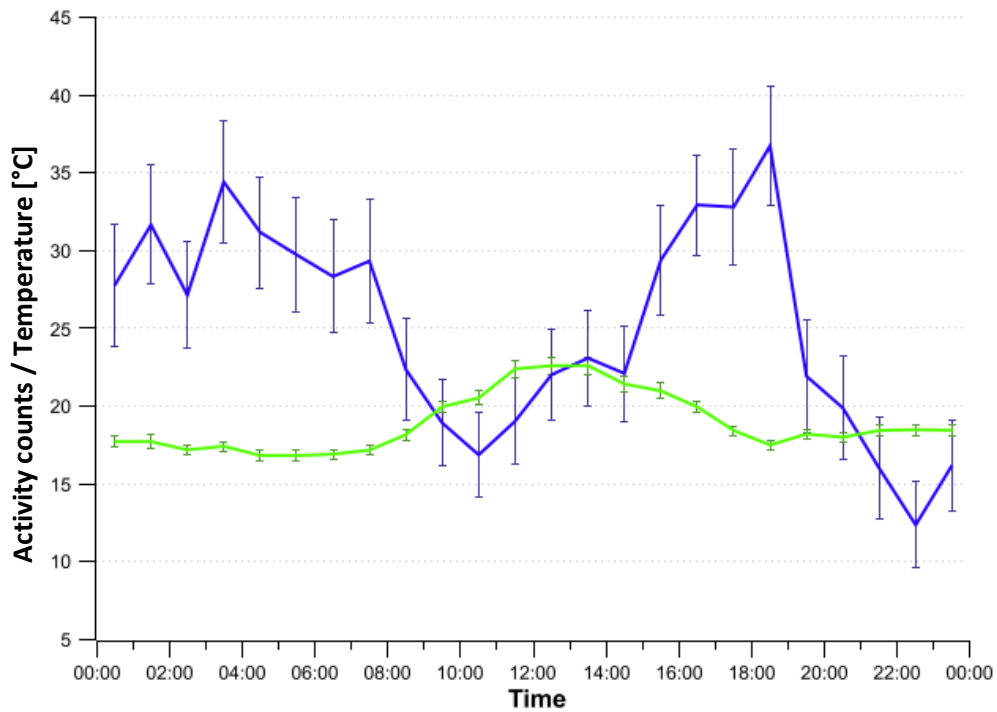
Figure 8. Activity of F10 over time of day during "winter". Activity blue, Temperature green (Mean ± 95 % confidence intervals).

In "summer" (2.5.3) acceleration data revealed two pronounced daily activity peaks from 06:00 to 07:00 and from 20:00 to 22:00 (Fig. 7). Diurnal activity was therefore clustered towards early morning and early night, while the lowest activity values were measured was during early afternoon (14:00 – 16:00), coinciding with the hottest temperatures of day, and late night (01:00 – 03:00). Activity pattern changed during winter, when activity peaks were much less pronounced, daily temperature levels were generally lower and daily activity levels higher (Fig. 8). Activity counts during the time of the day with the reached mean values as high as 20-25, the lowest activity of 12-16 was measured between 21:00 and 00:00.
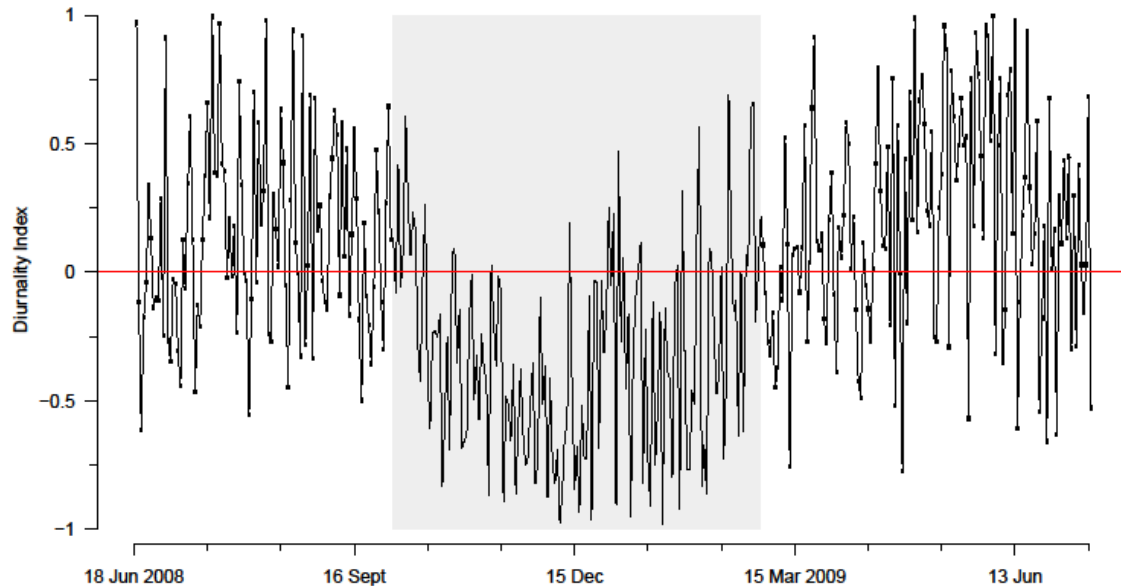
Figure 9. Diurnality Index for leopard F10 over 390 days of study period. Positive values indicate relatively more activity at daytime, negative values indicate relatively more activity at night-time. Grey field marks summer period October to February.

As shown in Figure 9, the Diurnality Index (DI) in summer was on average much lower than in winter. In summer, DI was predominantly below zero (mean±SD = -0.21 ± 0.42, 68.3%, of summer days). This value was even lower when including only data from the core months from October to February (mean = -0.32±0.39, 78.1%, of days). This means, F10 was primarily active during the period between sunset and sunrise in this time. Contrary,

27

during the winter months from April to August the DI was for the most part above zero (mean±SD = 0.2±0.43, 65.4%, of winter days) and activity occurred mainly during the day.
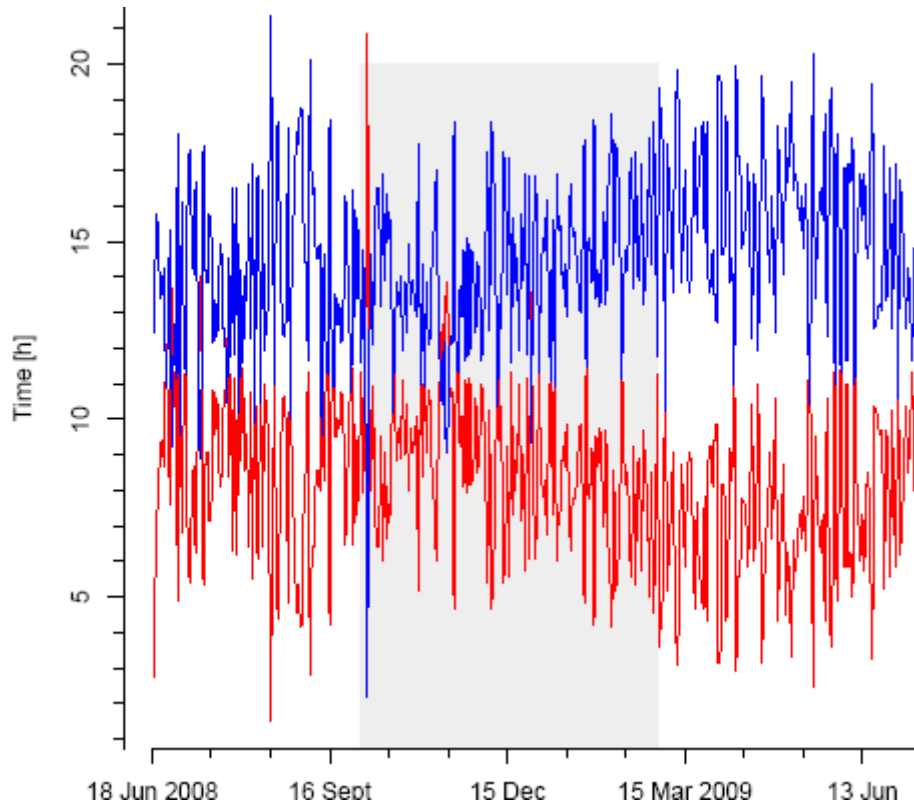
Figure 10. Total daily activity (red) and resting (blue) time for leopard F10 over 390 days of study period. Grey field marks summer period October to February.

Furthermore, there were changes in allocation of time budgets over the course of the year. From January 2009 daily activity time decreased considerably and resting time increased (Fig. 10). On 04.10.2008 an irregular change of time budget with unknown reason was recorded, with a sudden and extreme increase in activity time and accordingly a decrease in resting time. Figure 11 shows the averaged activity counts for each hour of the day and the distance covered within the same interval shown by leopard F10. Correlation of activity level and distance between two GPS positions over 24 hours measured is 0.62.
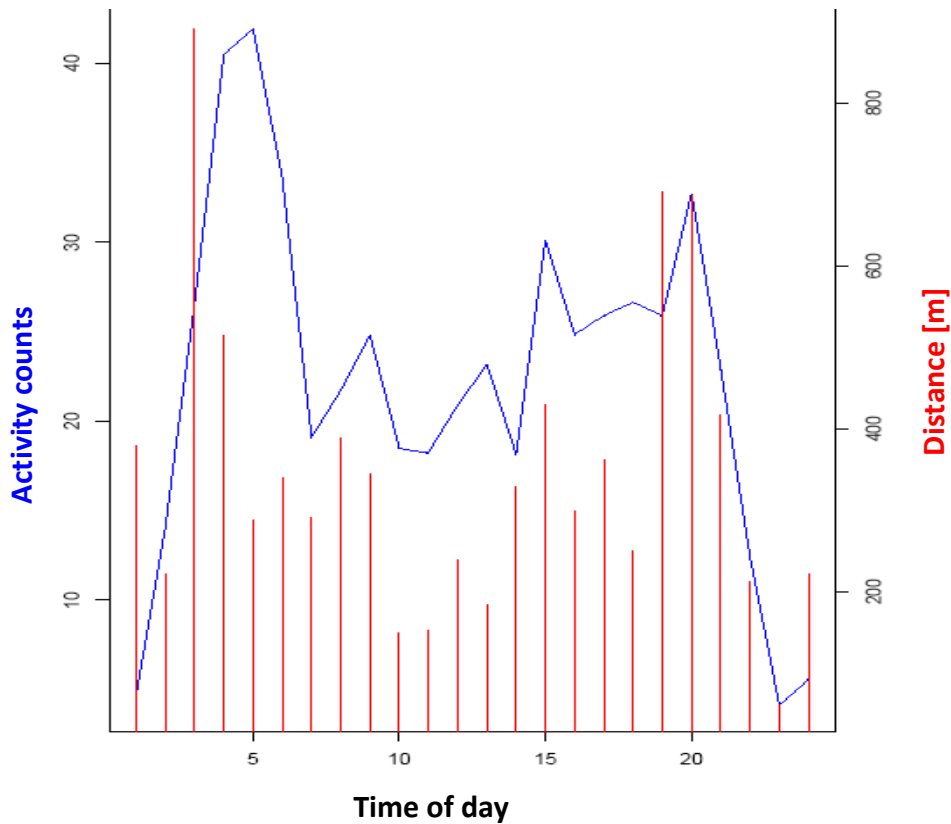
Figure 11. Activity level (blue line) and distance (red bars) between two GPS positionings for leopard F10 over 24 hours measured in hourly intervals (only days with fix schedule 24; see Tab. 3, Appendix I).

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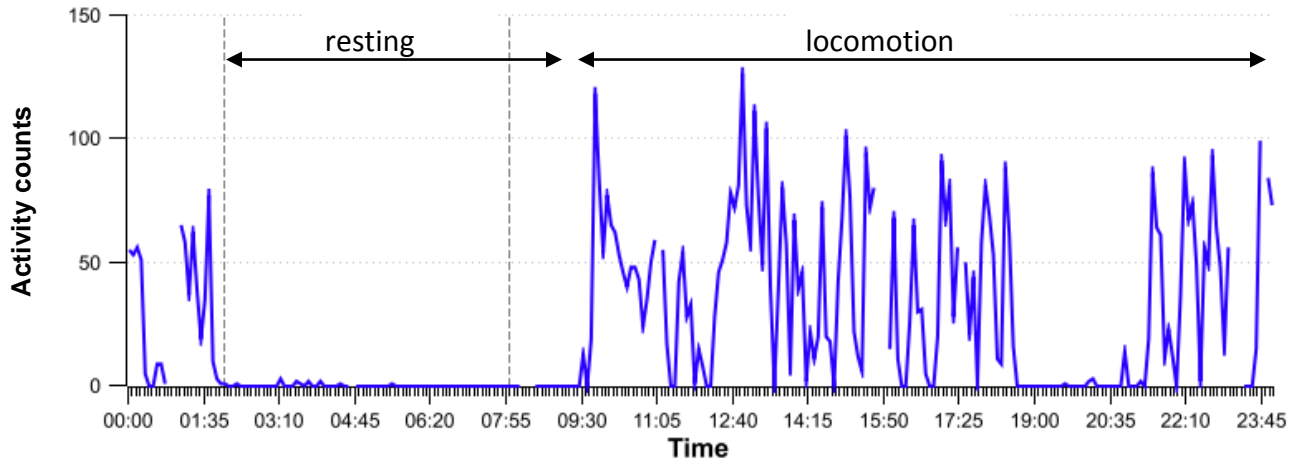
Figure 12. Daily activity curve from 25.11.2009 with 5 minutes measuring interval. Illustration of behavioural categories "resting" and "locomotion" recorded by activity sensors. Dashed lines confine a GPS location cluster.

Figures 12 and 13 show randomly selected activity curves to demonstrate different behavioural categories that can be visually determined from acceleration data. Sometimes it was possible to visually differentiate between behavioural categories locomotion, feeding and resting by using activity and location data. Locomotion is shown as uninterrupted or shortly interrupted activity in connection with large distance covered (small fix interval). Resting could be recognized from very low activity (< 5) over a longer period of time, and no distance is covered (Fig. 12). Feeding activity was expected where more or less rhythmic activity periods within a GPS location cluster occurred, no significant distance has been covered and a kill was found during field investigations (Fig. 13).
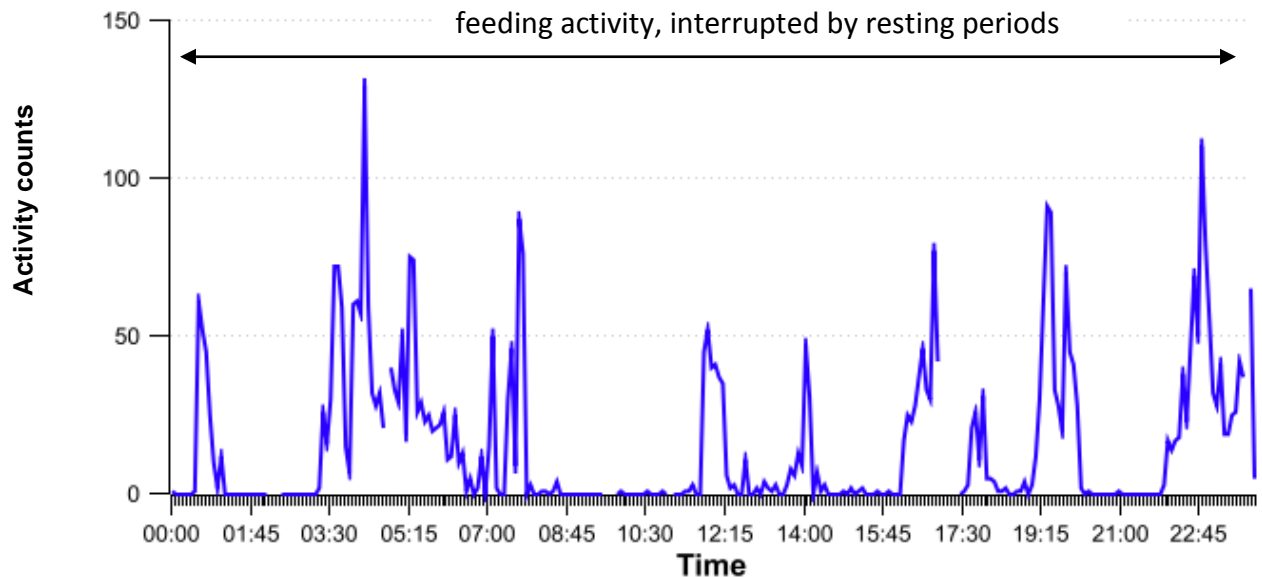
Figure 13. Daily activity curve from 18.11.2008 with 5 minutes measuring interval. Illustration of feeding activity within a 34 hour GPS location cluster (from 17.11.08, 14:00 until 19.11.08, 00:00) where a kill was confirmed by field survey, recorded by activity sensors.

30

3.2   Kill Cluster Analysis

3.2.1   Preliminary GPS location cluster analysis

Within the actual GPS-cluster study period from June 2008 to February 2009 (254 days), 78 potential kill sites from GPS data records of F10 were identified. Fifty-four sites were investigated 171 ± 91 days (range = 22-302 d) after the potential predation event which resulted in the detection of prey remains at 31 sites (confirmed kill sites). Success rate of finding kills using GPS cluster analysis was therefore 57.4 %. This corresponds to an approximate kill rate of eight days per kill for this female leopard. Twenty-two kill clusters (71 %) were initiated at night time (18:00 to 06:00). Figure 14 shows that first locations of confirmed kill sites were mostly identified in the early night time hours from 17:01 to 21:00, declined during the night (21:01 to 05:00) and increased again in the early morning from 05:01 to 09:00. The first location at confirmed predation sites was least frequent during the daytime hours from 09:01 to 17:00.
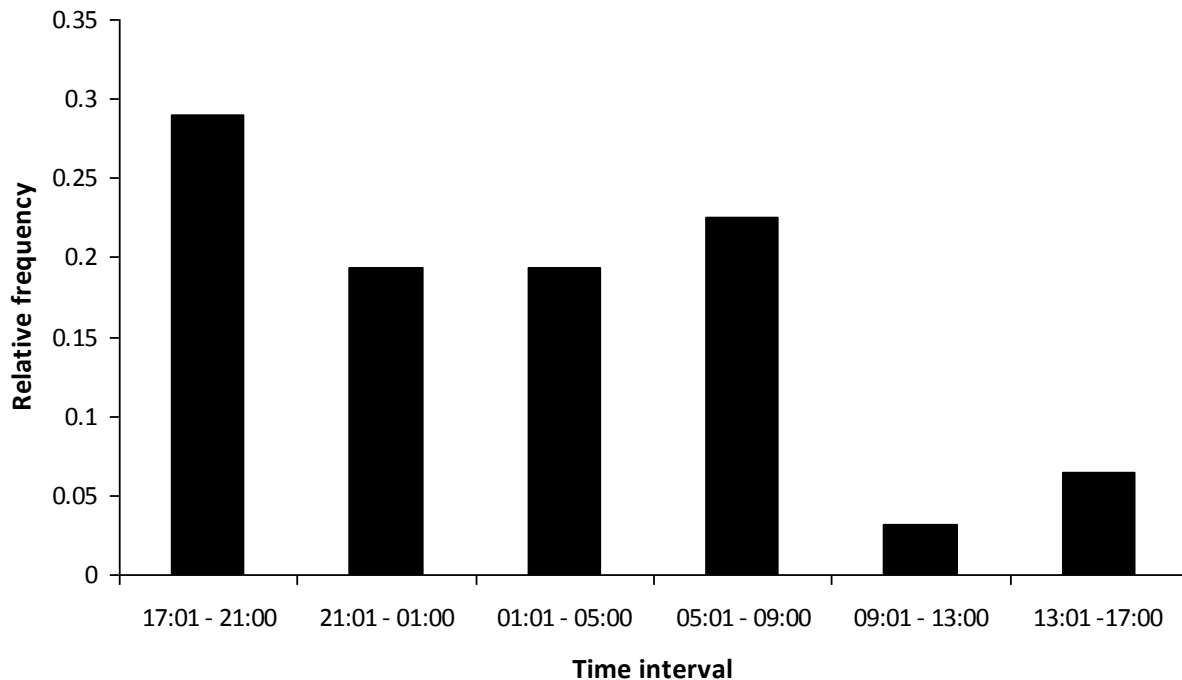
Figure 14. Frequency distribution of time intervals leopard F10 was first located at confirmed predation sites (n = 31) identified from GPS location clusters collected June-February, 2008-2009, in the Cederberg Mountains, South Africa.

Table 1 shows that the majority of prey items killed by F10 consisted of klipspringers (22.6 %) and rock hyraxes (55 %). Due to its weight klipspringer contributed most part of the consumed biomass, although fewer were killed. Other small antelope (grey duiker and cape grysbok) made up a further 9.7 % of kills. All prey species were in the < 20 kg class.

Table 2. Prey items found at kill sites of leopard F10

Prey species	Scientific name	N	Hours spent at kill site (range)	Mean weight (kg)	% of total biomass
Rock hyrax	*Procavia capensis*	17	7.7 (4 – 55)	3.8	29.3
Klipspringer	*Oreotragus oreotragus*	7	29 (10 – 48)	12.5	39.7
Grey Duiker	*Sylvicapra grimmia*	2	28 (24 -32)	19.7	17.9
Cape Grysbok	*Raphicerus melanotis*	1	6	10	4.5
Cape Porcupine	*Hystrix africaeaustralis*	1	17	9.4	7.9
Rock Rabbit	*Pronolagus rupestris*	1	4	1.6	0.7

In two cases no prey species could be determined because just a rumen or scats were found. However, they were considered as certain kills by the collectors (Q. Martins, pers. comm.). Kills where leopards fed on carcasses for >24 h consistently were antelopes weighing more than 10 kg like klipspringer and grey duiker. The average time spent within GPS location clusters was 17.4 hours (range 4 - 55), where prey remains were found (confirmed kill) and 8.5 hours (range 4 - 21) where no kill could be confirmed. 86 % (n = 14) of GPS clusters longer than 16 hours could be confirmed as kills sites. See Table 4 (Appendix II) and Table 5 (Appendix III) for detailed field survey data and a description of prey species including ecology and habitat.

3.2.2 Circular distribution of turning angles

The calculated Rayleigh's z for turning angles within kill-clusters was 1.335, which was smaller than the critical value $z_{0.05,80}$ = 1.645 (Zar, 1999). Thus, the Rayleigh Test failed to reject the null hypothesis H_0 [ρ = 0; the population of turning angles is uniformly distributed around the circle]. The same was found for turning angles outside GPS location clusters (z = 0.007, $z_{0.05,875}$ = 1.645). This implies there was no populations mean direction of

turning angles both within confirmed kill clusters and outside GPS clusters. Thus, the Rayleigh's Z was not used for further assessment of confirmed kill clusters.

3.2.3   Activity within GPS location clusters

Activity recorded by the dual-axis accelerometer shows a decrease with the formation of a GPS location cluster (Fig. 15 and Fig. 16). Within clusters of locations (relative time 0, 1, 2), recorded activity is generally lower than within intervals when distance between consecutive locations is above 200 m (relative time -3, -2, -1). According to Fig. 15, there is a larger range of activity for the first hour after cluster onset at confirmed kill sites, and for the second hour after cluster onset for the confirmed non-kill clusters.
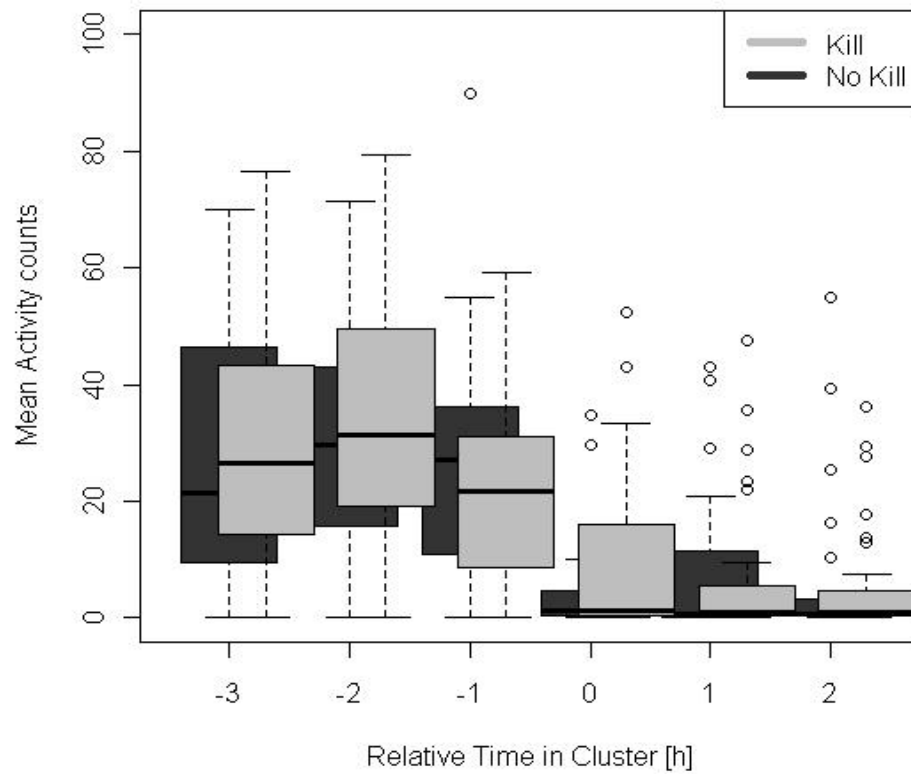
Figure 15. Boxplot of activity counts of F10 before and after cluster initiation, previously averaged over the particular hour relative to cluster onset. Black boxes indicate non-kills, grey boxes confirmed kills.

Comparison of activity within kill and non-kill clusters using binary Generalized Additive Modeling (GAM) did not reveal any significant differences (p = 0.345). A second GAM fits activity values (explanatory variable) against presence/absence of a kill (response variables). When comparing clusters where larger prey (antilopes) and smaller prey (rock hyraxes, rock rabbit) was found (model LargvsSmallPrey, see 2.5.4), GAM was able to detect a weak significant difference (p=0.07 for mean activity). Figure 16 shows that activity decreases sharply at small-kills sites and stays low for at least seven hours after the presumed time of kill, while activity at large-kill sites increases remarkably as soon as two hours after the kill again. Activity levels are similar before the kills. After Cluster-Onset, activity patterns within small-size kills and large-size kills differ from each other. After 2 hours an increase of activity within the large-kill clusters could be determined.
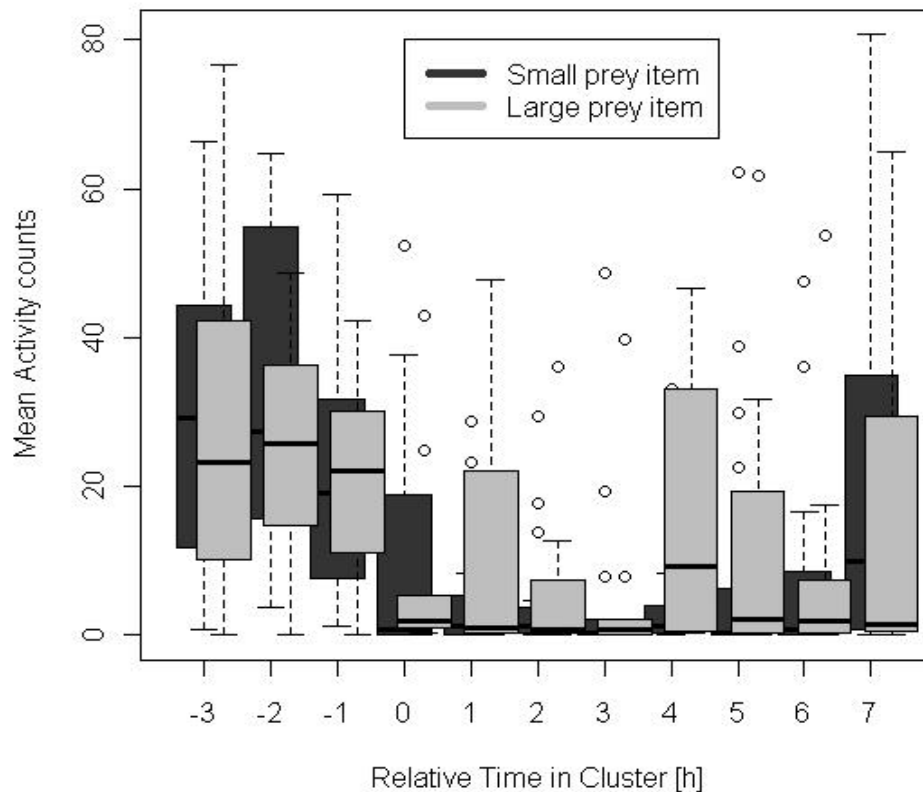
Figure 16. Boxplot of activity counts of F10 before and after cluster initiation, previously averaged over the particular hour relative to cluster onset. Black boxes indicate small prey items (rock hyrax, rock rabbit), grey boxes large kill items (antelopes).

3.2.4 Detection of periodic rhythms in activity data

To firstly illustrate the application of the Lomb–Scargle method on an evenly spaced time-series, periodograms were computed for two sections of activity data records, once for a kill cluster (Fig. 17) and once for a "normal" activity interval without known kill or feeding behaviour (Fig. 18). Because the eight kill clusters differed in length and frequency values are calculated in regular spaces, frequencies were initially pooled for every 0.5. The amplitude indicates how well the function fits to the data for the given period of 24 hours, more precisely proven using statistical significance (Confidence Interval of 0.95). Apparently significant amplitudes are distributed over several frequencies ranging from 1 to ca. 9 (means periods with a length of 24 hours to 24/9 hours) in the kill cluster (Fig. 17), while normal activity data only show significant amplitudes until frequencies of about 2.5 (means periods of 24/2.5 hours to 24 hours) (Fig. 18). These examples clarify that a single sample period < 24 hours can have more than one significant rhythm.
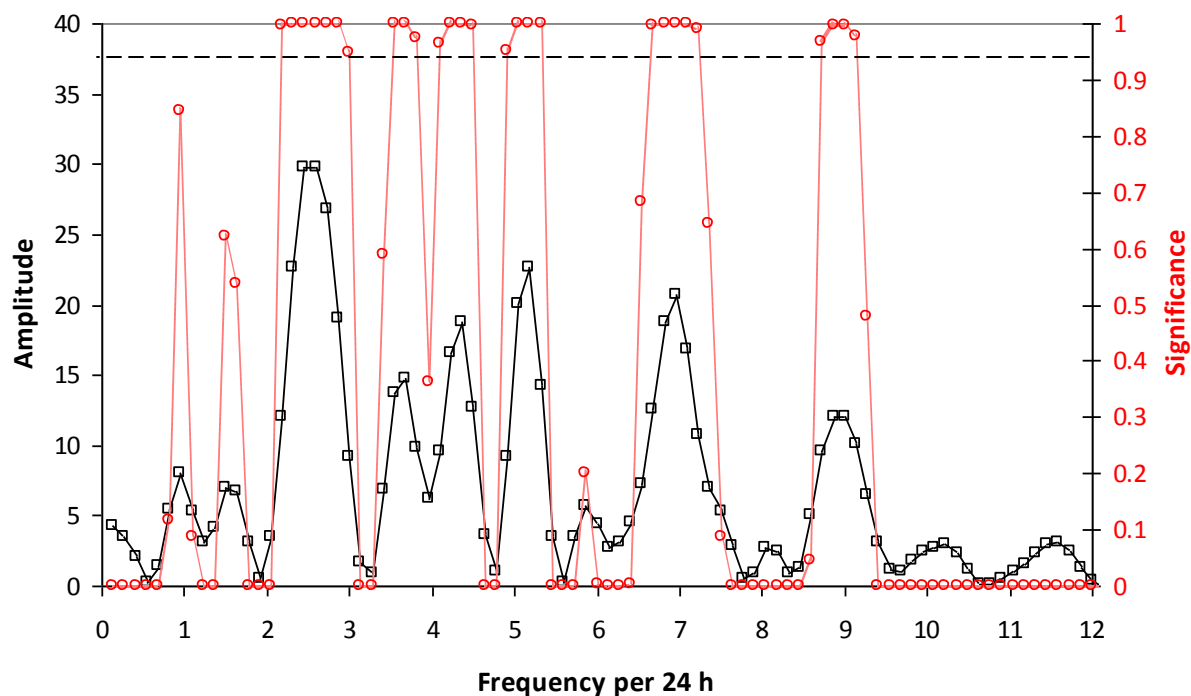
Figure 17. Lomb-Scargle periodogram of activity data for kill cluster of 45 hours (13. and 14.07.2008). Dashed line marks level of significance (p = 0.05).
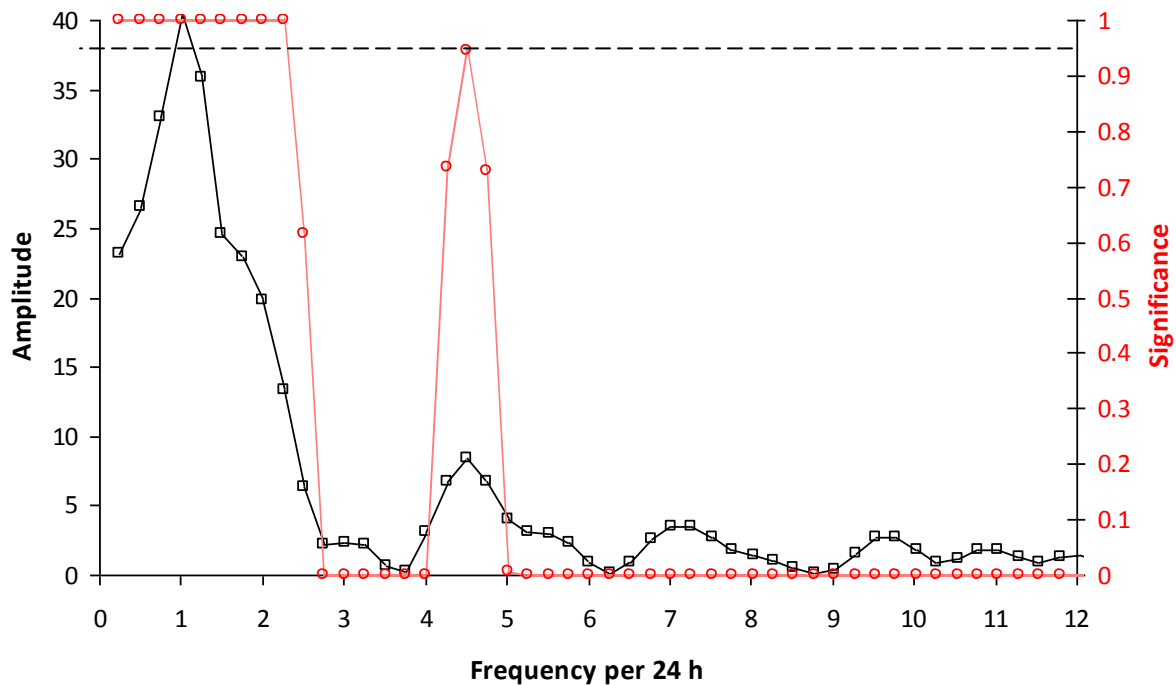
Figure 18. Lomb-Scargle periodogram of activity data for 48 hours of "normal" activity (31.10. and 01.11.2008). Dashed line marks level of significance (p = 0.05).

Figure 19 shows the respective proportion of sample (n = 8 for each feeding and "normal" periods) that showed significant activity counts for different period lengths. The Lomb-Scargle periodogram indicates that leopard activity at kill clusters and single positions differ remarkably in respect of the composition of their periodic components. The algorithm revealed a circadian rhythm with a period length of 24 hours within most "normal" activity intervals. However, this feature is missing in feeding cluster activity. In addition, the Lomb–Scargle periodogram picked up significant ultradian rhythms with a period < 24 (frequency > 1). This type of short-term rhythms with a fairly variable period was significantly more frequent in feeding cluster activity than in normal activity. At frequencies of 4.5 and 5 (period lengths of 4.8 to 5.3 the differences were significant (p < 0.05), at frequencies of 6.5, 8, 8.5 and 9 (period lengths of 2.7, 2.8, 3 and 3.7) even highly significant for this sample.

36
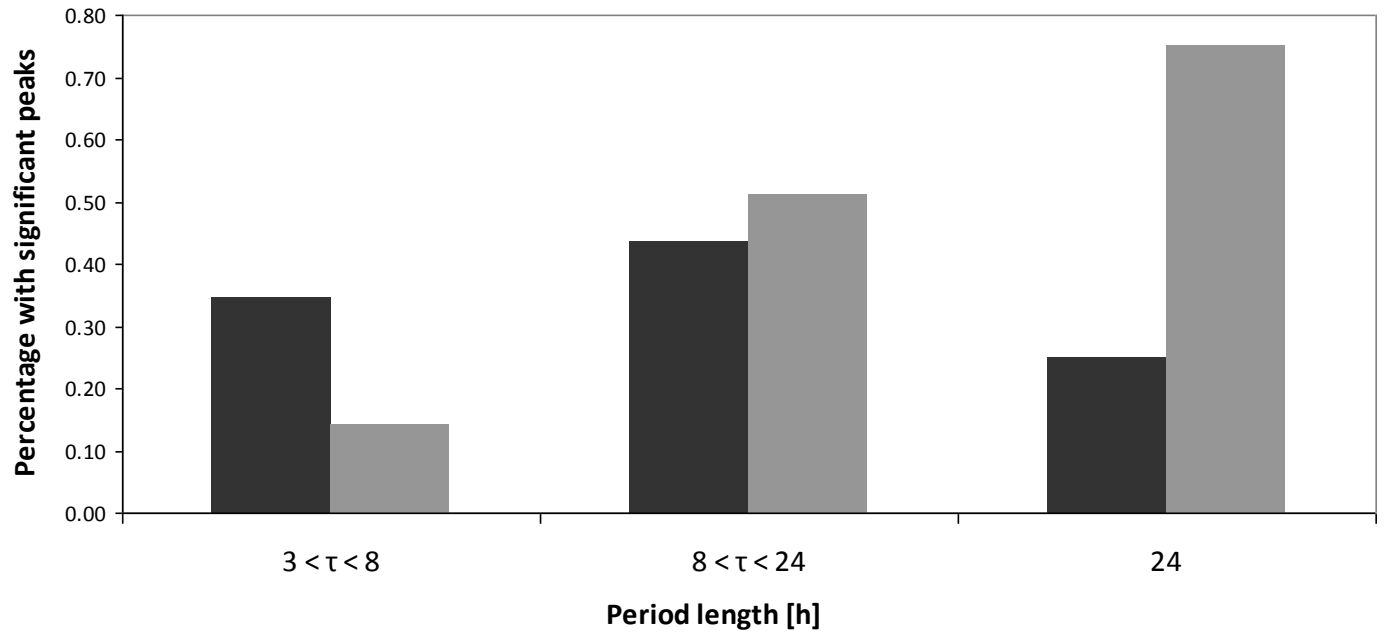
Figure 19. Detection of significant periodic components within confirmed feeding cluster (black bars) and no-cluster (grey bars) sites computed by Lomb-Scargle algorithm (n = 8).

4   DISCUSSION

4.1   Spatial use and activity

4.1.1   Home range of a female Cape leopard

F10 has concentrated her range in the central Cederberg, exclusively situated within the Fynbos biome of the Cederberg Mountains. Her home range size was far larger than previously suggested by Norton and Henley (1987) for leopards living in the Fynbos area of the Cederberg Mountains. However, they reported difficulty in capturing locality data, and Martins (2010) considered the VHF telemetry they used not as suitable for this mountainous, rugged terrain. But a change in food preference can be associated with home range size (Martins *et al.,* 2011), therefore a comparison of both studies might be difficult. This is corroborated by the home range sizes reported from the adjacent Boland area by Norton and Lawson (1985). More recent estimates (235 to 600 km^2; Martins and Martins, 2006) revealed that home ranges of male leopards in the Cederberg are among the largest previously recorded (e.g. Hamilton, 1976; Bailey, 1993; Marker and Dickman, 2005; Swanepoel, 2008). Their size is probably only exceeded by the leopards of the arid and flat Kalahari (1137±537 km^2; Bothma *et al.,* 1997). It has been reported that there is an inverse relationship between food availability and home range size in territorial animals. Previous leopard studies in Africa suggested that drier habitats with sparse prey distribution produce extremely large home ranges, and more humid and prey-rich habitats produce smaller home ranges (Odden and Wegge, 2005). Lindsay (2008) reported a range size of 147 km^2 for a female leopard of the Karoo Biome. This might be due to the fact that Fynbos comprises less open areas than Karoo, which are found to be avoided by leopards (Martins, 2010).

The method of home range estimation clearly affected results. Home range calculated by MCP was as much as 20 % larger as with 95 % Fixed kernel. MCP has frequently been used as home range estimator in leopard studies is criticised for its sensitivity to small sample size and the incorporation of large areas that are never used (Odden and Wegge, 2005).

4.1.2 Seasonal differences in activity patterns

African leopards are known to be active and mobile predators that will adapt their cycle of activity to specific situations as they do their hunting strategies (Hamilton, 1976; Bothma and Le Riche 1989, 1990; Bailey 1993; Jenny and Zuberbühler, 2005). However, data on the activity patterns of African leopards are rare (Bothma and Bothma, 2006) and different environmental factors need to be taken into consideration. For example, in an ecosystem such as the rainforests of West Africa, leopards appear to be more diurnal and crepuscular than nocturnal in their activity patterns because they follow the activity patterns of their main prey (Jenny and Zuberbühler, 2005). In semi-arid, savanna areas however, many leopard prey mammals prefer nocturnality in order to avoid heat stress (Bailey, 1993). However, female F10 showed a seasonally varying activity pattern and tended to be more active during the day in winter and during twilight in summer, which might be due to different feeding behaviour (see 4.3) and their manner of movement (Martins, 2010). Earlier studies also found that activity of female leopards abruptly increases around dusk and dawn (Grimbeek, 1992; Bailey, 1993). This pattern clearly differs from males, from which a higher activity level during the night has been reported in Kruger National Park (Bailey 1993), Southern Kalahari (Bothma and Bothma, 2006) and in the Cederberg Mountains (Martins, 2010). Current research on leopards in the Cederberg Mountains (Martins, 2010) revealed that they are predominantly nocturnal in this region, with a drop in activity between 22:00 and 02:00. Already Aschoff (1966) found that many nocturnal animals exhibit a double peak of activity, with the second peak being lower. The same pattern was found by Hamilton (1976) who studied leopards in Tsavo National Park, Kenya.

In this study, leopard activity during daytime was obviously related to season. F10 tried to avoid the hot temperatures in summer and was predominantly resting during the day, but also periodically rested during the night. Furthermore, time budget analyses showed that even though season does not influence the daily activity/resting time ratio (Fig. 10), it has obviously a significant impact on the day/night ratio of activity (Diurnality index, Fig. 9).

This means that for different seasons the leopard shifts its activity periods to different hours of the day rather than changing its time budget, e.g. through increasing resting time.

Contrary to forest leopards, savanna leopards have been reported to show no differences in seasonal behaviour (Bailey, 1993). However, the activity pattern reported by Bailey (1993) for the leopards in Kruger National Park was similar to the "summer" pattern found in the female leopard in this study. Bailey also recorded a sharp increase of night-time activity between 19:00 and 20:00; a sharp decline of morning activity between 04:00 and 07:00 and a minimum in the afternoons, from 13:00 to 14:00 (Bailey, 1993). During summer, F10 clearly avoided the increasing temperatures around midday. Bailey (1993) reported that, leopards were less active during the day in dry season compared to wet seasons (with reduced cover density). Other previous results from studies on leopard activity are also similar to the summer pattern of F10: Hamilton (1976) found that the main activity period of the leopards of Tsavo National Park was from the late afternoon to the next morning, with a major rest period during the daylight hours when they only moved around occasionally. Grimbeek (1992) found little daytime activity in two leopards studied in the Waterberg region of South Africa at a time when leopards were hunted actively there by cattle producers. Recorded movements during the daytime period were generally less pronounced and were possibly related more to seeking shade and shelter than to hunting (Bothma and Le Riche 1984, 1986).

4.1.3 Distinguishing categories of activity

Because GPS on its own provides only information about the location of an animal and not about its use, coupling of GPS locations and activity might be a good approach to differentiate between behavioural categories (Krop-Benesch *et al.,* 2010). For example, a high number of different locations in a short time can mean activity over a longer time span or a direct change of places with a high percentage of resting time. One aim of this study was to differentiate feeding activity from other behavioural categories in order to detect kills, measuring activity was therefore a valuable addition to GPS. However, determining the accuracy of behavioural data is essential to understand the behaviour of animals that are dif-

ficult to observe (Coulombe *et al.*, 2006). First studies to distinguish resting, slow and fast locomotion in red deer based on the acceleration measurements were done by Löttker *et al.* (2009). In a statistical comparison of values for different behavioural categories they found very highly significant differences between behavioural categories resting, slow locomotion, fast locomotion and feeding, except for the difference between feeding and slow locomotion. Activity includes a lot of behaviours during which the animal does not change its location, therefore activity is not necessarily low if no distances even though activity and distance correlate (Krop-Benesch *et al.*, 2010). In this study, GPS-data were included into the analysis and distance between two GPS-fixes was used as an additional criterion to differentiate between locomotion and non-locomotion activities. However, the possibility to differentiate between behavioural categories using the existing acceleration data of the female leopard is limited. An accurate generation and validation of threshold values would require the direct observations of tame or captive individuals (Löttker et al., 2009), conditions which are not feasible in harsh, inaccessible regions like the Cederberg Mountains.

4.2   Diet and hunting behaviour of a female leopard

GPS location cluster analysis and field investigation of kill sites provided important data on leopards' feeding habits. The results corroborate Martins *et al.* (2011), who found that klipspringers *Oreotragus oreotragus* and rock hyraxes *Procavia capensis* formed the majority of the leopard's diet in the Cederberg. The prevalence of klipspringers and rock hyraxes in both scats and GPS data suggests a preference for leopards hunting in rugged, rocky terrain, the preferred habitat for these preys (Skinners and Smithers, 1990). However, twenty-three species were recorded in the diet, using GPS data and scat analysis; similar diversity has been recorded in other studies and is indicative of the generalist feeding behaviour of Cape leopards. Small antelopes, in particular klipspringer, formed the greater part of the biomass consumed. A camera-trapping study in the Cederberg Mountains conducted by Martins et al. (2011) showed that, of 773 small antelope photographic captures, 73 % were klipspringer, 20 % grysbok, 6 % grey rhebok and > 1 % steenbok *Raphicerus campestris*. Therefore the found remains (Table 1) support the view that leopards in the

Cederberg take prey in proportion to their availability rather than being energy maximizers. The practice of eating and caching kills in trees or, where trees are scarce like in the Kgaladi Transfrontier Park, in holes, in order to avoid detection is known from most regions from Africa (Bailey, 1993; Bothma and Le Riche, 1986), but has not been observed in the Cederberg Mountains (Q. Martins, pers. comm.). The leopard is the only large predator in this region and interspecific competition is virtually absent, hiding their prey in order to avoid detection is therefore less necessary (Stander *et al.*, 1997; Martins, 2010).

Recent studies of predation patterns of other large predators such as cougars (Anderson and Lindzey, 2003) and wolves (Sand *et al.*, 2005) also using GPS technology showed that the majority of predation occurred at night. The data of the female leopard corroborate the common view that leopards are nocturnal hunters (Skinners and Smithers, 2003). The "kill peaks" at twilight times might be indicating of a preference of F10 to hunt at this time of the day, but confirmed kills are too scattered over the year to test this reliably. Moreover, it is known that leopards orient their activity times to that of their prey to increase hunting success in some regions (Jenny and Zuberbühler, 2005). This fact raised the question why the majority of prey items in this and other studies in the Cederberg (Norton and Henley, 1986; Martins *et al.,* 2011) consisted of diurnal species such as rock hyraxes and klipspringer. Martins (2010) examined hunting success of leopards in the Cederberg under different light conditions (new moon, half moon, full moon) and found that more kills were made in darker nights, when leopards have an advantage hunting diurnal prey in rocky habitat because it is then more difficult evade predation. Similar results are reported from lions by Tambling (2010).

Contrary to cougars which are killing at rates at the upper end oft those recorded for wolves in both frequency and biomass (Knopff *et al.*, 2010), leopards have been reported to have a low hunting efficiency with many unsuccessful attempts in their life (Bothma and Walker, 1999; Bailey, 1993). However, kill rate in this study might be seriously underestimated caused by non-detection of predation sites, e.g. due to delayed field surveys (see 4.4.4) or immediate consumption of prey items without forming a cluster. Le Roux and Skinner (1989) reported one kill every twelve days in Sabi Sand Game Reserve, Bailey

(1993) one kill every seven days in Kruger National Park. However, prey in these studies consisted mainly of impala (*Aepyceros melampus*) and other larger ungulates, the relative biomass consumed per day is therefore much higher. Female leopards in Kruger National Park consume 2.8 to 4 kg per day (Bailey, 1993). F10 made more large kills in summer than in winter, but sample size is too small to prove that season is a potential source of variation in leopard predation. This study provided data from only 8 months of the year, which may extrapolate poorly to annual predation rates (Sand *et al.*, 2005; Knopff *et al.*, 2010). Anyway, kill data from one single individual do not allow determining a kill rate for the leopard population of the Cederberg Mountains.

4.3   Prediction of kills from combined GPS and activity data

The GPS cluster analysis assumes that predators reach a cluster, stay for a certain amount of time and leave the cluster after the prey was consumed. It is well understood that time spent at a kill site is dependent on size of the prey item (e.g. Tambling *et al.*, 2010; Martins *et al.*, 2011). When predominance of biomass consumed by carnivores comes in relatively large, discrete packages, it results in clustered movements patterns owing to lengthy handling of prey (Merrill *et al.*, 2010). The finding that there was generally longer cluster duration in confirmed kill-clusters than in not-found clusters implies that the probability of finding of a kill predicted from GPS clusters increases with cluster duration and data of F10 seem to support the view that successful location of prey remains correlates positively with the length of time the leopard had spent in the vicinity of the kill (Martins *et al.*, 2011). Because there was a low probability of locating kills at sites occupied for less than 16 hours, these could have included resting as well as kill sites. In order to make sure that size of prey can be reliably detected using GPS location clusters, a detection of smaller-bodied prey is crucial to avoid biases in kill rate estimates towards larger prey and may require high-position frequency (Sand *et al.*, 2005; Webb *et al.*, 2008; Knopff *et al.*, 2009). More intensive GPS schedules may assist in refining the technique for finding smaller kills, although this may be prohibitively labour intensive and the effectiveness will be limited (Knopff *et al.*, 2009). Small prey such as rodents or birds may be consumed too quickly to be detected with a reasonable GPS location schedule. However, Martins *et al.* (2011)

43

claimed that the importance of this type of prey in terms of biomass consumed is negligible, as rodents and birds are an insignificant part of the diet of leopards in the Cederberg.

Turning angle analysis using the Rayleigh's Test for Circular Uniformity (Zar, 1999) was not able to differentiate kill sites from non-kill sites. Besides large fix intervals and GPS location errors dependent on number and position of available satellites, the reason for that might have been the manner of movement that has been reported for female leopards in the Cederberg (Q. Martins, pers. comm.). Contrary to males, which often use roads to patrol their larger territories, daily distances covered by females were significantly larger when using multiple instead of only one location per day for the calculation, suggesting that females are moving in a much less linear fashion than males (Martins, 2010). To put it another way, female movements lack the goal-directedness that are found in males and consecutive directions that are pursued are not likely to be a function of kill events. Turning angles will therefore be not a reliable measure for the differentiation between kill and non-kill clusters in female Cape leopards.

Because activity of an animal is usually correlated with locomotion or the distance that has been covered within a certain period (see 4.1.3), it is not surprising that recorded activity within clusters quickly decreased after onset, often to values just above zero. The GAM was not able to differentiate between kill-clusters and non-kill clusters, which might be due to small sample size and the high variety of activity at kill sites. However, several clusters could be rejected as potential kill clusters because of their low activity values. Activity data revealed that no or very low activity throughout the duration of clusters means they were probably resting sites or day bed locations (Anderson and Lindzey, 2003). Thus, the integrated acceleration sensor provides a helpful means to reject non-kill clusters *a priori* in order to reduce field study efforts. Activity at kill sites where rock hyraxes were killed differed from activity pattern at large-kill sites. As rock hyraxes provide only a fraction of the biomass of antelopes (Table 2), less effort is needed to kill this prey items and the carcass can be consumed in one continuous action. Therefore, no feeding activity pattern that is characteristic for small-kill sites was found. Handling of a large kill such as a klipspringer needs considerably more time and effort which is probably why extended periods of high

activity before most large-kill cluster onsets were recorded. Even when they hunt, leopards are seldom in a hurry and frequently stop to look and listen; locomotion remains generally slow and they almost never run (Bailey 1993). This is why it was concluded that intervals of high intervals before or during GPS location clusters reflect the time of kill. Furthermore, large-kill clusters with a long duration were characterised by a specific activity pattern that consisted of resting intervals with low recorded activity interrupted by feeding periods of variable length. However, because Cape leopards might have similar hunting success at capturing prey as leopards elsewhere (Bailey 1993), high activity in short time does not necessarily mean a kill but rather a kill attempt. Thus, it is a matter of fact that it is not possible to detect kill events from activity data alone, and studies of foraging ecology definitely have to make use of both data types.

The Lomb-Scargle periodogram revealed that the activity pattern at feeding sites lacks the circadian rhythm but exhibits various ultradian rhythms, recurrent activity periods repeated throughout a 24-hour circadian day. These are interpreted as feeding intervals that are needed to consume large prey entirely. Smaller prey items such as rock hyrax *Provavia capensis* and Rock rabbit *Pronolagus rupestris* are consumed immediately after the kill and are therefore not suitable for periodogram analysis. The handling of an antelope kill is thought to be noticeable from the activity pattern. Little is known about activity and behaviour of leopards at a kill site (Bothma and Le Riche, 1989). In terms of feeding behaviour, there is not much evidence in the literature that we find a specific feeding activity pattern in leopards. Bailey (1993) found that leopards in Kruger National Park fed on kills irregularly throughout day and night, with feeding activity once or twice before midnight, resting from midnight to early morning, fed once again before sunrise. The average uninterrupted feeding interval calculated by Bailey (1993) was 24 minutes (3-84 min), the average resting interval between feeding periods 164 minutes (32-324 min). However, the Lomb-Scargle periodogram provides additional means to differentiate kill clusters from non-kill clusters, given that the cluster duration is long enough (< 24 hours).

4.4 Sources of bias

When using remote techniques like GPS telemetry there is a considerable amount of factors that will influence results. Although some might be inevitable, others should get special consideration in future studies in order to facilitate work and generalize results.

4.4.1 GPS collar performance

Variation in fix acquisition represents a complex problem. Low fix success is more likely to approximate a random loss of data, as opposed to the strictly systematic data reduction due to large fix intervals (see paragraph 4.4.2), because this type of fix loss can contain runs of missed points, which is more likely to result in detection failure (Knopff *et al.*, 2009). Topography, vegetation, and animal behaviour may influence the performance of GPS telemetry collars, resulting in lower fix success rates and larger location errors, e.g. in areas with more rugged topography (Cain *et al.,* 2005). Although the GPS failure rates reported here are within the range or even below of what has been reported in some other studies on carnivores (e.g. Anderson and Lindzey, 2003: 17–40% for GPS-collars fitted to cougars; Sand *et al.*, 2005: 9-13 % for wolves; Swanepoel, 2010: 15–29% for GPS collars for leopards in the Waterberg Mountains of South Africa), several kill sites might not have been detected due to collar failure over > 6 hours or 2D-positions only (Anderson and Lindzey, 2003). However, accuracy of 2D locations is similar to 3D locations if the elevation from the last 3-D position is similar to that of the 2-D (Moen *et al.,* 1997). Additionally, Cain *et al.* (2005) found that shorter fix intervals are associated with higher fix success rates, which might be relevant as the fix schedules changed quite often. The influence of topography and fix interval on location error and fix success rates may bias GPS location data, resulting in under-sampling certain areas used by animals and non-detection of potential predation clusters.

4.4.2 Fix schedules and battery life dilemma

A major source of bias was the varying fix schedule that resulted consistently in long fix intervals (e.g, interval from 14:00 to 22:00). It was necessary to test collar performance in the first place; thus GPS acquisition was changed often in order to figure out an appropriate

schedule (Q. Martins, pers. comm.). The well-known "battery dilemma" describes the fact that a larger battery provides a huge amount of GPS fixes while affecting the animal in an unacceptable way, whilst a light battery has low impact on the animal, but is able to store only a very limited amount of data. Because of limited battery life and the high energy demands of GPS fixes, intervals between locations were often set as large as eight hours, with an average of six fixes obtained per day. When fix interval was too large, there was a high possibility that clusters might not form at some kill locations (Knopff *et al.*, 2009). Lower than average GPS acquisition might reduce the probability of cluster creation at some kills, biasing estimates of kill rate and prey composition. Where fix rate bias exists, sampling rate should be evaluated with this error in mind (Knopff *et al.*, 2009). For example, the presumed time of kill was estimated to 22:00, but according to extremely low activity data some kills actually must have occurred much earlier. That is why activity data were used to estimate correct cluster initiation and to adjust cluster duration. Webb *et al.* (2008) examined the effect of reducing the time between GPS location attempts (fix interval) on the probability of locating wolf-killed prey and found that kill rate for small prey was underestimated at longer fix intervals. The cluster technique in this study was designed to find prey > 3.7 kg (weight of rock hyrax, the smallest animal recorded) and prey less than or close to this value might be missed because handling time is too short to produce a cluster or because we did not locate remains at a cluster where prey was consumed. To further increase the precision of leopard kill rates in the Cederberg Mountains, an intensive programming schedule is needed. However, this option will significantly reduce the lifespan of GPS collars.

At the same time, monitoring periods must be long if accurate and precise estimates of carnivore kill rate and prey composition are required (Knopff *et al.*, 2010). Because handling time, search time, and species killed are all variable, and because leopard predatory events occur infrequently, long intervals of monitoring are required to accumulate a sufficient number of inter-kill intervals and prey types to encompass this variation. The duration of monitoring required for quality parameter estimation will depend on the variability and average length of inter-kill intervals and on dietary diversity (Knopff *et al.*, 2009). However, predators with shorter or less variable inter-kill intervals and lower dietary diversity will

require shorter monitoring periods. Although the Cape Leopard Trust was able to success-fully recollar F10 in July 2009 and data recording was not interrupted until March 2010, the large data set has not yet been used for GPS cluster analysis as no further field visits could have been made.

4.4.3 Handling of acceleration data

Because an old version of the GPS Handheld UHF terminal was used, remote download of data resulted in regular data gaps of three, and smoothing away faults was very laborious and time consuming. This technical problem has been resolved in the next UHF terminal generation and will not affect future studies (I. Heckmann, pers. comm.). Furthermore, the placement of the collar around the animal's neck accounts for the fact that the acceleration sensor is especially affected by head movements (Gervasi *et al.*, 2006). Therefore, head movements but also events like 'getting up', 'body shaking' and 'jumping' during a resting period caused higher activity values than usual for this period and thus lead to a shift from values that would normally be classified as resting to values that will be interpreted as feeding/slow locomotion (Löttker *et al.*, 2009). This is a technical problem resulting from the fact that activity data are mean values for a 5-minute interval. Moreover, the mobility of the collar itself represents a variable that accounts for an unknown percentage of values. If there are physiology-dependent changes, e.g. due to growth or nutritional condition, data recording will be influenced even if the behaviour is constant (Heckmann, 2007). The use of electronical measuring systems enhances the pool of tools for behavioural research on wildlife and bears advantages like continuity and long duration of data recording, but there are several technical limitations. Hence it is crucial to firstly become acquainted with the used collar system and the implemented data capturing modus in order to be able to infer from the data to the actual behaviour (Heckmann, 2007).

4.4.4 Delayed field visits

The time span between the kill event and field investigation of the kill site is critical to de-tect a carcass and to determine information such as prey species and cause of death (Merrill *et al.*, 2010). To date, average time spans have ranged from approximately 8–9

days (Zimmerman *et al.*, 2007; Sand *et al.*, 2005) to 200 days (Anderson and Lindzey 2003). Principally, GPS collars with remote data download via VHF, UHF, GSM or satellite link allow visitation of sites before decomposition and scavenging make field verification less reliable (Webb *et al.*, 2008). On the one hand, the time span should be long enough that field personnel will not interfere with the predator, one the other hand probability of finding a kill is generally higher the earlier a GPS cluster can be investigated (Swanepoel, 2008). In this study, field surveys of GPS clusters were undertaken comparably late (Knopff *et al.,* 2009; Ruth *et al.,* 2010; Tambling *et al.*, 2010), which might be one of the pivotal reasons why relatively few kills were detected. The decision to implement GPS cluster analysis in the Cape leopard research program evolved only over the course of the long-term study in 2009, which was in most cases long after clusters formed. Furthermore, leopards in the Cederberg spend the majority of their time in rugged terrain (Q. Martins, pers. comm.) which makes finding kills difficult. Although Martins *et al.* (2011) reported that they were able to locate kill remains for up to 3.5 years owing to the lack of scavengers in this area, it is very likely that many carcasses have been missed during field visits. After decomposition prey remains often consisted only of parts of a skull, hair or the rumen which are easily relocated or hidden by weather phenomena (e.g., wind and heavy rain) and passing animals. In addition, it was not possible to reliably assess seasonal variation in the composition of the leopard's diet due to the short length of the investigation period of eight months. Generally, it is advisable that clusters be investigated as soon as possible after they occur, because kills will be easier to locate (Tambling, 2010). Increasing availability of real-time GPS data will assist in rapid investigation of clusters (Anderson and Lindzey, 2003; Stotyn, 2005).

4.4.5   Small sample size

Lastly, but probably most importantly, the fact that all data of this study are obtained from one single individual prohibits any generalizations. Due to low population densities and difficult field conditions, capture and long-term monitoring of leopards in the Cederberg Mountains is challenging (Martins, 2010). The study animal F10 (also called "Spot") was to date the only individual for whom all three kinds of data (GPS location, activity and kill

data) were available. Kills from other collared leopards were also found using GPS-cluster analysis, but not a representative number. Home ranges of some collared individuals are situated in the Karoo biome of the Cederberg where prey remains are difficult to locate. Karoo terrain often consisted of rough, steep V-shaped kloofs formed along rivers with rocky slopes being difficult to access (Martins 2010). It is not a coincidence that "Spot" is known to be the "flagship leopard" of the Cape Leopard Trust, as it is the first leopard for whom long monitoring (locations and activity) and field surveys of GPS clusters were possible. It is well-known that small sample sizes can undermine inferences about the basic mechanisms of predation (Marshal and Boutin, 1999), and short monitoring periods can lead to prohibitively wide confidence intervals around parameter estimates (Hebblewhite *et al.,* 2004). Moreover, models could not be employed for predation parameter estimation.

However, a rather small sample size is also reported from other studies of large carnivores using GPS cluster analysis where population size is small (Sand *et al.*, 2005; Stotyn, 2005, Demma *et al.*, 2007). Intensive research for over seven years, including the use of camera traps, traditional VHF collars and scat analysis, support many results found also in this study on Cape leopards (Rautenbach, 2008; Martins, 2010). Anyhow, main concern of this Master's thesis was not an estimation of predation rates of Cape leopards in the Cederberg Mountains, like in extensive and well-funded cougar studies of Andersons and Lindzey (2003) or Knopff *et al.* (2009), but rather to explore the possibilities of a novel, combined analysis of different types of collar data that are simultaneously recorded. If one considers that it takes months or even years to conduct GPS cluster studies that involve capture and collaring of animals, data processing to detect clusters and field visits of potential kills (e.g., Sand *et al.*, 2005, Knopff *et al.*, 2010) it falls into place that a study to this extent would by no means be feasible within the scheduled period of six months for a Master's thesis.

4.5   Evaluation of methods

As leopards generally show high fidelity to kill sites and have extended handling times, investigating clusters from GPS location data proved to be an effective method in finding kills, especially in mountainous terrain. GPS data allow estimating time spent, distance traveled, and movement rates for leopards at sites where they were hunting, killing, and consuming prey of small as well as large size (Demma *et al.*, 2007). The harsh field conditions of the rugged Cederberg Mountains complicate the monitoring of leopard activity and the location of kills. Direct observation of leopards in the Western Cape is rare, therefore remote data collection was the only way to study their behaviour and movements (Martins *et al.*, 2011). Moreover, because GPS collars can be programmed to collect diurnal and nocturnal locations, GPS sampling resulted in detection of several night time only kills, which is impossible with VHF methods (Ruth *et al.,* 2010). Martins *et al.* (2011) reported that in many years of research they opportunistically encountered very few confirmed leopard kills in the Cederberg Mountains without GPS technology, whilst within one year they found more than fifty kills using GPS cluster analysis. Prey of leopards in this area is almost exclusively in the < 25 kg range and kills are often hidden under vegetation or rocks, therefore it is very unlikely to encounter kills occasionally (Martins et al., 2011). GPS locations can be used to provide an accurate measure of diet even when small prey such as rock hyrax *Procavia capensis* or rock rabbit *Pronolagus rupestris* is being taken.

To date, analyses of GPS-based movement patterns of large carnivores have focused on identifying periods of handling time that identify kill sites and the factors influencing handling time (Merrill *et al.*, 2010). Methods for identifying kill sites based on spatio-temporal patterns in the sequence of movement positions are evolving. As the approach is applied in more studies with a variety of species we will gain a better appreciation of how data sampling protocols and animal behaviour influence our ability to correctly distinguish a GPS-based kill site. In cougar studies estimates of behavioural parameters of predation were thought to be biased because they possibly consumed carcasses of animals they did not kill, creating GPS telemetry location clusters at scavenging sites that are misclassified as kills

(Anderson and Lindzey, 2003; Knopff et al., 2009). The fact that leopards in the Cederberg Mountains have large territories and no other large predators are present diminishes the effect of this form of bias.

However, due to the nature of GPS location and activity data and the lack of observational data, it was not possible to determine the actual hunting behaviour of the leopard. Demma *et al.* (2007) inferred that the kill-site use characteristics most likely represented the entire continuum of activities related to hunting prey including searching, capturing and killing, consuming and resting or sleeping after the initial feeding (Demma *et al.*, 2007). In order to investigate the feeding ecology of large carnivores in inaccessible areas, it is therefore advantageous to use a combination of different methods such as GPS cluster analysis, acceleration data analysis and camera traps. For the Cape leopard, measured activity seems to differ for different sizes of prey. Kills of large prey show usually a long handling time and might be rather suitable for statistical analysis than smaller kills with shorter cluster duration, because it was mostly difficult to differentiate the latter from resting sites.

In a GPS-cluster study on lions using Generalized linear regression models (GLM) and classification trees (CT), Tambling *et al.* (2010) found that the ratio of distance moved 24 hours before and 24 hours after a cluster of points proved to be the largest contributor to reliable discrimination between kill and non kill sites. Other logistic regression models have been used to predict presence or absence of kills in North American carnivores, with minimum length of time at a cluster as important predictor variable (Anderson and Lindzey, 2003; Sand *et al.*, 2005; Stotyn, 2005; Webb *et al.*, 2008). Due to varying fix schedules and small sample size (one individual and relatively few kills) these methods had to be omitted in this study. As soon as more kill data from more Cape leopards are available, it will be interesting to catch up on the above-mentioned analyses. However, modeling the probability of a cluster being a kill site is no substitute for field visits, but can guide field efforts (Sand *et al.*, 2005; Webb *et al.*, 2008; Knopff *et al.*, 2009). Factors related to handling time, such as prey size, size of predator social groups, environmental site factors (e.g. snow) and disturbance by humans have been identified by several authors (Zimmerman *et al.*, 2007; Webb *et al.*, 2008).

52

Model-based approaches for estimating predation rates in large carnivores are enhanced by developments in GPS collar technology (Anderson and Lindzey, 2003). Costs of GPS collars continue to decrease, which allows the purchase of more collars to increase sample size (A. Berger, pers. comm.). As a result, models can be employed, which may greatly reduce cost and effort associated with monitoring over the duration necessary to generate quality estimates. Furthermore, collars are becoming lighter and capable of collecting an increasing number of locations, mitigating the negative influence of the "battery life dilemma". With the use of timed drop-off devices collared leopards do not need to be recaptured and improvements in the reliability of remote downloading systems will allow more timely retrieval of data. The advancement of GPS technology provides opportunities to investigate more detailed hypotheses of predator-prey relationships and ecosystem processes.

5   CONCLUSION

Taken together, this Master thesis explored a new approach of combining GPS cluster analysis and activity data obtained from collar-integrated acceleration sensors in order to investigate the feeding ecology of Cape leopards of the Cederberg Mountains, South Africa. GPS and activity data from one female leopard were recorded continuously from June 2008 to July 2009, while field investigation of potential kills derived from GPS location clusters were only performed for the period June 2008 to February 2009. Consequently, 2580 GPS positions and more than 100.000 activity values were obtained, and 31 kills could be located using GPS cluster analysis. Most kills occurred during the night or twilight hours, and the majority of prey items consisted of diurnal and rock-dwelling species such as rock hyrax *Procavia capensis* and klipspringer *Oreotragus oreotragus*. Retrospective GPS analysis of leopard movements in the Cederberg Mountains provided an accurate demonstration of leopard dietary habits and is a valuable tool for studying the feeding ecology of elusive carnivores. The success in locating a kill seemed to correlate to both the length of time spent by the leopard at the kill site and the prey mass. Activity data turned out to be useful for *a priori* assessments of GPS location clusters, e.g. to differentiate between resting and potential kill/feeding sites. However, detection of kills by combined analysis of activity and location analysis is laborious, as activity data need to be allocated to the corresponding location data. Due to their different energy demands both data types are obtained in different frequencies, and analyses are further complicated when GPS fix schedules are irregularly changing like in this study. Furthermore, technical failures of collars and time lags between event recording and field visits have hampered utility of GPS data in locating kills. Nevertheless, the combination of different techniques such as GPS/VHF telemetry and activity data from acceleration sensors provides helpful means in remote mountainous areas where direct observation and scat collections are difficult. Further observations of spatial use, activity and hunting behaviour on more individuals of each age and sex class should be performed to take into account intra-specific variability. In order to generalize results, future studies on feeding ecology of Cape leopard require data from more individuals, smaller GPS fix intervals and a smaller time span between expected kills and surveys.

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56

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APPENDIX I

Table 3. Chronology of fix schedules for F10 during GPS cluster investigation period

N° start	N° end	Date start	Time start	Date end	Time end	Fix schedule
1	276	06/18/08	22:00:00	08/03/08	12:00:00	6a
277	280	08/03/08	14:00:00	08/04/08	00:00:00	12
281	329	06/08/08	02:00:00	08/06/08	02:00:00	24
330	360	08/08/08	04:00:00	08/11/08	04:00:00	6b
361	384	08/11/08	06:00:00	08/13/08	04:00:00	12
385	413	08/13/08	08:00:00	08/18/08	02:00:00	6b
414	461	08/18/08	03:00:00	08/20/08	02:00:00	24
462	492	08/20/08	04:00:00	08/25/08	04:00:00	6b
493	516	08/25/08	06:00:00	08/27/08	04:00:00	12
517	545	08/27/08	08:00:00	09/01/08	02:00:00	6b
546	593	09/01/08	03:00:00	09/03/08	02:00:00	24
594	624	09/03/08	04:00:00	09/08/08	04:00:00	6b
625	648	09/08/08	06:00:00	09/10/08	04:00:00	12
649	677	09/10/08	08:00:00	09/15/08	02:00:00	6b
678	725	09/15/08	03:00:00	09/17/08	02:00:00	24
726	757	09/17/08	04:00:00	09/22/08	04:00:00	6b
758	781	09/22/08	06:00:00	09/24/08	04:00:00	12
782	810	09/24/08	08:00:00	09/29/08	02:00:00	6b
811	858	09/29/08	03:00:00	10/01/08	02:00:00	24
859	1946	10/01/08	04:00:00	03/30/09	08:00:00	6b

Times of fix acquisition for different schedules (LMT)

6a	02:00, 05:00, 8:00, 12:00, 18:00, 22:00
6b	00:00, 02:00, 04:00, 08:00, 14:00, 22:00
12	00:00, 02:00, 04:00, 06:00, 08:00, 10:00, 12:00, 14:00, 16:00, 18:00, 20:00, 22:00
24	00:00, 01:00, 02:00, 03:00, 04:00, 05:00, 06:00, 07:00, 08:00, 09:00, 10:00, 11:00, 12:00, 13:00, 14:00, 15:00, 16:00, 17:00, 18:00, 19:00, 20:00, 21:00, 22:00, 23:00

APPENDIX II

Table 4. Field investigation of GPS clusters for leopard F10

Date START	Time START	Date END	Time END	Min hrs at site	Collection date	Area	Latitude	Longitude	Altitude (m)	Found (Y/N)	Species (Tab. 5)
22.06.08	22:00	23.06.08	02:00	4.0	20.04.09	Welbedacht	-32.4119	19.16845	1143	Y	PC
25.06.08	22:00	27.06.08	02:00	28.0	24.03.09	Uilsgat	-32.4007	19.1338	1217	Y	OO
29.06.08	05:00	29.06.08	12:00	7.0	22.04.09	Miedseberg	-32.4177	19.14053	1319	Y	PC
30.06.08	22:00	01.07.08	05:00	7.0	11.09.09	Panarama	-32.4249	19.192	1298	Y	PC
02.07.08	05:00	02.07.08	12:00	7.0	-	Uitkyk	-32.4087	19.11973	1094	-	-
09.07.08	08:00	10.07.08	02:00	18.0	21.04.09	Miedsekop	-32.4196	19.15102	1140	Y	OT
10.07.08	12:00	11.07.08	05:00	17.0	21.04.09	Miedsekop	-32.4211	19.15223	1155	Y	HA
13.07.08	05:00	15.07.08	02:00	45.0	09.10.08	Uilsgat	-32.402	19.13975	1060	Y	OO
16.07.08	05:00	18.07.08	12:00	55.0	08.10.08	Driehoek	-32.424	19.18552	1170	Y	PC
21.07.08	08:00	22.07.08	05:00	21.0	27.04.09	Uilsgat	-32.4046	19.14635	1005	N	SHB
25.07.08	02:00	25.07.08	05:00	3.0	-	Miedsekop	-32.4131	19.14678	1119	-	-
28.07.08	05:00	29.07.08	08:00	27.0	15.04.09	Uitkyk	-32.4192	19.13574	1057	Y	OO
03.08.08	05:00	03.08.08	12:00	7.0	-	Shaleband	-32.4196	19.19648	1514	-	-
04.08.08	19:00	05.08.08	00:00	5.0	-	Uilsgat	-32.3904	19.1407	1257	-	-
05.08.08	06:00	05.08.08	12:00	6.0	-	Uilsgat	-32.3878	19.12218	1423	-	-
05.08.08	20:00	06.08.08	04:00	8.0	-	Uitkyk	-32.4039	19.10494	1026	-	-
05.08.08	20:00	06.08.08	04:00	8.0	-	Uitkyk	-32.4044	19.10692	1055	-	-
07.08.08	22:00	08.08.08	02:00	4.0	20.04.09	Welbedacht	-32.4182	19.17472	1125	Y	PC
10.08.08	22:00	11.08.08	06:00	8.0	21.04.09	Miedsekop	-32.4246	19.15591	1032	N	-
12.08.08	06:00	12.08.08	10:00	4.0	-	n/a	-32.4013	19.10584	1106	-	-
12.08.08	20:00	13.08.08	02:00	6.0	-	n/a	-32.4075	19.12483	1260	-	-
15.08.08	02:00	15.08.08	08:00	6.0	28.04.09	Waterkloof	-32.4339	19.20401	1275	N	-
16.08.08	22:00	17.08.08	08:00	10.0	21.04.09	Miedsekop	-32.4256	19.15415	1146	Y	PC
16.08.08	08:00	16.08.08	14:00	6.0	21.04.09	Miedsekop	-32.4174	19.14965	1107	N	-
17.08.08	14:00	18.08.08	06:00	16.0	22.04.09	Miedseberg	-32.4147	19.14395	1214	N	-
19.08.08	06:00	19.08.08	13:00	7.0	27.04.09	Uilsgat	-32.4014	19.14792	1100	N	-
20.08.08	22:00	21.08.08	04:00	6.0	-	Miedseberg	-32.405	19.12354	1400	-	-
21.08.08	22:00	22.08.08	04:00	6.0	-	Uitkyk	-32.3965	19.10303	1186	-	-
25.08.08	18:00	26.08.08	04:00	10.0	22.04.09	Miedseberg	-32.4189	19.13728	1200	Y	OO
29.08.08	02:00	29.08.08	14:00	12.0	22.04.09	Miedseberg	-32.4169	19.13224	1070	N	SB
01.09.08	07:00	01.09.08	13:00	6.0	22.04.09	Uilsgat	-32.4014	19.13368	1235	Y	PC
01.09.08	14:00	01.09.08	22:00	8.0	24.03.09	Uilsgat	-32.4005	19.13574	1133	N	-
02.09.08	00:00	02.09.08	12:00	12.0	24.03.09	Uilsgat	-32.4104	19.143	1065	Y	OO
02.09.08	17:00	03.09.08	00:00	7.0	22.04.09	Miedseberg	-32.4182	19.14356	1322	Y	PC
05.09.08	22:00	06.09.08	08:00	10.0	20.04.09	Uilsgat	-32.4079	19.16136	1144	N	S
07.09.08	22:00	08.09.08	06:00	8.0	14.05.09	Uilsgat	-32.4016	19.13419	1227	Y	PC

09.09.08	10:00	09.09.08	18:00	8.0	-	Uilsgat	-32.4057	19.15607	1254	-	-
12.09.08	14:00	13.09.08	14:00	24.0	14.04.09	driehoek	-32.4413	19.20295	1087	Y	PC
15.09.08	08:00	15.09.08	11:00	3.0	-	Uitkyk	-32.4167	19.11647	1040	-	-
15.09.08	17:00	16.09.08	06:00	13.0	-	Uitkyk	-32.4143	19.10872	1286	-	-
21.09.08	00:00	21.09.08	04:00	4.0	21.04.09	Miedsekop	-32.4216	19.15268	1159	Y	PC
24.09.08	22:00	25.09.08	02:00	4.0	-	Uitkyk	-32.3938	19.10462	1250	-	-
27.09.08	22:00	28.09.08	04:00	6.0	14.05.09	Uilsgat	-32.4037	19.13638	1186	Y	PC
27.09.08	04:00	27.09.08	14:00	10.0	27.04.09	Uilsgat	-32.4069	19.14979	998	N	Scats
28.09.08	22:00	29.09.08	02:00	4.0	-	Middelberg	-32.4001	19.12156	1619	-	-
29.09.08	19:00	30.09.08	02:00	7.0	24.03.09	Uilsgat	-32.3971	19.13653	1109	N	-
03.10.08	00:00	03.10.08	04:00	4.0	12.08.08	Driehoek	-32.4248	19.12842	1014	N	-
14.10.08	22:00	15.10.08	04:00	6.0	27.02.09	Kalkoenfon-	-32.452	19.22567	1040	Y	PC
08.11.08	00:00	10.11.08	00:00	48.0	04.02.09	Driehoek	-32.431	19.1658	933	Y	OO
17.11.08	14:00	19.11.08	00:00	34.0	25.02.09	Driehoek	-32.4235	19.18637	1210	Y	OO
07.12.08	04:00	08.12.08	04:00	24.0	19.03.09	Driehoek	-32.4287	19.19101	1105	Y	SG
13.12.08	22:00	14.12.08	04:00	6.0	-	Uilsgat	-32.3931	19.12849	1336	-	-
15.12.08	02:00	15.12.08	08:00	6.0	22.04.09	Miedseberg	-32.4128	19.14203	1190	Y	RM
15.12.08	22:00	16.12.08	04:00	6.0	-	Miedsekop	-32.4126	19.14416	1134	-	-
21.12.08	08:00	22.12.08	04:00	20.0	18.04.09	Uilsgat	-32.411	19.16209	1045	N	-
23.12.08	08:00	23.12.08	14:00	6.0	15.04.09	Uitkyk	-32.4185	19.1172	1084	Y	PC
23.12.08	22:00	24.12.08	04:00	6.0	-	Uitkyk	-32.4082	19.89962	1267	-	-
25.12.08	14:00	26.12.08	04:00	14.0	-	De Rif	-32.443	19.21438	1216	-	-
27.12.08	22:00	28.12.08	02:00	4.0	18.04.09	Uilsgat	-32.4101	19.15739	1000	N	-
01.01.09	22:00	02.01.09	04:00	6.0	27.04.09	Uilsgat	-32.4089	19.14385	1062	N	-
03.01.09	00:00	03.01.09	04:00	4.0	-	Shaleband	-32.3988	19.158	1574	-	-
06.01.09	00:00	06.01.09	04:00	4.0	27.04.09	Uilsgat	-32.4119	19.14729	1065	Y	PC
09.01.09	00:00	09.01.09	04:00	4.0	28.04.09	Waterkloof	-32.4312	19.19918	1174	N	-
10.01.09	00:00	10.01.09	04:00	4.0	18.04.09	Uilsgat	-32.4107	19.16117	1142	Y	PR
16.01.09	08:00	16.01.09	14:00	6.0	27.04.09	Uilsgat	-32.4027	19.14903	1135	Y	Hair
22.01.09	22:00	23.01.09	04:00	6.0	22.04.09	Miedsekop	-32.421	19.14549	1300	N	-
26.01.09	08:00	26.01.09	14:00	6.0	-	Uitkyk	-32.4061	19.10079	1053	N	Scats
28.01.09	00:00	28.01.09	04:00	4.0	22.04.09	Miedsekop	-32.4151	19.13856	1324	-	-
29.01.09	08:00	21.01.09	22:00	14.0	20.04.09	Welbedacht	-32.4166	19.16999	1047	Y	PC
03.02.09	22:00	04.02.09	04:00	6.0	25.02.09	Uilsgat	-32.4084	19.15121	980	-	-
05.02.09	08:00	05.02.09	14:00	6.0	20.04.09	Welbedacht	-32.4188	19.1705	984	Y	PC
13.02.09	02:00	13.02.09	08:00	6.0	21.04.09	Miedsekop	-32.4173	19.14813	1169	N	-
15.02.09	00:00	15.02.09	08:00	8.0	13.03.09	Driehoek	-32.4283	19.15191	1020	N	-
16.02.09	22:00	17.02.09	02:00	4.0	-	Welbedacht	-32.4086	19.18392	1433	-	-
19.02.09	00:00	19.02.09	04:00	4.0	-	Uitkyk	-32.4091	19.11998	1054	-	-
21.02.09	08:00	21.02.09	14:00	6.0	22.04.09	Miedseberg	-32.4145	19.13938	1347	-	-
25.02.09	22:00	27.02.09	08:00	32.0	14.04.09	Driehoek	-32.4503	19.21042	954	Y	SG

APPENDIX III

Table 5: Prey characteristics and distribution (Skinner and Smithers 1990; IUCN 2010)

Species name	Latin name	Order	Weight (kg)	Activity pattern	Social org.	Nutrition	Habitat	Distribution	IUCN Status
Rock Hyrax (PC)	*Procavia capensis*	Hyracoidea	1.8 - 5.4	diurnal	groups of 50 - 80 individuals	grasses, forbs and shrubs	rocky outcrops, mountains, cliffs and scree slopes	sub-Saharan Africa, with the exception of the Congo basin and Madagascar	LC
Klipspringer (OO)	*Oreotragus oreotragus*	Artiodactyla	8 – 18	diurnal	monogamous	browser; herbs and low foliage	rocky and mountainous terrain, occurring up to elevations of 4000 m	north-east to southern Africa, with a few isolated populations in central Africa.	LC
Cape Grysbok (RM)	*Raphicerus melanotis*	Artiodactyla	10	nocturnal	solitary	browser	fynbos, thickets and shrublands with dense cover	endemic to South Africa, coastal regions of the Western Cape and Eastern Cape provinces	LC
Grey Duiker (SG)	*Sylvicapra grimmia*	Artiodactyla	15 - 18	crepuscular	solitary	broad-leaved forbs, trees and bushes	savanna woodland, but also open country and alpine zone in some mountainous areas	sub-Saharan Africa, excluding the rain forests of Central Africa	LC
Porcupine (HA)	*Hystrix africaeaustralis*	Rodentia	6 – 16	nocturnal	monogamous	leaves, twigs and green plants	rocky outcrops and hills	sub-Saharan Africa, excluding the south-western deserts of the continent	LC
Smith's Red Rock Hare (PR)	*Pronolagus rupestris*	Rodentia	2	nocturnal	solitary	sprouting grasses, herbs, shoots of shrubs	rocky slopes and the tops of rocky outcrops of mountains and hills, where grass or scrub vegetation occurs	South Africa , Kenya, Malawi, Tanzania, and Zambia.	LC

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Hiermit versichere ich, dass ich die vorliegende Masterarbeit erstmalig einreiche, selbstständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.

Marlen Fröhlich

Berlin, den 15.06.2011