Ecology and population status and the impact of trophy hunting of the leopard *Panthera pardus* (LINNAEUS, 1758) in the Luambe National Park and surrounding Game Management Areas in Zambia

By

Rena-Rebecca Ray

Dissertation for the degree of Doctor of Sciene (Dr. rer. nat.) in Zoology of the
Rheinische Friedrich-Wilhelms-Universität, Bonn

Bonn, August 2011

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zur
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Abstract

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Rena-Rebecca Ray

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Academic dissertation for the Degree of Doctor of Science (Dr. rer. nat.) in Zoology at the
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In this study that was carried out in Zambia, population size and density, diet, activity pattern and habitat use of leopards (*Panthera pardus*) were studied in Luambe National Park (LNP) and a bordering Game Management Area (GMA-A) where trophy hunting takes place. It was further aimed to find out if an impact of trophy hunting exists in this region.

By camera trap pictures individual leopards were identified. Capture and recapture models were used to analyze the leopard population abundance and the density in both the study sites. Two female and three male leopards were radio tracked to determine their activity pattern and habitat use. 416 fecal samples of leopards collected inside LNP were analyzed to investigate prey spectrum of leopards and biomass consumed by leopards.

Offtake quotas of leopards from 2004 to 2010 were analyzed in order to get an insight of the hunting pressure on leopards.

Population estimates resulted in 12 individuals for LNP 2008 and 10 for GMA-A. The selected part inside the GMA-A which is smaller in area, reflected a population density estimate of 4.79 ± 1.16 per 100 km², higher than that recorded in the National Park at 3.36 ± 0.64.

This result could be influenced by one or two factors. The area in the GMA that was selected for the study is considered to be congested due to surrounding environmental and habitat pressures. Furthermore, the higher density within this relative small sized area could also be due to a transient leopard population, and the impact of hunting may cause higher intra-specific competition and therefore also more often infantizid than within the LNP.

Home range sizes resulted in 28-56 km² (MCP-95%) / 33-81 km² (Kernel) for males and 3-42 km² (MCP-95%) /3-17 km² (Kernel) in females. Analyses of activity pattern showed that all observed leopards moved significantly more during night than day times, males were moving much longer distances than females, movements of females during night times were less than movements of males. In terms of habitat use most of the observed leopards favored dense habitat types. However, females showed a higher preference for dense vegetation like Combretum-Terminalia-woodland, dense Mopane forests and thickets whereas males implied also a preference for open vegetation like grassland. Home ranges, activity pattern and habitat preferences are more likely dependant on prey choice, but also on concealment and safety possibilities especially in respect of females.

The prey spectrum included in total 18 different species. Ungulates made up the main part of the biomass consumed (LNP: 90.67%; GMA-A: 88.12%). Leopards showed differences in prey choice between LNP and GMA-A. While in LNP it preyed on species of >15-30 kg (e.g impala, bushbuck) but also on heavier species suach as puku, it preferred in GMA-A species' of >1-15 kg (e.g. Sharpe Grysbok, primates, young warthogs). This implies that the leopard is in competition with human hunters in the GMA because middle sized antelopes are trophy hunted in a higher quantity than small sized antelopes in the GMA.

Analyzes of offtake quotas constituted that 43% of the country wide hunting quotas for leopards are covered by hunting blocks located in the Luangwa Valley, and 43% of the "Valley-wide" quotas is brought out from the four GMA's surround the LNP. Further, GMA-A showed the highest hunting intensity among the four hunting areas around LNP. The findings of this study showed that an impact of hunting on the leopard exists and that it is exposed to a high hunting pressure in this region.

To take precedence against overexploitation effective conservation measures have to be adopted. In this context the quota of leopards needs to be reduced to 2 individuals per 1000 km² to let the population recover.

Key words: Felidae, leopard, *Panthera pardus*, population estimate, home range, habitat use, activity pattern, diet, impact of trophy hunting, Luangwa Valley, Zambia, Africa.

Zusammenfassung

Ökologie und Populationsstatus des Leoparden *Panthera pardus* (LINNAEUS, 1758) sowie Einfluss der Trophäenjagd im Luambe National Park und in umgebenden Jagdgebieten

by
Rena-Rebecca Ray

(August, 2011)

Dissertation zur Erlangung des Doktorgrades (Dr. rer. nat.) in Zoologie an der Mathematisch-Naturwissenschaftlichen Fakultät der Rheinischen Friedrich-Wilhelms-Universität Bonn

Im Rahmen dieser Doktorarbeit, die im Luambe National Park (LNP) und einem angrenzenden Jagdgebiet (GMA-A) in Sambia stattfand, wurde die Größe der Population und Dichte sowie der Streifgebiete von Leoparden erfasst. Im Weiteren wurden das Aktivitätsbudget, Habitatpräferenzen und Beutespektrum untersucht. Ein Ziel war unter anderem festzustellen, ob in dieser Region ein Einfluss der Jagd auf den Leoparden besteht.

Anhand von Fotofallen und der Verwendung von Fang- und Wiederfang Modellen, der Besenderung und telemetrischen Verfolgung von zwei weiblichen und drei männlichen Leoparden sowie der Analyse von 416 Kotproben, wurden diese Themen bearbeitet. Zudem wurden die Abschussquoten der Jahre 2004 bis 2010 durchgearbeitet, recherchiert und entsprechende Rückschlüsse daraus gezogen.

Die Schätzung der Populationsgröße ergab 12 Leoparden in LNP und 10 in GMA-A, sowie eine Dichte von 3.36 ± 0.64 pro 100 km² in LNP und eine höhere Dichte von 4.79 ± 1.16 in GMA-A obwohl der ausgewählte Bereich des Jagdgebietes kleiner war als der Bereich des National Parks. Dies könnte allerdings darin begründet sein, dass mit der Entnahme von Männchen durch die Jagd Territorien frei werden, um die mehrere neu hinzu gewanderte Männchen konkurrieren. Dadurch würde sich ein erhöhter innerartlicher Konkurrenzdruck ergeben, der zudem in unnatürlich vermehrten Infantizid resultieren könnte. Zudem wäre es möglich, dass der ausgewählte Raum, aufgrund der Habitatverhältnisse eine Art Ballungszentrum für Leoparden und andere Arten sein könnte.

Die Streifgebietsgrößen variierten zwischen 28-56 km² (MCP-95%) / 33-81 km² (Kernel) für Männchen und zwischen 3-42 km² (MCP-95%) /3-17 km² (Kernel) für Weibchen. Das

Aktivitätsbudget wies im Allgemeinen für alle Leoparden eine höhere Aktivität während der Nacht als am Tag auf. Allerding bewegten sich Weibchen während der Nachtstunden weniger als Männchen, welche zudem größere Distanzen zurücklegten als Weibchen.

Alle Leoparden bevorzugten prinzipiell dichteres als offenes Habitat. Die Weibchen zeigten allerdings eine größere Präferenz für dichte Vegetation wie z.B. Combretum-Terminalia-Wald, dichter Mopanewald sowie Dickicht, als Männchen. Diese hingegen wiesen ebenfalls eine erhöhte Nutzung für offene Vegetation wie Grasland auf. Die Lage der Streifgebiete, Aktivitätsbudget und Habitatwahl stehen u.a. im Zusammenhang mit der Beutewahl, zeigen jedoch im Falle der Weibchen auch erhöhte Ansprüche an diverse Schutzmöglichkeiten.

Das Beutespektrum beinhaltete insgesamt 18 verschiedene Taxa. Obwohl in beiden Gebieten Paarhufer den größten Teil der Biomasse darstellten (LNP: 90.67%; GMA-A: 88.12%), zeigten sich Unterschiede bezüglich der Beutewahl zwischen LNP und GMA-A. Im LNP wurden hauptsächlich Arten mit Körpergewichten von >15-30 kg (z.B. Impala und Bushbock), aber auch schwerere Antilopen wie Puku gefressen, während im GMA-A zum größten Teil Arten von >1-15 kg (z.B. Sharpe Grysbock, Primaten, junge Warzenschweine) konsumiert wurden. Aufgrund der Tatsache, dass im Jagdgebiet mehr mittelgroße als kleine Antilopenarten geschossen werden, lassen die Ergebnisse auf eine Jagdkonkurrenz schließen, in die der Leopard mit Trophäenjägern steht. Um diesen Konkurrenzdruck auszuweichen, schlägt der Leopard im Jagdgebiet somit kleinere Beutetiere als im LNP.

Die Analyse der Jagdquoten ergab, dass 43% der landesweiten Quoten für Leoparden von Jagdgebieten innerhalb des Luangwa Tals bestritten werden. 43% von diesen „talweiten" Quoten werden alleine von den vier Jagdgebieten um den LNP hervorgebracht. Die Ergebnisse dieser Arbeit zeigen, dass definitiv ein starker Einfluss der Jagd auf den Leoparden besteht und dieser einem hohen Jagddruck ausgesetzt ist.

Um eine Übernutzung der Quoten zu vermeiden müssen effektive Schutzmaßnahmen ergriffen werden. Der erste Schritt in diese Richtung wäre hier die Senkung der Abschussquoten auf 2 Leoparden pro 1000 km².

Schlagwörter: Leopard, *Panthera pardus*, Habitatnutzung, Aktivitätsbudget, Streifgebiete, Trophäenjagd, Luangwa Tal, Sambia, Afrika

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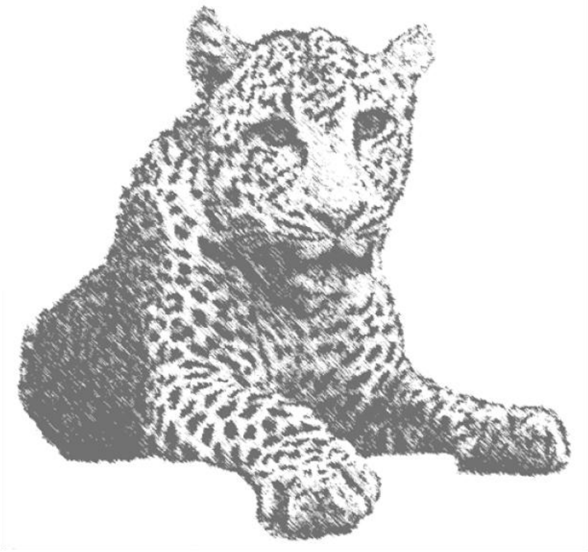
DMT	Distance moved between traps
GMA	Game Management Area
GMA-A	Game Mangement Area Chanjuzi
GMA-B	Game Mangement Area Mywana
GMA-C	Game Mangement Area Nyampala
GMA-D	Game Mangement Area Luawata
HB	Hunting block
HMMDM (½ MMDM)	Half mean maximum distance moved
HRr	Radius of averaged home ranges
Juv.	juvenile
KDE	Kernel (Polygon)
LNP	Lumabe National Park
MCP	Multi Convex Polygon
MMDM	Mean maximum distance moved
RAI	Relative abundance indices
ZamBio	Zambian Biodiversity Project
ZAWA	Zambia Wildlife Authority
ZFMK	Zoologisches Forschungsmuseum A. Koenig (Zoological Research Museum A. Koenig)



Das Beste steht nicht immer in Büchern, sondern in der Natur, nur haben die Menschen oft nicht die Augen es zu sehen

(Adalbert Stifter)

……After the Ethiopian had daubed spots on the leopard, he told the leopard,
"You can lie out on the bare ground and look like a heap of pebbles.
You can lie out on a leafy branch and look like sunshine sifting through the leaves;
And you can lie right across the centre of path and look like nothing in particular."………
(R. Kipling, 1902)

1 General Introduction

1.1 The conservation status of leopards in Zambia and concern of this study

Most cat species are solitary, secretive, and in many cases nocturnal. Except for cheetahs and the social lions with their preferences for open habitats, the largest parts of the known cat species inhabit inaccessible and inhospitable landscapes. These circumstances make it very difficult for a researcher to observe and study these animals.

In their computer habitat model that included numerous African countries, Martin & De Meulenaer (1988) estimated a potential population of over 700,000 in Africa and of 46.000 leopards in Zambia. It was based on habitat availability and human population densities for which they used a rate of 9.4 humans/ km² in Zambia. This study has been critically debated among specialists as presenting a high overestimate and has thus been rejected (Martin & De Meulenaer 1989, Norton 1990, Nowel & Jackson 1996). Moreover, today, now almost 20 years later, the human population of Zambia has increased (likely doubled), followed by habitat fragmentation and cultivation of former wildland by human settlements (Purchase & Mateke 2008).

Purchase et al. (2007) reviewed the status, distribution and levels of human-carnivore conflicts in the network of protected areas in Zambia and stated that little is known about leopards in this respect. Unprotected areas were not considered in that study.

Although summary of available knowledge about leopards in Zambia (Purchase & Mateke 2008) showed that most data are either anecdotal or based on subjective observations, it also led to the recognition that leopards have been disappeared from two protected areas in this country. Reports of infrequent sightings in several Game Management Areas (GMA's) are further cause for concern (ZAWA information, Purchase & Mateke 2008).

No scientific research on leopards has been carried out or field surveys on this cat have been conducted in Zambia (ZAWA information, Purchase & Mateke 2008), except for studies which included the leopard species as for example Martin & De Meulenaer (1988) or Mitchell (1965) who determined the predation on large mammals in the Kafue National Park in Western Zambia, or Ansell (1978) who described the mammals of Zambia.

My study deals with the African leopard (*Panthera pardus pardus*) in Zambia, the investigation of its population status in an undisturbed and in a disturbed region in the Luangwa Valley, and the possible impact of hunting on this species. While the alarming situation of the African lion (*Panthera leo*) throughout its range (Bauer 2008, Henschel et al. 2010, IUCN 2008) has already become recognized in Zambia, the leopard appeared somewhat neglected at the time I began the research. This is due to the belief that leopards are the most abundant and adaptable among the large cats, and not sensitive to habitat changes. The impact of trophy hunting on leopard populations is unclear, but excessive hunting of lions, for example, has often been discussed as influencing their demography and population levels, and conservation requirements have gained public awareness in Zambia (ZAWA-Off-Take Quota 2007).

Ansell 1978 mentioned in his “Mammals of Zambia” that the leopard in the Luangwa Valley “*can only be described as abundant*”. Although this source is more than thirty years old, this, and interviews with hunting operators and photographic tourist guides led me to the conclusion that the Luangwa Valley is a potential core area for leopards in Zambia, especially the North- and South-Luangwa National Park. However, it is possible that in areas outside the undisturbed regions, encompassing mainly GMA’s, various anthropogenic caused circumstances influence leopard occurrence. This is because unlike National Parks that are fully protected areas, GMA’s are partly protected regions with agricultural areas, villages and trophy hunting activities.

My study is the first research of this kind about leopards in Zambia. It was conducted in cooperation with the Zambia Wildlife Authority (ZAWA). The Luambe National Park (LNP) in the Luangwa Valley was a convenient place for this kind of study for several reasons: a) I confirmed by own observations that leopards are abundant in the region, b) it is surrounded by GMA’s c) it encompasses a relative small size of 354 km² which made it possible at least for one person to survey, and d) the professional hunters in the surrounding GMA’s were open to cooperation with my research, which allowed me to select an additional study area

of about 137 km² in the bordering GMA for comparison with the LNP. Information gleaned from interviews with professional hunters and park managers concurs with the general opinion that leopards are found in “very high abundance” in the study area. To verify these assumptions, it is necessary to figure out if the LNP, as an apparently undisturbed area, shows signs of being influenced by utilization of its surrounding environment.

1.2 The primary objectives of this study

The LNP as well as the selected part of the bordering GMA provided an appropriate study area (see Chapter 1.1). Data acquisition took place from 2006 to 2008, primarily during the dry seasons (May to October) with a cummulative stay of 17 months. I attempted to address the following topics:

1) The leopard population size in both study sites
   - What is the population size and density of leopards inside the LNP and in the bordering GMA?

2) Home range, activity pattern and habitat preference
   - What are the leopard home-range sizes in the region?
   - How are the overlaps of the home ranges with LNP and the hunting area?
   - What is the activity pattern of the different leopards and are there significant differences between them?
   - What are the habitat preferences and are there any differences between the home ranges in habitat availability and use?

3) Prey composition
   - What is the leopard’s prey spectrum in the region?
   - Are there differences in choice of prey between the two area types?
   - Is there a relation between prey choice and trophy-hunting of the potential prey by humans within the GMA?

4) <u>Possible impact of trophy hunting on the leopard populations</u>

- Are there any signs which indicate an impact of trophy hunting on the leopard populations in this region?
- Can the LNP be considered as a fully protected area that is not influenced by the GMA's?

<u>The major methods that were used to answer these questions were (numbers correspond to topics):</u>

1. Systematic placing of digital-camera traps in the study areas, which provided photographic capture-and-recapture data along with the identification of individual leopards.

2. Compilation of telemetrical data to determine home ranges, activity patterns and habitat preferences. For this purpose it was first necessary to locate trees that were preferred by leopards in order to place baits and trap the animals. Due to the size and strength of this large cat, a steel-live-trap was built especially for this purpose. Trapped leopards were tranquilized, radio collared and then radio tracked.

3. Analysis of leopards fecal samples collected at the different study areas revealed the prey composition.

4. Analysis of all the results in relation to the offtake quotas (provided by the Zambia Wildlife Authority) provided insight into possible impacts of trophy hunting in the study area.

Claudia Stommel did her master thesis within my PhD-Project (Leopard-Monitoring Project) and was supervised by me. Therefore, some data are taken from her master thesis (STOMMEL 2009, unpublished).

1.3 The Leopard - background

Although different studies regarding the leopard, have taken place in the past, one of the most intensive study about leopards was conducted by Bailey in the 1970s, in the Krueger National Park in South Africa. This study was first published in 1993 and republished in 2005.

1.3.1 Description and taxonomy

The leopard is the largest spotted cat in Africa and Asia. Its coat is marked with rosettes that cover most of its body including the back of the neck, shoulders, flanks, back, hips and the upper parts of the limbs. Black spots of varying size and density cover the lower limbs, throat, belly and face (Guggisberg 1975, Smithers 1983, Turnbull-Kemp 1967). The spots on the throat often coalesce to a collar.

Due to its spot pattern this large cat is difficult to detect, especially when it remains motionless. The fur and coat pattern varies according to its geographical distribution. The background color of the fur is also highly variable, and it is presumed that animals inhabiting humid forests are of darker than those in arid areas (Pockock 1932, Divyabhanusinh 1993).

Size and weight of leopards also vary geographically.

Within the family Felidae the leopard belongs to the “larger cats” (Pantherinae), which are divided in the genera *Neofelis, Unica* and *Panthera.* The leopard is the smallest of the cat species in the genus *Panthera*. Further members are the tiger (*Panthera tigris*), lion (*Panthera leo*) and jaguar (*Panthera onca*). The snow leopard, which can sometimes be as classified as the genus *Panthera* (depending on the taxonomy) has been placed in its own genus *Uncia* (Wilson & Reeder 2005).

In an older, classic taxonomic classification (Pocock 1930, 1932), 27 subspecies were described primarily, but based on morphological and genetic analyses, the species *Panthera pardus* was divided into nine subspecies (Mithapala et. al. 1996, Uphyrkina et al. 2001). According to this classification, all continental African subspecies were subsumed under "*Panthera pardus pardus*".

The nine current subspecies and their geographical distribution (IUCN 2008):

Panthera pardus pardus (Linnaeus, 1758): Africa
Panthera pardus nimr (Hemprich & Ehrenberg, 1833): Arabia
Panthera pardus saxicolor (Pocock, 1927): Central Asia
Panthera pardus melas (Cuvier, 1809): Java
Panthera pardus kotiya (Deraniyagala, 1956): Sri Lanka
Panthera pardus fusca (Meyer, 1794): Indian Sub-Continent
Panthera pardus delacourii (Pocock, 1930): Southeast Asia into southern China
Panthera pardus japonensis (Gray, 1862): Northern China
Panthera pardus orientalis (Schlegel, 1857): Russian Far East, Korean peninsula and northeastern China

Due to very small sample sizes, the recognition of *Panthera pardus melas* and *Panthera pardus nimr* is considered tentative (IUCN-Red List of Threatened Species 2008).

1.3.2 Distribution

The leopard has the greatest geographic distribution of all felid species. It occurs from the Middle East to the Far East, northwards to Siberia and south to Sri Lanka and Malaysia as well as the southern parts of Africa. Leopards inhabit tropical rainforests, the mountainous regions and some desert regions. In historical times leopards were distributed across eastern and southern Asia as well as east and west of the Sahara on the African continent (SMITHERS 1983, STUART 1981, HARRISON & BATES 1991, HEPTNER & SLUDKIJ 1980, MYERS 1976, GASPERETTI 1985, CORBET & HILL 1992). A comparison of the historical distribution range with the present one indicates that the species has suffered large parts of its original distribution (Figure 1.1)

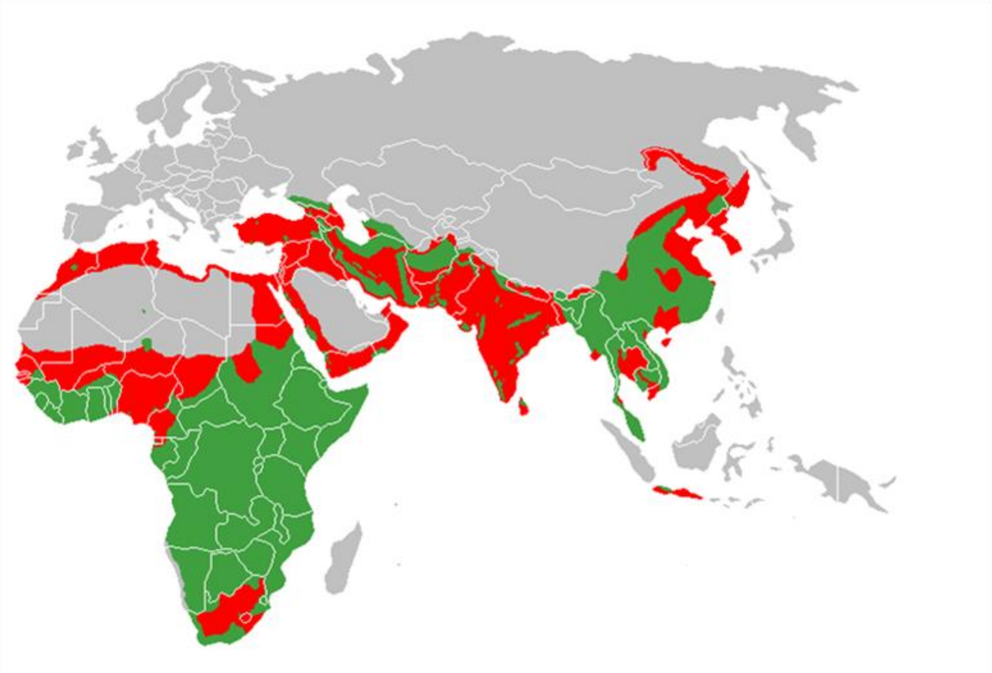


Figure 1.1: Current and historical distribution, (green and red respectively) of leopard (*Panthera pardus*). Based on data from IUCN Red List of threatened species 2010 (current) and HEPTNER & SLUDSKIJ 1980 (historical), modified from original map at: http://www.ofcats.com/2007/05/leopard-distribution.html

It has been estimated that leopards had disappeared from at least 36.7% of their historical range in Africa (RAY et al. 2005). Apparently, they suffered the largest range loss in the Sahel belt, Nigeria and South Africa. Due to the lack of confirmed records in Zanzibar since 1996, it is believed that leopards are probably extinct in this area (HUNTER et al. in press). Among the most serious threats to leopards are habitat fragmentation and intense persecution. This becomes obvious especially in cases of livestock loss and competition for prey with human hunters. Sharing the same habitat with humans in a restricted space can also lead to attacks on humans.

In India leopards are feared for their attacks on people (Singh 2005, Singh et al. 2008). In Tanzania, an average of 4.7 people were killed and 7 injured annually by leopards between 1993-1999 (Games & Severre 2002). In Uganda, 114 leopard attacks on people are reported between 1923-1994, resulting in 37 death cases (Treves & Naughton-Treves 1999, Loverigde et al. 2010). Reports rarely distinguish between unprovoked attacks and those that happen when the cats are hunted or harassed.

In Indo-Malaysia the major threat to leopards, apart from habitat loss, is the poaching for illegal trade (Nowell & Jackson 1996). In West-Asia leopards are mainly restricted to protected areas, which are often too small to facilitate sustainable populations (Breitenmoser et al. 2006, 2007). It is believed that leopards are still numerous in marginal habitats in sub-Saharan Africa, where other large felids have disappeared. The North-African leopards, in contrast, are on the verge of extinction.

Nevertheless, leopards are still known to be the most widely distributed big cats in the world and are considered to live in almost every type of habitat. This is true at least for the African leopard (*Panthera pardus pardus*), which is considered the most abundant and widespread large felid in Africa at the present. Due to their ability to adapt to many habitats and feed on prey like arthropods (Fey 1964) and small reptiles (Bailey 2005), they gained the reputation of being the most adaptable large felid, which can therefore cope with habitat changes relative easily. This, among other reasons, led to classifying leopards as being of “least concern” in the IUCN Red List between 1996 and 2007. Leopard hunting has been practiced for centuries in Asia and Africa. However, legal hunting of wild large cats in Asia for trophies has been abolished due to their population decline. Nowadays, the legal international traffic concerning the leopard is allowed under the CITES Appendix I quota system by 12 African countries at the moment (2011) (Cites 2011). It is limited largely to exports of skins and hunting trophies (IUCN 2011).

The Asiatic lion (*Panthera leo ssp. persica*) for example survives in an isolated single population in Gir Forest in India, showing reduced genetic variation due to its small population size (O’Brien et al. 1987). The tiger (*Panthera tigris*) has lost 91% of its historic range (Sanderson et al. 2006) and in the last ten years, its range shrunk by 41% (Dinerstein et al. 2007).

Until the 1980s, the leopard was one of the most threatened species listed by IUCN. This changed with the study of Martin & De Meulenar (1988), who suggested a population of leopards of about 700,000 in Africa, which was criticized and largely discredited from the scientific community (Martin & De Meulenar 1989). Members of the IUCN Cat specialist group mentioned their doubts of the estimates from this habitat model (Martin & De Meulenar 1989). Nevertheless, the result was that CITES increased the international hunting quotas for the African leopard, despite the lack of reliable continent-wide estimates of its population size. Since 2008 the African leopard is regarded as “Near threatened” (Henschel et al. 2008), while two of its sub species (*P.p. nimr* and *P.p. melas*) are “Critically endangered” and another two (*P.p. kotiya* and *P.p. saxicolor*) are “Endangered” (IUCN 2008). The leopard’s general trend is of population decline, mainly due to progressing habitat loss and fragmentation aggravated by hunting for trade and pest control (IUCN 2010). These threats may soon significant enough to justify listing the species as “Vulnerable” under Criterion A (IUCN 2010), a status it held in 1990 for the last time.

1.3.3 Life history

Due to their elusiveness, leopards are difficult to locate. They are solitary and usually avoid each other (Bailey 2005), although home ranges of same sexes very often overlap. They are perfect climbers and stalk hunters, capable of carrying prey twice their weight into trees to make it less accessible to scavengers. Leopards appear to be primarily nocturnal. Some reports suggest that leopards are less nocturnal and more territorial in areas lacking other large predators such as tigers and lions, as, for example, in Sri Lanka (Eisenberg 1972, Grassmann 1999, Karanth & Sunquist 2000).

1.3.4 Reproduction

Leopards are non seasonal breeders and cubs are born any time of the year after a gestation period of 100 days (Mills & Hes 1997). Females become sexually mature at 2-3 years, males likely a bit later, at 2-4 years (Bailey 2005, Nowell & Jackson 1996). Mating usually takes place over two to three days (Mills & Hes 1997). Females are polyestrous, and if mating was not successful, they get into oestrus again every 20 to 50 days (Bailey 2005; Bothma & Walker 1999).

It appears that mating success is not always guaranteed. In Kruger National Park, Bailey (2005) observed 13 alleged courtship associations between males and females, of which only two (15%) resulted in the birth of cubs. This is comparable with the reproduction success of lions, whose mating contacts resulted in only 20% conception (Schaller 1972).

1.3.5 Trophy hunting

The use and trade of diverse wildlife species and products is a billion Euro business worldwide, comprising billions of animal species annually (Große et al. 2001). A big part of this trade is of important regional economic significance and is subjected to national conservation and hunting and fishing conditions. On a national level, the utilization of wildlife species is regulated by laws of species conservation, hunting and fishing. In an international context, most countries on a convention that is supposed to protect 33.000 wildlife species against uncontrolled trade and overexploitation, as for example CITES, which regulates the international trade of endangered species.

The excessive worldwide trade in leopard fur (*Panthera pardus*) in the 1960s and 1970s led to an alarming situation for this species. Therefore, in 1975, the leopard was included in Appendix 1 of CITES that aimed to prohibit international trade in skins and other products of all subspecies.

Nevertheless, the leopard remains one of the most demanded trophies in Africa. Although the facts mentioned in Chapter 1.3.2 are considered the primary threats, the impact of trophy hunting on the leopard populations is unclear (IUCN 2010) and should not be underestimated. Selective hunting of carnivores and ungulates can have demographic side effects (e.g. Milner-Gulland et al. 2003, Milner et al. 2007).

The present research and the resulting knowledge are not meant to be used against trophy hunting activities in general. Trophy hunting safaris are an important economical factor in Zambia and throughout Africa. Apart from that, many inhabitants of the different local villages are employed by and earn good salaries at the hunting camps, and meat from animals shot during hunting safaris is given to the villages. There are very few alternatives for well paid jobs in this area and meat is not easily available within the villages, apart from poaching. Furthermore, a certain percentage of the revenues from trophy hunting are required to be given to the village communities (CRBs) (see Chapter 1.4.3).

The conservation of the leopard and big predators in general should be a common project of trophy hunters and scientists. The more we know the better we can develop an efficient conservation management plan emphasizing the commonalities and bridge differences.

Although the leopard still appears to be widely distributed, caution is necessary in order to avoid reaching the same alarming situation of its family members, the tiger and lion. It will also serve the interest of hunting communities if trophy animals of high economic significance do not become endangered.

1.4. The study area

1.4.1 Zambia and its Geography

Zambia is a landlocked country between the Tropic of Capricorn and the Equator that encompassing an area of 752,614 km² (more than twice the size of Germany). It lies in southern-central Africa between latitudes 8° and 18° S, and longitudes 22° and 34° E, and is situated in the tropics. Neighboring countries are Angola in the West, the Republic of Congo in the North, Tanzania to the North-East, Malawi in the East, Mozambique in the South-East, and Zimbabwe, Botswana and Namibia in the South.

Two major river basins shape the country, the Zambezi basin in the south that covers about three quarters of the country, and the Congo basin in the north that encompasses one-quarter of the country. In the center of these regions lakes and swamps are surrounded by floodplains that have important ecological functions (Schulz 1983). Zambia's largest rivers are the Kafue River and the Luangwa River that are tributaries of the Zambezi. The Luangwa runs from its source in the Mafinga Hills in northern Zambia to its confluence with the Zambezi near the border with Mozambique (ASTLE 1999).

Zambia experiences three seasons, a cool dry season from May to August, a hot dry season from September to October, and a warm rainy season from November to April. Annual rainfalls lie between 800 and 1500 mm. July and October are months with average temperatures of 17.2 °C and 30 °C, respectively. These are the coldest and warmest months across the country (KÜPPER 2001). Due to the modifying influence of the altitude, the Zambian weather is more sub-tropical than tropic and humid during the dry seasons, which won the country the name of “the air conditioned state” (KÜPPER 2001).

In the east, at the border with Malawi, the escarpment region is 1800-2150 m above sea level, and tropical-cool average temperatures are below 17.5°C. Average monthly temperatures in the high plateau at 1000-1500 m above sea level are between 17.5°C-22.5°C. In the valley regions, at 300-600 m above sea level, temperatures are higher and reach average values of 25°C (SCHULZ 1983) (Figure 1.2). The hottest regions of Zambia are Sesheke and the Luangwa Valley, where the temperatures reach 45°C in October. Seasonal differences in temperatures and the duration of the rainy season decrease from north-east to south-west. Thus, the rainy season in the North of Zambia lasts about 190 days and in the south only 120 days.

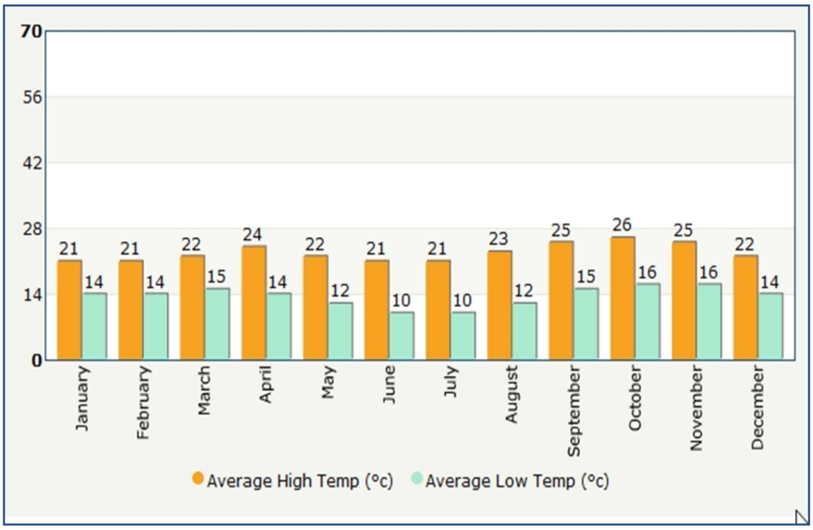


Figure 1.2: Average temperature for Mfuwe (C°), (Luangwa Valley) source: www.worldweatheronline. com

In general there are 8% of Zambia conservation areas in National Parks, together; National Parks and so called Game Management Areas comprise approximately 30% of Zambia's area (HUPE & VACHAL 2006).

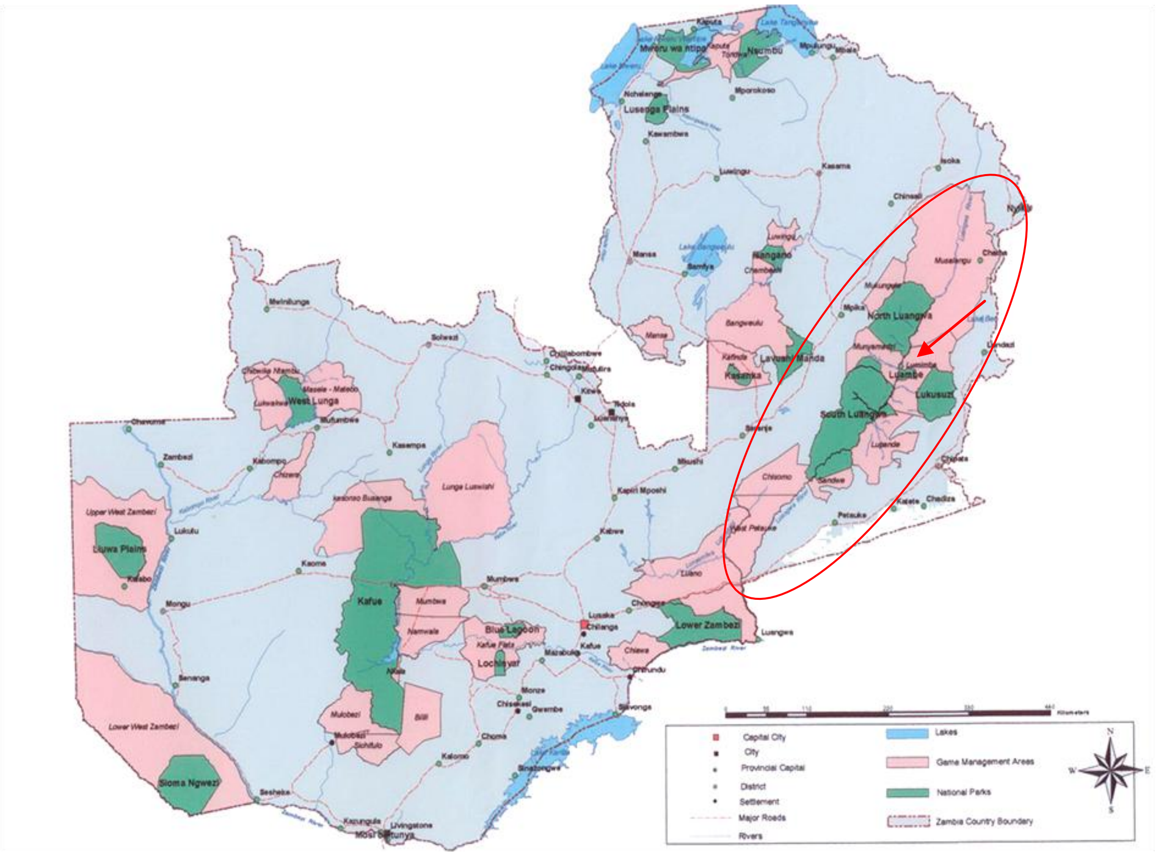


Figure 1.3: Map of Zambia with an overview of National Parks and Game Management Areas, red: Luangwa Valley, red arrow: Luambe National Park

1.4.2 The Luangwa Valley

The Luangwa Valley, located in the east of Zambia, (Figure 1.3), is 800 km long and 100 km wide (DRESCHER 1998). It is an extension of the Great Rift Valley that runs from the Dead Sea in Israel down along East-Africa (DRESCHER 1998). The two branches of the Great Rift Valley comprise Lake Malawi in the east and the Luangwa Valley (Figure 1.4) in the west.

The Valley houses the naturally flowing Luangwa River and its numerous tributaries that are formed and filled during the rainy season and dry out during the dry seasons.

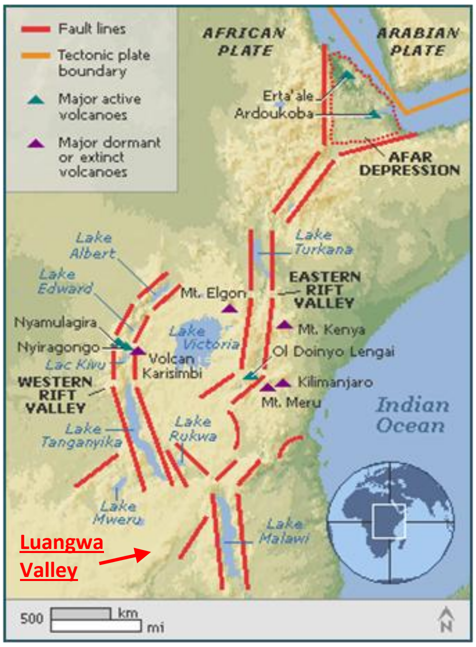


Figure 1.4: The Rift Valley with the Luangwa Valley in the west and the Lake Malawi in the east. Source:http://people.eku.edu/davisb/Geo100/RiftValley.gif

The Luangwa Valley was famous for the high abundance of game in historical times but also notorious for excessive poaching in the last decades, which caused depletion of the once richness of wildlife.

This region is home to most of the typical southern Africa savannah species, including several threatened species such as Black Rhinoceros (*Diceros bicornis*), the African wild dog (*Lycaon pictus*), and the African elephant (*Loxodonta africana*).

Certain ungulate species such as the Thornicraft's giraffe (*Giraffa camelopardalis thornicrofti*) and the Cookson's wildebeest (*Connochaetus taurinus cooksoni*) are endemic to the Luangwa Valley (Wilson & Reeder 2005). Dominant antelope species are the puku (*Kobus vardoni*) and the impala (*Aepyceros melampus*) (see Figure 1.5).

Four National Parks are located in this area: the South-Luangwa, the North-Luangwa, Luambe, and Lukusuzi, and these are separated by nine Game Management Areas. In the ZAWA-annual reports (2004-2008), the South Luangwa NP and the North Luangwa NP are classified as prime National Parks whereas the Luambe National Park is considered secondary (see Table 1.1) National Park and the Lukuzui as under stocked (see Table 1.1).

1.4.3 The Game Management Areas

The Game Management Areas (GMA's) in the Luangwa Valley cover a much larger area than that of the National Parks. In GMA's, the use of natural resources by local people is allowed: agricultural areas and villages occur in GMA's, and stock of trees can be used as timber and firewood. Sport and trophy hunting activities are allowed and are officially limited by hunting quota. All these activities are regulated by ZAWA. GMA's support also a wide diversity of flora and fauna and are intended to provide buffers and wildlife corridors between and around the National Parks.

Community Resource Boards (CRBs) and Village Action Groups (VAGs), with the chiefs as patrons, constitute a link between ZAWA and the communities within the GMA's. They are expected to navigate the management of natural resources in the GMA's and co-negotiate agreements for hunting safari operators. As part of this arrangement, 45% of all revenue from hunting safaris are paid to the CRB, 5% go the chief, and 50% remains for ZAWA. The CRBs are authorized to use revenues at their discretion, e.g. for building schools or hospitals. Although this concept is good in its intentions, disadvantages and shortcomings, as mismanagement in many cases (Musumali et al. 2007), have been recognized.

Table 1.1: Categories of Game Management Areas (ZAWA 2004-2009)

Prime:	Areas with highly abundant populations of diverse wildlife species, especially highly valued trophy species such as leopard, lion, roan and sable. These areas can accommodate several classical safaris and mini safaris per hunting season
Secondary:	Areas with fairly abundant populations of diverse wildlife species that can generally sustain 3-4 classical safaris and a minimum of five mini safaris per hunting season
Specialized:	Areas where species such as lechwe, sitatunga and tsessebe are the most abundant species. Their distribution is generally restricted to such areas
Under stocked:	Areas with occurrence of different species but of sparse populations
Depleted:	Areas with fragmented species populations, with much of the wildlife generally demised. The recommendation is that Safari hunting and any further hunting activities should not take place in these areas

Four Game Management Areas are described below in more detail (Table 1.2) because they surround the main study area (LNP) (Chapter 1.4.4).

Table 1.2: Characteristics of LNP and the four GMA's, surrounding it

Study site	*Type*	*Land-use, status of hunting*
LNP	Luambe National Park	Prohibited, qualified as secondary
A	Game-Management Area (GMA-Chanjuzi), (actually divided into two hunting blocks, bordering the LNP in the north	Commercial and trophy hunting permitted; land use by villagers; prime area at the border with LNP, 2nd hunting block in the north; secondary area
B	Game-Management Area (GMA-Mwanya), bordering LNP in the south	Commercial and trophy hunting permitted, land use by villagers; prime area
C	Game-Management Area (GMA-Nyampala), south-west of LNP, separated from LNP via the Luangwa River	Commercial and trophy hunting permitted, land use by villagers, prime area
D	Game-Management Area (GMA-Luawata), north-west of LNP, separated from it by the Luangwa River	Commercial and trophy hunting permitted, land use by villagers; prime area

1.4.4 The Luambe National Park and the bordering GMA-Chanjuzi

The Luambe National Park (LNP) is the smallest park inside the Luangwa Valley and is situated at the east side of the Luangwa River. Among the four GMA's (see Table 1.2) that are surrounding the LNP, the GMA-Chanjuzi (GMA-A) is of main interest in this study. Although officially designated as a National Park since 1972, LNP remained neglected for a long time and excessive poaching took place in this region. Due to its geographical position that is characterized by heavy rainfall, the park is not accessible during the rainy season. The size of the park is unclear: Its size is often cited as being 254 km², but a calculation of the boundaries based on the data provided by the Zambia Wildlife Authority (ZAWA) reports 354 km². As a result of misunderstandings (about the current boundaries) that hark back decades ago, the bordering GMA-Chanjuzi (GMA-A) overlaps with portions of the LNP. It appears that activities such as movement of villagers, fishing, firewood and timber harvesting, as well as trophy hunting take place inside the National Park. But this may not be the case because it is unclear exactly where the current border between the LNP and adjacent GMA runs.

Thus, it caused conflicts between the tourist lodge situated inside the LNP, the chief of the area, and the professional hunters who rented the GMA. For certain parts of the region it is not clear if they belong to the LNP or the GMA:

Although according to maps these areas are actually included in the LNP, villagers use natural resources and trophy hunting activities take place within them. I therefore, refer to these parts of the region as the "controversial area". To deal with this uncertainty regarding the borders of the LNP, I calculated the size of the studied area of the LNP using Geographical Information System (GIS) because certain borders of the LNP were unclear, which resulted in 338 km².

Between 2005 and 2008, the infrastructure of the park was relatively undeveloped and contained very poorly maintained roads (2-3). Parts of the park, especially the eastern side, were hardly accessible. Until the start of the present research project, neither scientific game counts for population estimates nor mammal species inventories existed. As a matter of fact, no other detailed information has been published about this region.

At the beginning of this research project several game species behaved very shyly and timidly and were difficult to observe. Elephants reacted very aggressively towards cars and humans, which resulted in several cases of death among villagers in the bordering Game Management Areas. This behavior of the different game species can be attributed to the previous poaching activities.

The LNP is now considered as a corridor for migrating species between the Luangwa and the escarpment in the back-up area (Hupe & Vachal 2004).

The total size of the bordering Chanjuzi-GMA is about 2,555 km². Human habitation and settlements are prohibited within the boundaries of the LNP. In contrast, several villages are situated approximately 15 km away from LNP and are under dominion of Chief Chitungulu. Various agricultural activities in the area include cultivation of rice and cotton (see Table 1.2). Due to the occurrence of the tsetse fly - the carrier of the sleeping sickness that affects domestic animals - the raising of livestock is not possible. Trophy hunting occurs only during the dry season, and therefore at the same time when this study took place. To avoid the main disturbance of hunting safaris and due to logistical difficulties, I selected an area of 137 km² within the GMA-A that borders directly with the LNP.

During rainy season a large percentage of the area is not accessible, specifically not by automobile. Due to these circumstances the primary portion of the research had to be completed during dry season.

Figure 1.5: Zebra and puku (top left); Cookson’s wildebeest (top right); Thornicroft giraffe (bottom left), impala (bottom right)

1.4.5 Fauna

The following middle-sized and large mammal species were observed inside the Luambe National Park as well as within the selected area of the bordering GMA during the present research project:

Table 1.3: Observed mammal species in the LNP and the GMA-A

Ungulates	Non Ungulates	
Giraffidae	***Proboscidea***	***Carnivores***
Thornicroft's giraffe *(Giraffa camelopardalis thornicrofti)*	African elephant (*Loxodonta africana*)	African lion (*Panthera leo*)
		African leopard *(Panthera pardus)*
		Serval *(Leptailurus serval)*
Bovidae	***Rodents***	African wild cat (*Felis sylvestris)*
Cookson's wildebeest (*Connochaetus taurinus cooksoni*)	Bush squirrel (*Paraxerus cepapi)*	Spotted hyaena (*Crocuta crocuta)*
		Wild dog** *(Lycaon pictus)*
	Mouse (*Mastomys* spec.)	
Buffalo *(Syncerus caffer)*	(*Gerbiliscus* spec.)	Honey badger *(Mellivora capensis)*
Eland (*Taurotragus oryx*)	Rat (*Pellomys* spec.)	Civet *(Civettictis civetta)*
Greater kudu *(Tragelaphus strepsiceros)*	Porcupine (*Hystrix africaeaustralis*)	Genet *(Genetta genetta)*
Waterbuck (*Kobus ellipsiprymnus*)		Slender mongoose (*Herpestes sanguina*)
Roan* (*Hippotragus equinus*)	***Lagomorpha***	Banded mongoose (*Mungos mungo)*
Puku (*Kobus vardoni)*	Scrub hare (*Lepus saxatilis*)	Marsh mongoose (*Atliax paludinosus*)
Impala (*Aepyceros melampus)*		Dwarf mongoose (*Helogale parvula*)
Reedbuck (*Redunca arundinum*)	***Primates***	
Bushbuck (*Tragelaphus scriptus)*	Vervet monkey (*Cercopithecus aethiops*)	
Oribi (*Ourebia ourebi*)		
Sharpe's Grysbok (*Raphicerus sharpei*)	Baboon (*Papio cynocephalus)*	
	Galago (*Otolemur crassicaudatus*)	
Suidae	***Tubulidentata***	
Warthog (*Phacochoerus africanus*)	Aardvaark (*Orycteropus afer*)	
Bushpig *(Potamochoerus larvatus)*		
Equidae	***Macroscelidae***	
Zebra (*Equus quagga crawshayi)*	Elephant shrew *(Petrodromus tetradactylus)*	

* observed only inside the GMA; ** very rarely observed

1.4.7 Vegetation

The *Miombo* constitutes the most common type of vegetation, covering approximately four-fifths of Zambia's area (Ansell 1978). However, the open Mopane forest, with *Colophospermum mopane* as the dominant tree species, is characteristic for the valley regions of the Zambezi and the Luangwa. Dambos occur in extreme flat regions, and temporary flooded depressions are covered by grass (Mäkel 1975).

The vegetation of the LNP consists of forest and bush formations that constitute ca. 82.5% of the park's area. Grassland covers around 17.5% of the park (Anderson 2009). Determination of the following different vegetation types is based on physiognomy and identification of certain characteristic plant species by Anderson 2009.

Table 1.4: Composition of vegetation inside the LNP (after Anderson 2009)

Category	***Cover (%)***
Clay pan / Aquatic Association Grassland	2.63
Combretum-Terminalia woodland	34.19
Thicket	9.38
Mopane scrub woodland	10.58
Mopane woodland	23.36
Riverine Woodland and Thicket	4.99
Grassland	14.84
Water (includes only river parts)	0.03

Because the flora of the studied area of the bordering GMA-A was very similar to that of the LNP, the above listed were also used for the GMA-A.

2 Population estimate of the leopard (*Panthera pardus*) in Luambe National Park and a bordering Game Management Area in the Luangwa Valley of Zambia

This chapter deals with the estimation of population size and density of leopards using capture-recapture models inside the Luambe National Park and a selected area within the Game Management Area Chanjuzi close to the border of the National Park. Questions to be answered are:

- What is the population size and density of leopards in Luambe National Park and the selected area in Game Management Area -A?
- Are there any differences in the population estimates?

2.1 Introduction

The African leopard (*Panthera p. pardus*) has recently been relisted by IUCN from “least concern” to “near threatened” (IUCN 2008). But until now, this species is still considered to be the most abundant large felid in Africa (Hunter et al. in press).

In several countries where leopards are allowed to be hunted for trophies, the status of leopard populations remains unclear, and apart from the computer model based estimates by Martin & De Meulenaer (1988) (Chapter 1.1) no reliable research estimating the leopard population size and density has taken place since then. Zambia is one of these countries. The Luangwa Valley in the east of Zambia is historically famous for its once high game abundance but also notorious for decades of excessive uncontrolled poaching which apparently has caused depletion in animal stocks in an area once so rich in fauna. However, the Luangwa Valley is still a popular destination hot spot for hunting safaris and several Game Management Areas (GMA’s) are established in the area where controlled hunting is allowed. Information gleaned from interviews with professional hunters and park managers concur with the general opinion that leopards are common in “very high abundance” in the study area.

To prove these assumptions it is necessary to explore if the Luambe National Park (LNP), as an apparently undisturbed area, shows signs that it is influenced by the event disturbances within its surrounding environment. This research is a first step to provide

some knowledge about leopard distribution and population status in Zambia and more specifically within the Luangwa Valley.

2.1.1 Study area

The LNP (encompassing 338 km² in this study) and a selected part (137 km²) from a GMA (see Chapter 1.4.4) that borders directly onto it (see Figure 2.2) provided an appropriate area to determine leopard population estimate due to its compact size and the fact that it is completely surrounded by GMA's.

The LNP is surrounded by four GMA's in total, in the North by the GMA–A, which is the primary considered GMA in this study, and in the South by GMA-B (for detailed description of the study area, see Chapter 1.4.4). Villages exist and agricultural activities take place in the GMA's and hunting for game meat as a source of food, as trophy hunting, is allowed (see Table 1.2).

Due to rainfall (see Chapter 1.4.1) and other circumstances (see Chapter 1.4.4) data acquisition had to take place during the dry season. Data for this study was therefore collected during the dry periods from 2006-2008 from the leopard population inhabiting the LNP and the bordering GMA-A. The total size of the GMAA is about 2,555 km² from which I selected 137 km² for my study.

Choosing an area deeper within the GMA-A was not a realistic option due to safari hunting activities which were taking place at the same time. But I had been informed that the area in the GMA-A where I had decided to place the cameras and carry out my study hunting of big cats had not been successful at this time.

2.2 Methods

2.2.1 Camera trapping

To estimate leopard population density in LNP and the direct bordering GMA-A camera traps surveys were used. Camera traps were generally set 2-5 km apart. Due to the limited numbers of the traps, especially in the beginning of the study (2006 = 6 traps /2007= 9 traps/ 2008 = 20 traps) trap stations had to be changed regularly. Photo traps were left on each station for a period of at least 1-2 weeks (KARANTH & NICHOLS 2002); locations were then changed, so that finally all important domains of the LNP could be covered (KARANTH &

NICHOLS 2002) as well as the part of GMA-A. Three different brands of camera traps were deployed during the study and these were provided by the companies Mennekin, Bushnell and Stealth Cam. They were equipped with memory cards (XD, SD) between 32 Mb to 1 Gb which enabled space of between 40 and 2,000 pictures.

Camera traps were set on prominent game trails, waterholes, trees and vehicle tracks or along the Luangwa River, as well as along small tributaries (Figure 2.3). I also set camera traps in trees that were known as “leopard trees” (trees that are frequently used by leopard, see Figure 2.4). On certain locations I placed baits in trees, or I dragged 3-5 day old meat or intestines in order to attract leopards. Very effective was the use of intestines that had been allowed to stand in their own liquid for 2 days in a hermetically sealed bucket.

To facilitate the identification of leopards it would have been ideal to use subsets of camera traps to get pictures from the left and the right side of individual leopards. But due to the limited number of camera traps, as well as damage by animals and cases of theft this option was impossible.

Figure 2.1: Leopard track on a road, next to tracks of tyres (left).

Although most typical leopard trees and tracks (see Figure 2.1) were found in denser forest area along the Luangwa River, I set photo traps in grassland also because leopards were seen and had also been located there via radio tracking (see Chapter 3). I also set photo traps in areas where I did not find any signs of leopard presence to prove it as a 0-test (see Figure 2.2). 69,151 photo-trap pictures were taken in total within the trapping periods between 2006 and 2008.

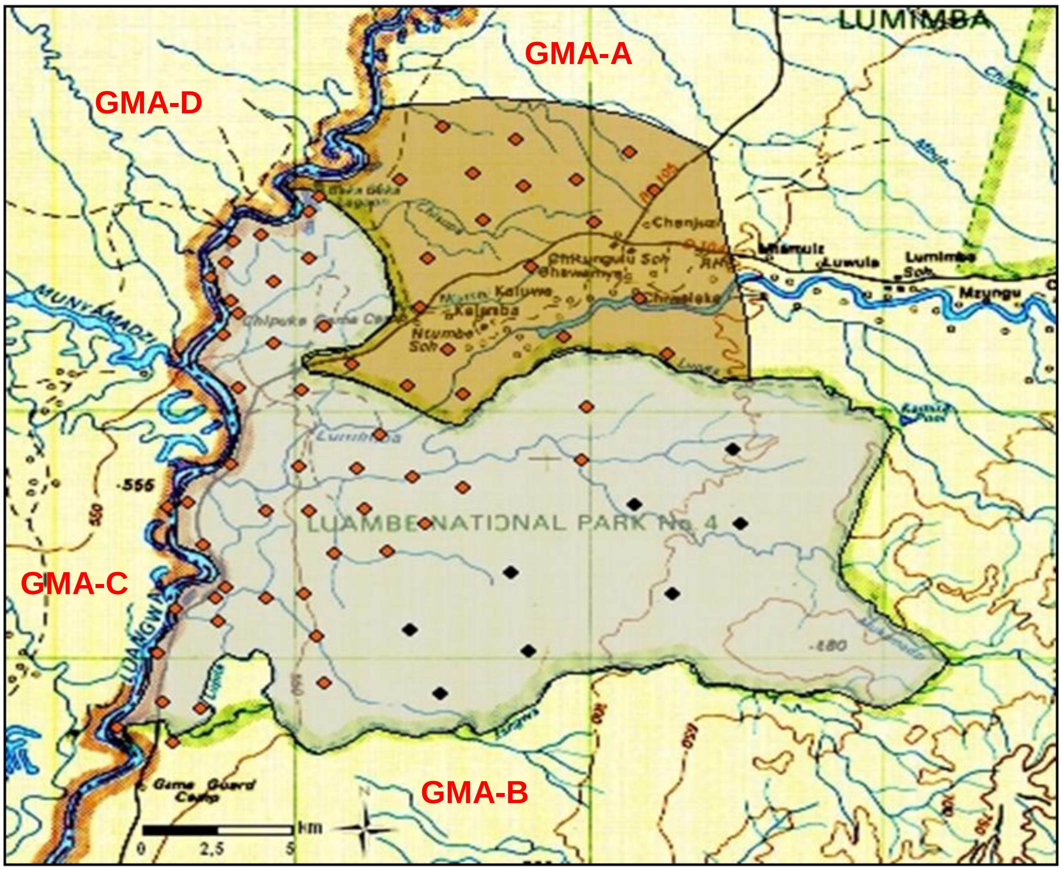


Figure 2.2: Example overview of the area covered by camera traps (grey: LNP; brown: selected part of the hunting area, GMA-A), red and black representing camera trap stations. Red spots show the cover by camera traps 2008 because the highest number of traps was available in this year. Black spots show the "zero-test", the cover of the eastern part of the LNP (2006/2007) where no pictures of leopards and hardly pictures of other species were taken.

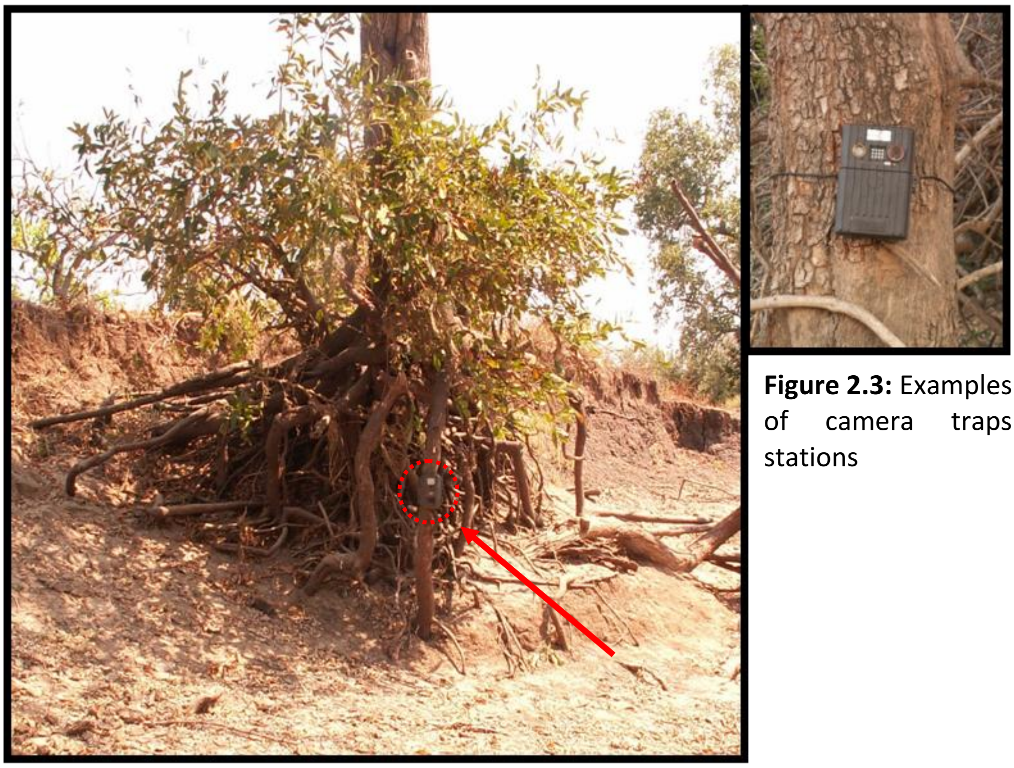
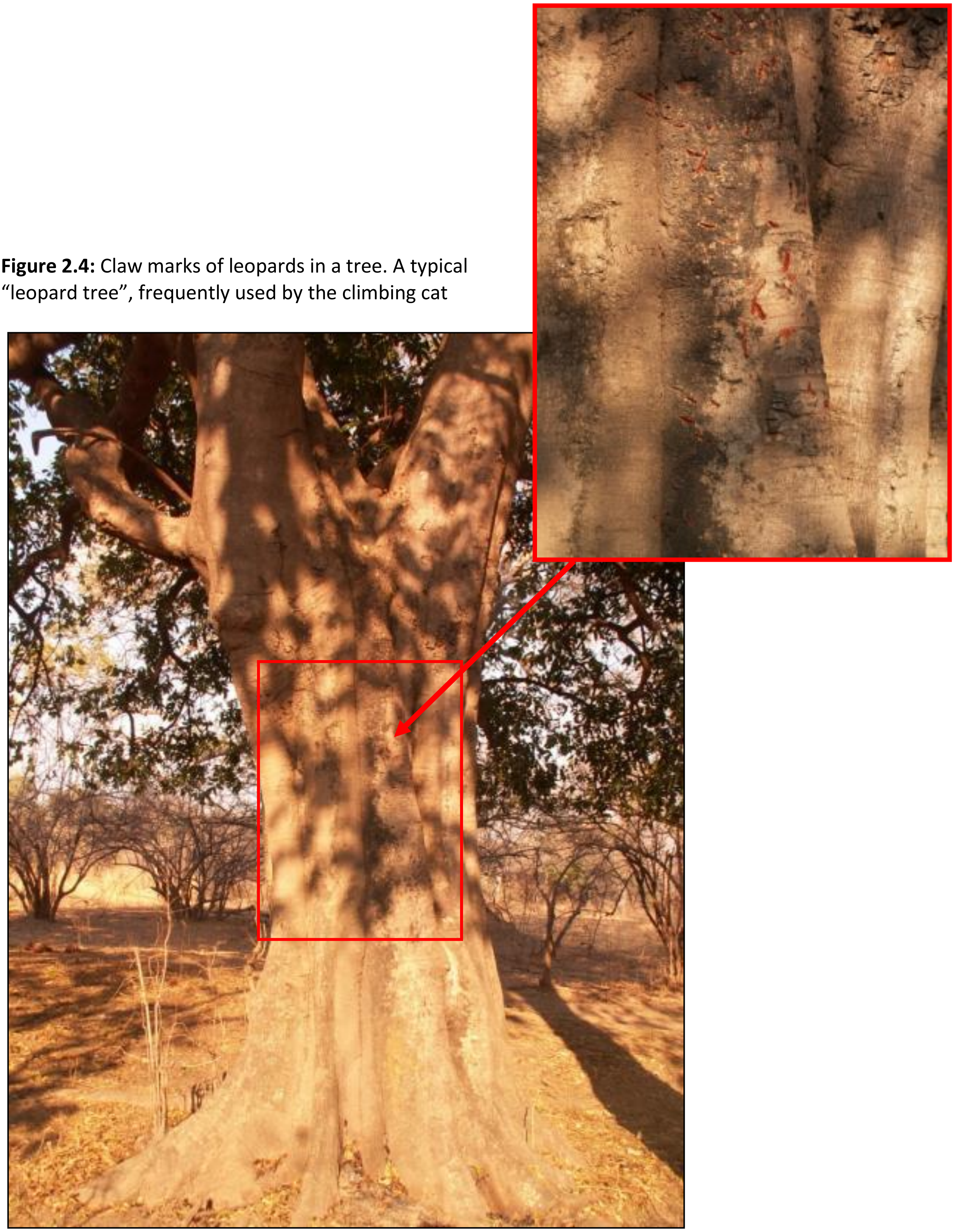


Figure 2.3: Examples of camera traps stations

Figure 2.4: Claw marks of leopards in a tree. A typical "leopard tree", frequently used by the climbing cat



2.2.2 Identification of single individuals

Pictures of leopards which have been taken during this study period were used to identify single individuals. Because every individual looks different and every spotted animal has a unique spot pattern, I compared the spot pattern of the leopards photographed (see Figure 2.5).

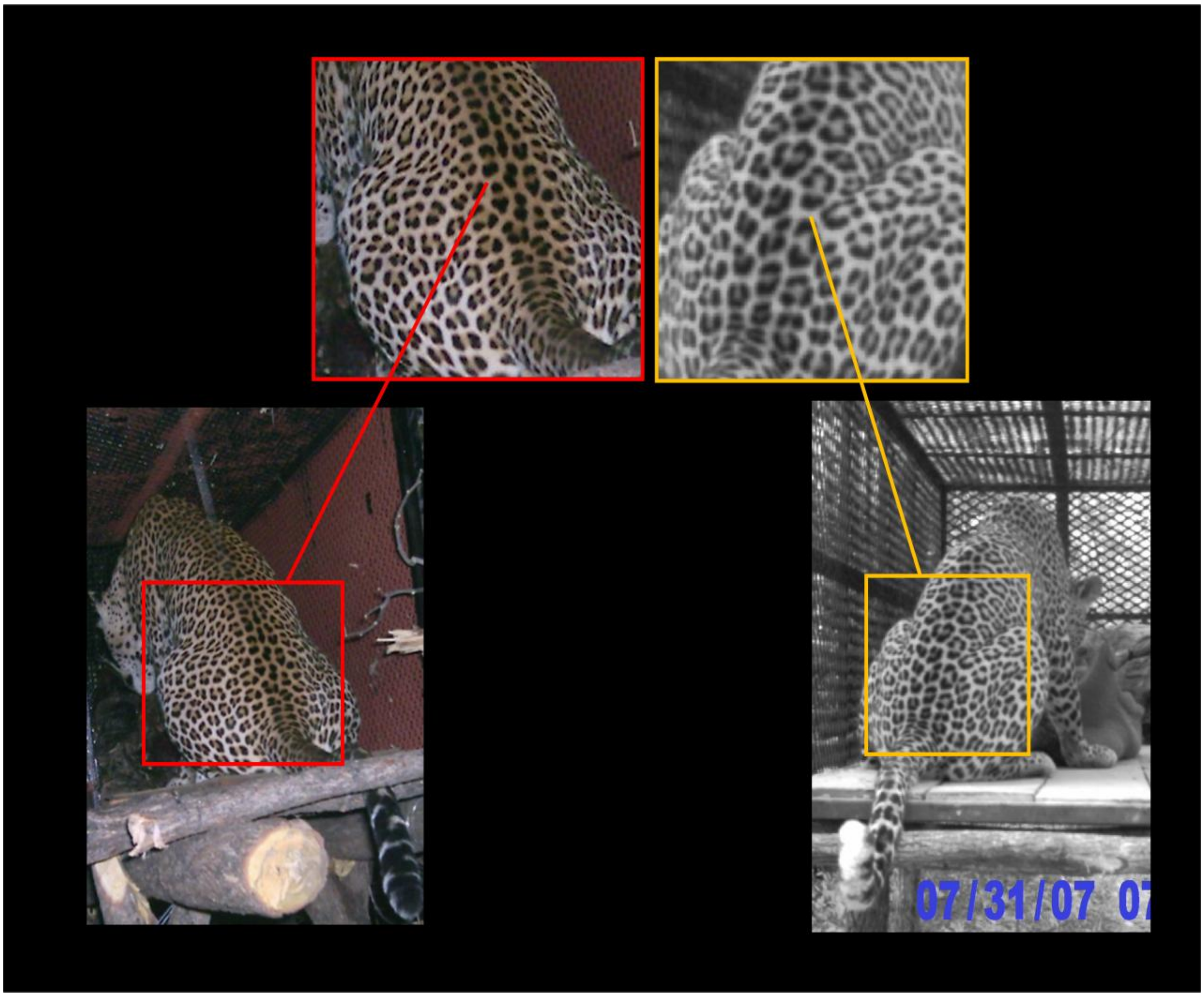


Figure 2.5: Example for identification of individual leopards based on their individual unique pattern of spots and rosettes. The figure shows two different leopards (red and yellow).

2.2.3 Analyses of population estimates

After identification of the leopards, I compiled capture histories for individual leopards in the program CAPTURE (Rexstad & Burnham 1991), using X-matrix and assigning with “1” if the individual was captured or with “0” if the individual was not captured on each capture occasion (7 days = 1 occasion).

I used the model selection function to determine which estimator best fits the data in question. CAPTURE offers seven different models to estimate population size and gives values ranking 0.0-1.0 with higher values indicating a better fit (Otis et al. 1978). I tested population closure with the program CLOSURE (Stanley & Burnham 1999); because the test for population closure within CAPTURE is known not to be statistical robust and unaffected by heterogeneity in capture probabilities.

CLOSURE presents a test for time specific data that tests the null hypothesis of closed-population model M_t against the open-population model Jolly-Seber as an alternative (Stanley & Burnham 1999). This test should be most sensitive to permanent emigration and least sensitive to temporary emigration and of intermediate sensitivity to permanent or temporary immigration. P-values below 0.05 suggest that the population is not closed (Stanley & Burnham 1999). The definition of a closed population excludes emigration, immigration, births and deaths during the time of the study (Karanth & Nichols 2002, Thompson et al. 1998). In their study on tigers Karanth & Nichols (2002) recommend a maximum sampling period between 8-12 weeks. CAPTURE produces for each selected model an estimate of capture probability and a resulting population size with confidence limits and standard error.

I calculated the size of the effectively sampled area covered by camera traps plus a circular buffer around the outer traps to account for an additional area from which individuals may enter the trapping polygon (White et al. 1982). The width of this buffer zone should be equivalent to the radius of an average home range, and for trapping studies half the mean maximum distance moved (HMMDM) by leopards photographed more than once. The mean maximum distance moved (MMDM) can be used as an approximation of home range diameter (Wilson & Anderson 1985). In my study I calculated the MMDM by both the ways described above, since I also determined the home ranges of leopards in the study area (see Chapter 3). I calculated leopard density by dividing the population size estimated by CAPTURE for each site with the corresponding sampled area.

Due to the fact that the two study areas border against each other, leopards could move freely across the boundary. In order to differentiate the population of the LNP and the GMA-A, I defined those leopards belonging to the LNP or GMA-A population that were captured only or mostly in LNP or GMA-A. This applied especially to three leopards, two of these were radio-collared (see Chapter 3), that lived close to the boundary.

2.2.4 Calculating relative abundance indices of prey species and species of inter-specific competition

I used photographic rates to compare prey availability among the two study sites and calculated the relative abundance indices (RAI) for the main prey species of leopards in these regions which will be described in Chapter 4.

The RAI was used in studies on tigers (O'BRIEN et al. 2003, JOHNSON et al. 2006) but also in further studies dealing with camera trap data (BALME et al. 2010, HENSCHEL 2008; ILEMIN & BEZAT 2010) and is defined as the number of independent photographs (captures) taken of each species per 100 trap days. Following this, each photograph was identified to species level and sorted by “dependent” and “independent” captures, with “independent” defined as consecutive pictures of different individuals of the same or different species taken more than 0.5h apart or non-consecutive pictures of the same species (O'BRIEN et al. 2003). I also deployed the photograph captures to get an idea of inter-specific competition. In most of the camera trap stations with baits or odor, hyaneas (*Crocuta crocuta*) and lions (*Panthera leo*) were captured beside leopards. Consequently, I used the captures of lions and spotted hyenas to calculate the RAI of inter-specific competition in the study areas. African wild dogs (*Lycaon pictus*) are known to compete occasionally with leopards (CREEL et al. 2001), and I have one record of an observation were a group of wild dogs within the GMA-A chased a leopard into a tree. But because this was only one record and wild dogs occurred very rarely in those areas during the study period and were captured just once by a camera trap (never at a bait station), I assume that their influence on leopards was insignificant.

2.2.5 Statistical methods

In order to analyze if there were significant differences in population sizes and RAI-values I used non parametric statistical hypothesis tests such as the chi^2-test (SPSS 13.0). The chi^2-test is applied to see if the sampling distribution of the test statistics is a chi square distribution when the null hypothesis is true (Mühlenberg 1993).

2.3 Results

2.3.1 Camera trapping and identification of individual leopards

Across the study periods from 2006 to 2008, I operated 94 camera trap stations in the survey area over durations of 56-77 days resulting in 6,715 trap days in total (see Table 2.2). During the years seven camera traps have been either stolen or damaged by elephants, hyenas or lions. In total 69,151 camera-trap pictures were taken which included 5,454 leopard pictures (see Table 2.1).

Table 2.1: Number of captures of camera trap surveys conducted in the LNP and adjoining GMA-A, between 2006-2008

Survey area (Year)	Number of pictures in total	Number of leopard pictures
2008 (LNP)	31,260	1,351
2008 (GMA)	20,109	1,839
2007 (LNP)	14,014	1,652
2006 (LNP)	3,768	612
In total	**69,151**	**5,454**

Table 2.2: Camera trap sampling effort at the study area from surveys between 2006-2008

Survey area (Year)	Maximum duration (days)	Camera stations	Trapping polygon size (km²)	Trap days
2008 (LNP)	77	30	150	2,310
2008 (GMA)	75	20	77	1,500
2007 (LNP)	77	21	98	1,617
2006 (LNP)	56	23	66	1,288

From 5,454 captures (representing 333 independent leopard captures) I identified (e.g. Figure 2.6 and Figure 2.7) 23 individual leopards which I assigned respectively either to the population living in the LNP (fourteen individuals identified, within from 2006-2008) or to the population living in the GMA-A (nine individuals identified). Three individuals of the LNP and one of the GMA could not be identified to sex level, but reliably differentiated due to their individual spot pattern. The eight to sex level identified leopards in the GMA-A 2008 show a sex ratio of 1 female/male (4 females/4 males). The sex ratio of the seven leopards identified in the LNP 2008 results in 1.3 females/males (4 females/3 males). Three cubs in total that were recognized within the study period are not included in the estimate. Of the fourteen leopards identified in the LNP six individuals were captured during more than one census period.

Figure 2.6: Identification of individual leopards by dorsal spot pattern. Picture A and B show the two different individuals, male (red) and female (yellow), at the same bait station.

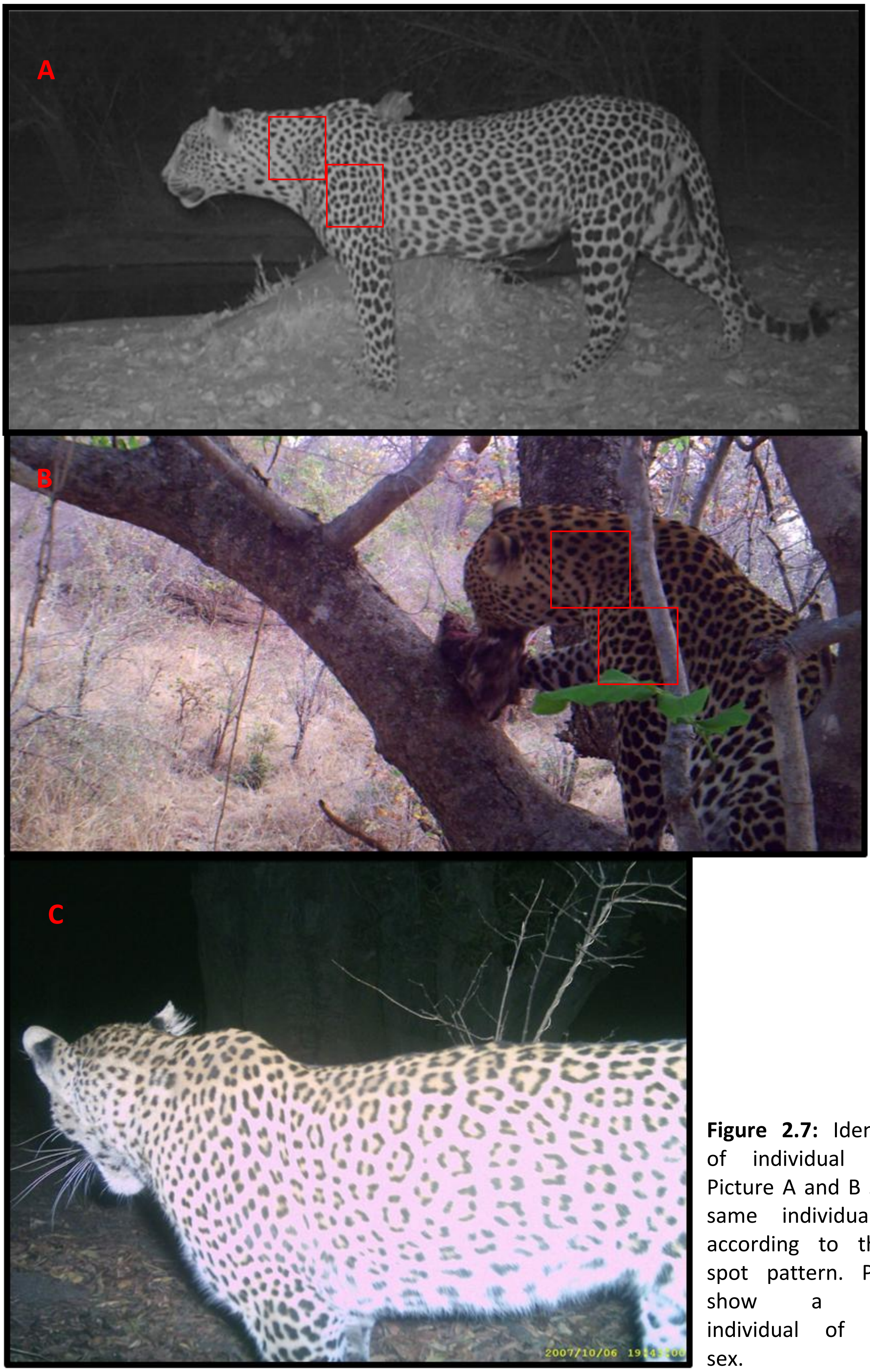


Figure 2.7: Identification of individual leopards. Picture A and B show the same individual (male) according to the same spot pattern. Picture C show a different individual of unknown sex.

In the study periods from 2006 until 2008, 17-27 captures and recaptures were obtained representing 7-10 individual leopards (see Table 2.3). The CLOSURE test results confirmed population closure during the time of the survey (Table 2.3). In the CAPTURE model choice function the model M_h scored highest for all study surveys, and only at the 2006-survey model M_{bh} scored highest. Both models test for heterogeneity in capture probability between different individuals, but M_{bh} assumes also behavioral differences in capture probability. Some individuals might avoid camera traps, having a negative reaction to the camera flash upon initial capture and may decrease the likelihood of the individual being recaptured (JACKSON et al. 2005), and therefore only initial captures and no recaptures are used to estimate the population size.

Table 2.3: CAPTURE and CLOSURE results for both the study areas, showing capture & recapture data with capture probability=p, and high P-values indicating the closure of the populations.

Survey area (Year)	Captures + recaptures	Individuals identified	Individuals recaptured	p	Closure test	
					df	**P**
2008 (NP)	27	10	7	0.22	9	0.33
2008 (GMA)	17	9	4	0.29	5	0.31
2007 (NP)	18	9	6	0.17	6	0.25
2006 (NP)	20	7	4	0.36	6	0.25

The population sizes (LNP; GMA-A) differ not significantly from each other (p=0.519). The population sizes in the GMA-A and in the LNP of the year 2008 (see Table 2.4) were estimated at 10 ± 2.03 (with 95% confidence interval from 10-21) and 12 ± 1.96 (with a 95% CI from 11-20) with corresponding population densities of either 4.79 ± 1.16 or 3.35 ± 0.64 (HRr) (or of either 7.69 ± 1.67or 4.38 ± 0.85 (DMT)). The two densities were calculated as well with the ½ MMDM resulting from the averaged home ranges (HRr) (2.83 ± 0.54) as with the ½ MMDM resulting from the distance moved (DMT) by animals which were photographed at more than one camera trap station (1.25 ± 0.25/ 1.73 ± 0.48), (see Figure 2.8).

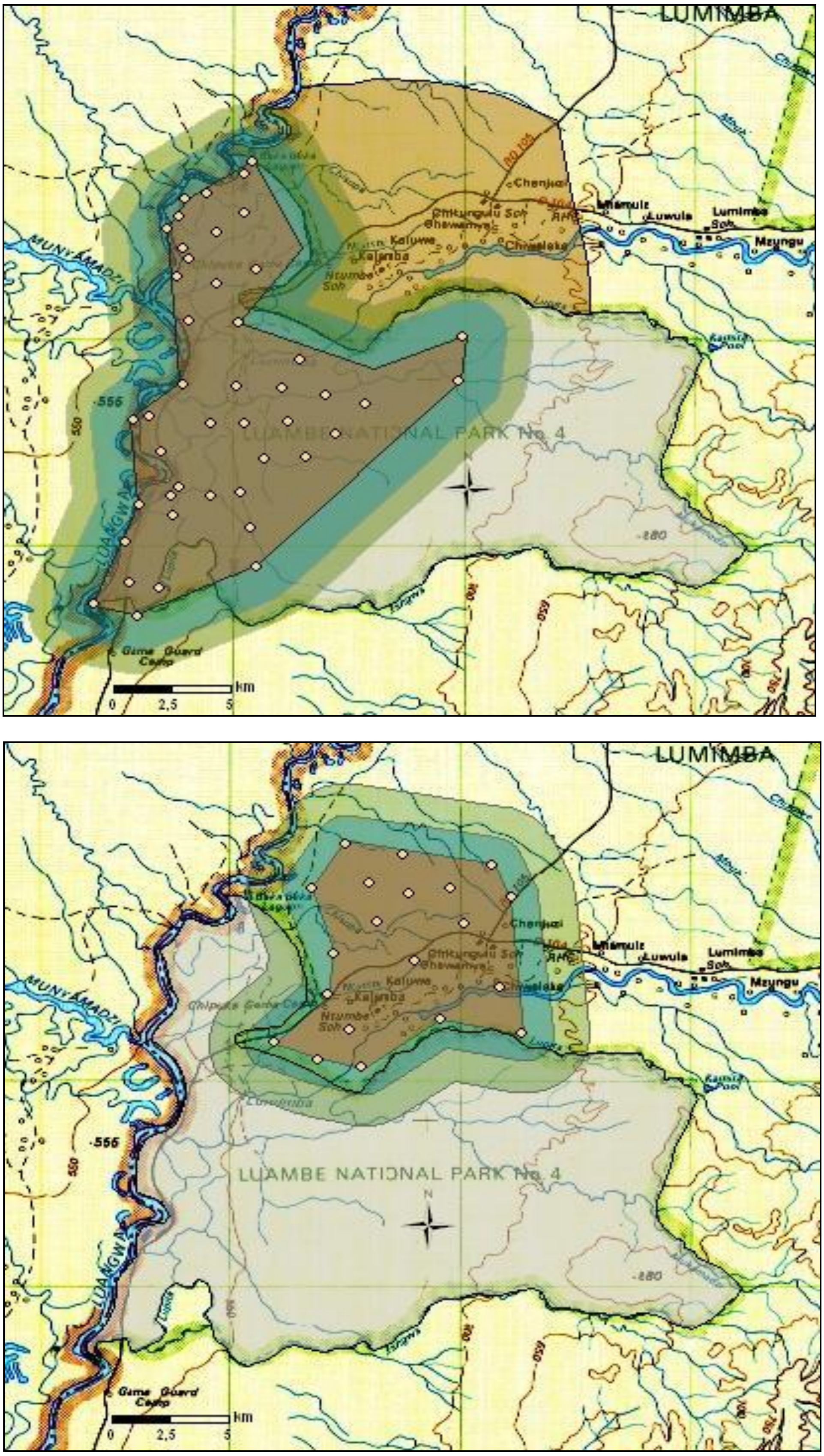


Figure 2.8: Study site of the LNP (grey) with a sketch of the selected part of the GMA-A (light brown) and the study site inside the GMA-A (below). Showing the camera trap locations (yellow spots), the trapping polygon (dark brown) and the effectively sampled area calculated by ½ mean maximum distance of an animal moved between traps (DMT) (blue) and by the averaged home ranges of the radio-tracked leopards (HRr) (green).

In the years 2006 and 2007 (see Table 2.4) the population size estimate ranged from 7 ± 0.00 (with a 95% CI from 7-7) to 10 ± 2.76 (with a 95% CI from 10-26) inside the LNP. The population sizes of the LNP 2006, 2007 and 2008 did not differ significantly ($p=0.670$). Population densities calculated with the ½ MMDM resulting from the averaged home ranges varied (HRr) from 3.47 ± 0.47 to 3.85 ± 1.16. The density values calculated with the ½MMDM resulting from the linear distance moved (DMT) by animals between successive captures resulted in 5.51 ± 0.22 and 5.37 ± 1.75. I calculated the population density by using these two available methods to see which method fits best to this study. This topic will be discussed later (Chapter 2.4.1).

Table 2.4: CAPTURE results for study area LNP observed for 3 years, showing population size (using model Mh, Mbh), boundary strip width as determined by the half mean maximum distance moved (½ MMDM), calculated by a) the radius of averaged home ranges (HRr) and b) the distance of animals trapped more than once (DMT=distance moved between traps), and the resulting population density

Survey area (Year)	Population size ± SE	95% confidence interval (CI)	½ MMDM (km) ± SE		Effectively sampled area (km²)		Density (per 100 km²) ± SE	
			HRr	DMT	HRr	DMT	HRr	DMT
2008 (LNP)	Mh:12 ± 1.96	11 - 20	2.83 ± 0.54	1.73 ± 0.48	359	274	3.35 ± 0.64	4.38 ± 0.85
2008 (GMA)	Mh:10 ± 2.03	10 - 21	2.83 ± 0.54	1.25 ± 0.25	209	130	4.79 ± 1.16	7.69 ± 1.67
2007 (LNP)	Mh:10 ± 2.76	10 - 26	2.83 ± 0.54	1.63 ± 0.67	260	166	3.85 ± 1.16	5.37 ± 1.75
2006 (LNP)	Mbh: 7 ± 0.00	7 – 7	2.83 ± 0.54	1.38 ± 0.13	202	127	3.47 ± 0.47	5.51 ± 0.22

2.3.2 Relative abundance indices (RAI)

I obtained 8,005 independent pictures of six mammal species which belonged to the main leopard prey species (4 ungulate species, 2 primate species) in the study area (see chapter 4) and 244 independent pictures of two carnivore species (lion and hyena, Figure 2.9) which were assumed to be the leopards competitors inside the study area. All the mentioned species of ungulates, primates and carnivores were captured on both study sides, and also every year from 2006-2008 in the LNP. Impala and puku were the most regularly photographed prey species comprising 41.5% and 37.3% of the independent captures, whereas bushbuck and warthog covered 2.57% and 1.62%. Primates contained 17% of captures.

The RAI for 2008 of 153.25 for all the six prey species in the LNP was higher than in the GMA-A with 70, and the highest of the years from 2006 to 2008 (see Table 2.5). The highest RAI was observed in impala (*Aepycerus melampus*) and puku (*Kobus vardoni*) and differed significantly from RAI of previous years ($p < 0.001$). Bushbuck (*Tragelaphus scriptus*) and warthog showed the lowest RAI values within the ungulates group and did not differ significantly from each other.

Figure 2.9: The leopards competitors: Capture of a young male lion that climbed in the tree to feed on a bait placed for leopards (top), and a hyena at the live-trap station for leopard (bottom)

The RAI of the primates was also highest in the LNP 2008 (48.58; p=0.001), as well as the RAI of the possible competitors like lion and hyena (5.88). The RAI values of the carnivores between the years (2006-2008) in LNP and GMA did not differ significantly from each other (p=0.637).

Table 2.5: Relative abundance indices (RAI) of six main leopard prey species and two competitor species of leopards photographed in camera-trap surveys in LNP and adjoining GMA-A, 2006-2008

RAI (photographs/100 trap days)

Species	**LNP**			**GMA**
	2006	**2007**	**2008**	**2008**
Ungulates				
Impala *(Aepyceros melampus)*	27.10	29.56	78.40	45.60
Puku *(Kobus vardoni)*	33.31	42.30	67.58	21.07
Bushbuck (*Tragelaphus scriptus)*	0.78	2.16	5.45	2.33
Warthog *(Phacochoerus africanus)*	0.39	4.21	1.82	1.00
Total	***61.58***	***78.23***	***153.25***	***70***
Primates				
Baboon *(Papio cynocephalus)*	3.11	2.91	41.65	7.60
Vervet monkey *(Cercopithecus aethiops)*	0.93	0.43	6.93	1.00
Total	***4.04***	***3.34***	***48.58***	***8.60***
Large Carnivores				
Leopard (*Panthera pardus*)	3.42	5.57	4.59	5.33
Lion (*Panthera leo*)	0.31	1.24	3.20	2.13
Hyaena *(Crocuta crocuta)*	0.54	1.86	2.68	1.00
Total (without leopard)	***0.85***	***3.1***	***5.88***	***3.13***
Total	***4.27***	***9.53***	***10.38***	***8.46***

2.4 Discussion

2.4.1 Estimate of leopard population abundance and density by camera trapping

This was the first systematic attempt to estimate the population status of the leopard in a part of Zambia. The use of camera traps to estimate the leopard population density is a proven method that has been successfully employed in prior studies to large cryptic felids as e.g. tigers, jaguars, snow leopards, and also leopards (Karanth & Nichols 1998, Karanth et al. 2004a, Silver et al. 2004, Jackson et al. 2005, Henschel 2008, Balme et al. 2009, Balme et al. 2010). Therefore, it was judged as appropriate for this kind of study. For the population density estimates I used the MMDM calculated by the averaged home ranges (HRr) of the radio-tracked leopards as well as the MMDM calculated by mean maximum distance (DMT) of an individual moved between traps. This compares the two estimates resulting in more reliability for this study. The results of the DMT-MMDM are 1-1.5 smaller than those of the HRr-MMDM and the population density values calculated by the DMT-MMDM are much higher (difference of 1-3 animals/km²) than the values calculated by the HRr-MMDM. The DMT-MMDM do not differ significantly between the study periods or between the LNP and the GMA-A. Results of former camera trapping studies suggest that bias may occur if trapping polygons are too small to perceive the true maximum distance moved (Maffei & Noss 2008) but this is not the case in the present study. Maffei & Noss 2008 indicated that camera traps across an area have to be set in a distance of at least three to four times an average home range. Due to the home range sizes resulting from a concurrent radio-tracking of the leopards (see Chapter 3), and in order to avoid overestimation, I assume that the results of using the home range MMDM fit the density data best.

The population size estimates over the years 2006 to 2008 for the LNP did not differ significantly from each other (Table 2.4). The population size of seven leopards in 2006 is finally equal to the total number captured and identified individuals with reasonable certainty. One adult male leopard was seen regularly in the LNP only in 2006 and was never trapped again in the following years. One of the male leopards that had been collared in 2007 left the area in 2008 (see Chapter 3).

Due to the fewer number of camera traps for the survey periods 2006 and 2007 the area could not prove the same coverage as the camera traps as in the following year, 2008.

Apart from natural circumstances as deaths, immigration and emigration, it is also likely that leopards captured in 2008, were permanently resident in the area during the previous years, too but avoided detection by camera traps.

The estimate of the population size for the LNP in 2008 was twelve. In the GMA-A it was ten, which is comparably high considering the smaller size of the study area inside the GMA-A. Despite of the smaller study size inside the GMA-A the population density resulted in a higher estimate (4.79 ± 1.16) per 100 km² than inside the LNP (3.36 ± 0.64). However, CLOSURE results supported a closed population during the study period in the GMA-A while hunting activities were going on. Although professional hunters from this GMA said that they did not shoot a leopard in the selected part of the GMA-A where this study took place, it is still possible that a leopard was trophy hunted. This leopard might have extended its excursions and overstepped the buffer zone of the effective sampled study area.

A male leopard that was killed inside the GMA-study area left an empty space ("empty range"), which was soon taken by another male (according to personal observations and interviews with professional hunters). This "vacuum-effect" was e.g. previously described in African lions (*Panthera leo*) in the context of sport hunting (Loveridge et al. 2007), as well as in other carnivores such as lynx (*Lynx canadensis*) populations depleted by fur trapping (Bailey et al. 1986) and badgers (*Meles meles*) depleted by bovine tuberculosis control operations (Cheesemann et al. 1993). These resulting empty territories were recolonized by immigration of immediate neighbors, causing social perturbation (Tuyttens & Macdonald 2000) in these populations. That critical situations like this perhaps also affect leopard populations was also suggested by Balme & Hunter (2004) and Balme et al. (2010).

In the GMA, it is also possible that more than one new coming leopard tried to take over the "empty range" and competed with other individuals. The successful male chased competitors away, which could explain the high number of captures but lower numbers of recaptures in this study area in comparison to the LNP. Thus, such circumstances could result in a temporarily high density of leopards in a relatively small area.

In addition to that, it is possible that the sample area was favored because most of the selected area within the GMA-A comprised grassland and Combretum-Terminalia woodland. These are important leopard hunting habitats (Chapter 3), as opposed to the drier areas in

the east (and in the LNP), which support less game, and to north-western areas, where villages cause disturbance for leopards.

However, certainly, new leopards are also attracted by the increase of mating opportunities ("vacuum effect") and that may increase intra-specific conflicts in this area. Leopards live in a land tenure system, where well established male resident leopards possess the older breeding rights that are associated with permanent stable land occupancy and territorial behavior like scent marking and vocalization (Bailey 2005). Only resident and usually older males are associated with females long enough to breed. Females seem to be less aggressive towards other females, but both sexes defend territories against same-sex invaders (Bailey 2005, Le Roux & Skinner 1989).

However, they seem to tolerate familiar neighbors rather than strangers (Bailey 2005) that e.g. Ydenberg et al. (1988), Falls (1982) and Fisher (1954) described as "dear enemy effect" where territorial residents discriminate between neighbours and non-neighbours. Consequently, this land tenure system appears to be dependent on the stability of long term relationships (Bailey 2005).

Intra-specific competition could be a strong limiting factor for carnivore populations (Creel 2001). Usually the home ranges of male leopards encompass the home ranges of several females, and although male leopards do not seem to show high parental care, the resident male's presence constitutes a protection of the cubs towards intruders thus preventing infanticide. This was also assumed in Balme & Hunter (2004) and Balme et al. (2010) in their study about leopards in the Mhkuze-Phinda complex in South Africa.

One argument against excessive trophy hunting of lions was that it could be critical to kill male lions younger than a certain age of 6 years. After that they will have more likely successfully reproduced and protected their cubs up to a subadult age from which they are not really threatened by new males (Whitmann et al. 2004, Packer et al. 2006).

There are perhaps not as many studies (comparable with lion studies) concerning infanticide in leopards, but e.g. Ilani (1986; 1990) documented for an isolated leopard population in the Judean Desert, in Israel, that infanticide was the main reason that not a single individual was integrated into the adult population during a five-year period. Balme & Hunter (2004) suggested in Phinda (a protected private game reserve) in South Africa that female reproductive levels might decline significantly when males are removed constantly from the population.

Does not this imply that these factors can also seriously influence leopard populations?

I witnessed a case of infanticide by following a radio collared male that left the study area (it presumably was chased away), and tried to settle in an area about ca. 80 km away from the study site (see chapter 3). His new “range” was inside a National Park, but also inside a bordering hunting area. He killed a cub of a resident female and within the time I could observe him there I could not find any signs of an adult male. This observation led to the assumption that the “sire” of this range was dead. He was probably shot due to the fact that inside the bordering GMA-A trophy hunting took place and leopards moved freely across the boundaries. I assume that the intra-specific competition inside the GMA-A is higher than inside the LNP caused by the impact of trophy hunting.

Although the LNP is an apparently undisturbed area, I believe the leopard population living there is influenced by the hunting activities outside from the Park.

On the one hand leopards can move freely across the borders, even temporarily, for short excursions, and thus, it simply happens, that “National Park” - males are getting shot thus leaving young cubs unprotected. On the other hand leopards (e.g. subadults) will naturally migrate out of the LNP into the GMA in search of a territory.

2.4.2 Relative abundance indices (RAI) and inter-specific competition

The RAI index for ungulates, primates and large carnivores inside the LNP increased from 2006 to 2008. This may be attributed to the increased number of available camera traps covering the area.

When the research commenced in 2006, only twelve cameras were in use and in the following year the number of cameras was increased to eighteen. Therefore, the values of the RAI index of 2008 inside the LNP which was the highest within these three years were a result of the higher amount of camera traps (38 in total) and also camera models of better quality which were provided at this time.

A few cameras were seriously damaged by animals or stolen by people, eliminating some data from analyses. Furthermore, improved protection of animals in the LNP (due to presence of a tourist lodge and the research camp) were likely leading to a general increase in game population and could be an additional reason for the increased RAI index figures. The RAI values from inside the GMA-A for potential prey species were lower than inside the

LNP. But results from scat analyses do not indicate a lesser abundance of the potential prey species in the GMA-A than inside the LNP (see Chapter 4).

Therefore, this difference is - on the one hand - conclusively substantiated in those areas that were covered with fewer camera traps. Most cases of camera trap thefts occurred inside the GMA-A. On the other hand, that could have been due to the size of the selected area being much smaller than the study area inside the LNP. Taking all this information into consideration, the RAI values for the ungulate species of the GMA-A may not differ significantly from the LNP.

The values of the primates differ significantly between the areas and are explained with the choice of camera trap stations. Primates were in general less captured on camera in denser habitat which was mostly chosen due to the increased possibility of leopard captures. The highest capture rate of baboons and vervet monkeys inside the LNP was in places very close to the research camp, mostly at a waterhole not far from the camp. This is not surprising since water is the limiting factor for these monkey groups (e.g. Norton et al. 1987). The high abundance of the primates around human habitations is most likely due to food supplies and the production of organic waste (e.g. Muoria et al. 2003, Maples et al. 1976, Wolfheim 1983).

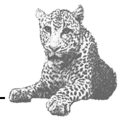
Every year, the RAI-Index of the leopards inside the LNP was higher than the values of lion abundance. This is also applicable for the GMA-A 2008. According to interviews with local people (villagers, scouts), professional hunters and the Zambia Wildlife Authority lion abundance had decreased over the years. Although the critical lion situation seemed to be highly discussed (but without scientific proof) hunting activities were going on with apparently successful lion harvest (see Chapter 5). During the entire time of my research I observed on two occasions a mature male lion inside the LNP. The presence of at least one male mature lion had to be assumed because a group of 2 lionesses with cubs were regularly seen. Camera traps only captured groups of 2 or single immature male lions, or lionesses with cubs or single lionesses, also at bait stations for leopards. Due to the very close neighborhood of the hunting area a male lion was always at risk of getting shot as soon as it overstepped the boundary.

Nevertheless, lions are competitors to leopards. To avoid “kleptoparasitism” (Sunquist & Sunquist 2002, Jenny 1996, Hart et al. 1996, Bertram 1982) leopards cache their kills and drag them into trees in this area. From eight leopard kills and their remains that I discovered

during the study period none were cached on the ground and I witnessed several times that a leopard was chased away from baits by lions. It was also very difficult to capture leopards in the live-trap for telemetry studies as long as lions were attracted from the bait inside the live-trap. Leopards disappeared as soon as lions appeared and returned once lions were gone. I also observed a leopard scavenging on an impala carcass (of unknown death cause) on the ground. The leopard immediately disappeared as two lionesses approached and finally finished the carcass.

Consequently, the competition by lions can definitely be confirmed in this area, but probably due to the extensive lion harvest by trophy hunting the leopard abundance increased or remained higher than the lion abundance. This was documented previously in Tanzania, where hunting blocks with highest average lion harvests showed the largest increases in leopard harvests (Packer et al. 2009, Packer et al. 2010).

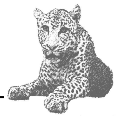
Hyenas, for which RAI-index of the LNP and the GMA-A was lower than that of the leopards, were obviously also competitors to leopards especially due to their scavenging life style, and appeared at bait stations more often than lions. However, in these cases, a leopard was the one that chased the hyenas away primarily if it dealt with a single individual. Because RAI value of the hyenas remained lower than that of the leopards during the years, it could also be that this is related to the hyena harvest by trophy hunting (see Chapter 5).



2.5 Summary

In this study that was carried out in Zambia, the aim was to determine the population size and density of the leopard (*Panthera pardus*) in the Luambe National Park (LNP) and a bordering Game Management Area (GMA-A) where trophy hunting takes place. By photographic camera trap pictures individual leopards were identified and capture and recapture models were used to analyze the leopard population size and the density in both the study sites. The highest estimate of the population size resulted in 12 individuals for the LNP 2008 and ten for the GMA-A. The selected part inside the GMA-A which is smaller in area reflected a population density estimate of 4.79 ± 1.16 per 100 km^2, relatively higher than that recorded in the LNP at 3.36 ± 0.64 per 100 km^2.

This result could be influenced by one or two factors. The area in the GMA-A that was selected for the study is considered to be congested due to surrounding environmental and habitat pressures. Furthermore, the higher density within this relative small sized area could also be due to a transient leopard population. It could be argued that the impact of hunting may cause higher intra-specific competition and therefore also more often infanticide than that within the LNP, and thus the LNP will be influenced by these circumstances as well. Results of relative abundance indices (RAI) of large carnivore species and the leopards' main prey species supported the inter-specific competition between large carnivores (lion and hyena). But it perhaps is also an indication, based on the difference in abundance values, of the impact of hunting.



3 Home ranges, activity patterns and habitat preferences of leopards in an undisturbed area (Luambe National Park) and a disturbed area (Game Management Area) in the Luangwa Valley in Zambia

This chapter deals with home ranges, their physical size and the activity patterns of collared leopards inside the Luambe National Park, and those that occur inside the Game Management Area Chanjuzi close to the border of the National Park. Questions to be answered are:

- What is the size of the home ranges?
- How much do the home ranges overlap with each other?
- Are there any differences of the home ranges in habitat availability and use?
- To which extent do the home ranges overlap with the Luambe National Park and the hunting area?
- What is the activity pattern of the leopards and are there significant differences between the individuals?

3.1 Introduction

Leopards are by reputation the most adaptable large felid of the big cat group and therefore find it easy to deal with habitat changes. Due to progressive habitat loss and fragmentation African leopards are declining in their range, further aggravated by hunting for trade and pest control (IUCN 2010, Ray et al. 2005). Critically, hunting quotas were being issued without adequate knowledge regarding the status of leopard population in every country nor about their life style. Previous studies about leopards so far showed that home range sizes of leopards are extremely variable (6-1,200 km^2) and dependant on environmental circumstances as well as the habitat preferences and activity patterns of these cats.

In Zambia, leopards have never previously been studied with this in view. However, Zambia is one of the countries that allows professional hunting and has responded positively to the high demand for lion and leopard trophies (see Chapter 5). The primary aim of this study is to gather more detailed information about leopards for a better understanding of this species and in order to develop an efficient conservation management plan.

3.1.1 Study area

Data was collected between July 2007 and November 2008 from the collared leopards residing in the Luambe National Park (LNP, encompassing around 338 km²) and the bordering Chanjuzi Game-Management-Area (GMA-A). This park is located inside the Luangwa Valley, in the east of Zambia. It is surrounded by four GMA's in all, in the north by the GMA-A, which is the main considered GMA in this study and in the south by GMA-B. In the west it is separated from two GMA's, C and D, by a natural border, the Luangwa River.
(For further description of the study area, see Chapter 1.4.)

Recently a map has been prepared by ANDERSON 2009, recognizing the following vegetation types that characterize the study area of especially the LNP.

Thickets

Two kinds of thickets can be found in the study area (Figure 3.1). One kind consists of dense leafed bushes and leafed trees with characteristic species such as *Schrebera trichoclada* and *Diospyros quiloensis*. The other thicket type consists of dense or open scrubland with different species of the genus *Combretum*, mainly of *Combretum obovatum.*

Figure 3.1: Dense thickets along the main road leading through the park (left); scrubland (right)

Riverine woodland and thicket

River vegetation (Figure 3.2) grows near water along the river and river arms as well as at lagoons. It consists mainly of large and small trees and thickets of characteristic species such as *Diospyros mespiliformes, Kigelia africana, Trichilia emetica, Feretia aeruginescens, Combretum obovotum* and other diverse *Combretum* species.

Figure 3.2: Riverine woodland and thicket along a tributary of the Luangwa

Combretum and Terminalia forest

Combretum-Terminalia forest (Figure 3.3) is the dominating vegetation-form in LNP and surroundings. It is often accompanied by dense undergrowth vegetation and characterized by species such as *Terminalia sericea* and *Combretum imberbe* and further *Combretum* species.

Figure 3.3: Combretum-Terminalia forest (Picture taken by R. v. d. Elzen)

Acacia Forest

Acacia forest (Figure 3.4) does not occur in all areas of the study sites. It shows a continual, dense growing of *Acacia kirkii.* This vegetation type is common in the north-west of the study area and close to river side’s. Further typical species are *A. sieberiana* and *A. polyacantha*.

Figure 3.4: Acacia forest (Picture taken by V. Rduch)

Mopane forest

Wide areas of the study sites are characterized by Mopane trees which appear in two different types, of large dominating trees and short, dense bushes. The big, dominating trees between 15 m - 30 m height are categorized here as "open Mopane forest" with typical species such as C*ollophospermum mopane*. The short bush type which is usually shorter in height is not that common as the large tree type and categorized here as "dense Mopane forest" (Figure 3.5)**.**

Figure 3.5: Dense Mopane forest

Grassland

Grass species are common, which can reach up to three meters. The major part of this vegetation form is distributed over the flood plains of the rivers. Grasses (Figure 3.6) also characterize the picture of sandbars and cut off meanders. A few tree species which characterize the grassland are *Combretum obovatum*, *Collphospermun mopane* and *Acacia.*

Figure 3.6: Grassland

Semi permanent water / aquatic association grass

This habitat type spreads out in seasonal flooded areas, also on small waterholes and lagoons close to the meandering Luangwa River. Those areas (Figure 3.7) have high water storage capacities which enable the growing of diverse grasses and herbs. One tree species of these seasonal wetlands is *Combretum imberbe.*

Figure 3.7: Semi permanent water/aquatic association grass

Water

The term “water“, represents in this case, only parts of the Luangwa River and its meanders (Figure 3.8). Waterholes and lagoons are not included in this definition.

Figure 3.8: Example for “water”, which only includes parts of the Luangwa River

3.2 Methods

3.2.1 Baiting and collaring of the leopards

Collaring leopards requires first baiting and trapping the cat. Extra for this purpose a live-trap was constructed. It consisted of steel with a weight of 250 kg to guarantee solidity.

The live-trap was placed underneath trees frequented by leopards (Figure 3.9) and equipped with bait. Mainly meat of goat, hippo, impala and puku was used. The attempt to bait leopards with meat of warthog, domestic pig or chicken was not successful. I recorded the number of days a leopard needed to respond to the bait and calculated an average time for LNP and GMA-A.

For positioning baits and the live-trap I chose trees that were preferred by leopards, according to observations of their tracks, and photo trap pictures. Some leopards became relative quick habituated to the live-trap (Figure 3.11). The locations for the live-trap had to be changed constantly. Therefore, as well as building up this trap on the platform of 2 m height I employed 4 people from the village. Further I trained them for the procedure of trapping and collaring of leopards. For the latter I employed two armed scouts to support our security.

Figure 3.9: Leopard live-trap made of steel (250 kg) and placed on a platform of 2m height

All immobilization were conducted by a veterinarian or a licensed darter in compliance with the Zambia Wildlife Authority (ZAWA).

Experiences showed that covering the trap with leaves and branches, reduced the possibility of injuries to the trapped animal, usually caused by panic and anxiety as soon as it became aware of us. The cats got tranquilized with Zoletil.

While tranquilized, in addition to collaring, further information was collected in the form of measurements of the cats, body size, weight, as well as blood and hair samples (Figure 3.10). Only adult leopards were collared.

The tranquillized leopards have been aged mostly according to their tooth wear (STANDER 1997), colour of the nipples in females, size of their neck, and size of the testicles in males, and their body weights. Adult leopards tend to have yellow teeth with slightly too much worn tips. Large adult males that are among the favourite for trophy hunters, have a massive neck and long canines.

Figure 3.10: Collaring of a leopard (left); taking measurements of body and head (middle) as well as measurements of dentition and assessment of tooth wear (right)

The testicles were checked for size as it is an indicator whether a male leopard is an adult or not (personal observation, and experiences of professional hunters). After collaring we put the leopards back into the trap which we had placed two meters above floor to avoid lions and other scavengers. We stayed close to the trap for observation to make sure that the cats were fully recovered from the effects of the tranquilizer and back to normal condition before being released. Generally this was when they were able to keep their balance.

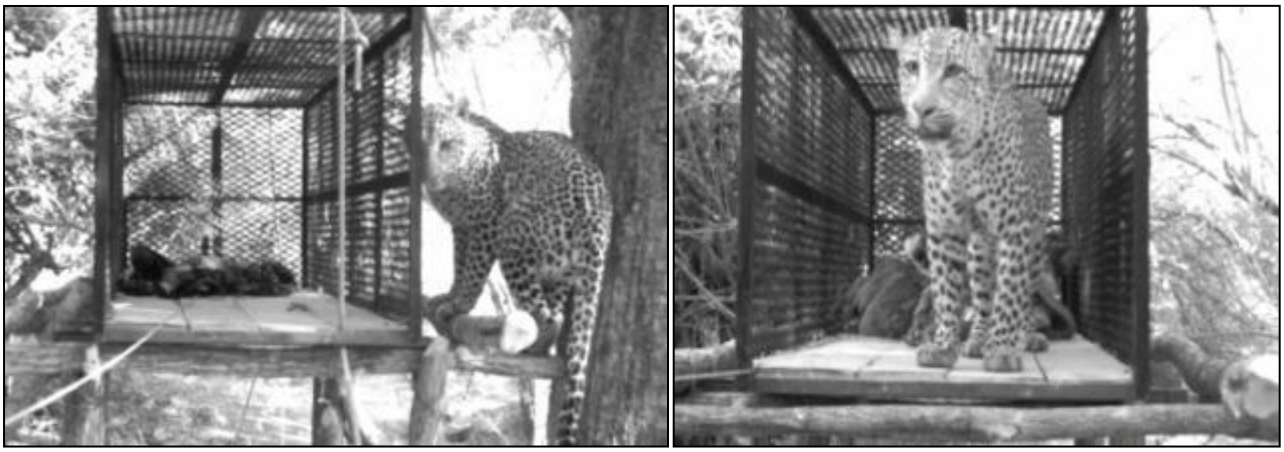


Figure 3.11: A leopard is inspecting the live-trap, which was inactive.

Figure 3.12: Female F1 was collared 2007

It took around 1.30 hrs (± 30) for females to raise their head and look around, another 30 (± 10 minutes) to sit up and take first steps. Generally it would take 3.5 to 4 hrs before the leopards were fully awake.

After another 15-20 min. of observing the animals for good health and condition we set them free from the trap. No complication occurred during any of these procedures.

On a few occasions we noticed a huge pride of lions close to the trap. In these cases we released the leopard in the morning to avoid any unnecessary risk.

3.2.2 Locations through VHF tracking

Observing individual leopards and also tracking them by spoor alone is very difficult due to their elusiveness. It has been proven in previous research that radio telemetry is the most effective method of gathering information on wild felids (AMLANER & MACDONALD 1980, SCHEMNITZ 1980, KENWARD 1987, BOOKHOUT 1994, WILSON et. al 1996).

Radio telemetry implies to equip cats with radio transmitters which broadcast signals that can be received by stationary or mobile receivers at remote locations. Transmitters on different cats are tuned into different radio frequencies thus permitting the researcher to locate and track the individual collared animal.

Figure 3.13: Tracking of a leopard with a VHF receiver.

The most common information obtained from radio telemetry is the location of the animal, but other data such as levels of movement activity can also be collected. Telemetric data can answer a wide range of questions related to behaviour, use of space, and intra-specific social relationships which are impossible to answer otherwise.

Two female (F1 and F2, e.g. Figure 3.12) and three male leopards (M1, M2 and M3) were equipped with VHF radio collars (Wagner Tracking, Germany). The leopards were located with an E 121-VR500 with HB9CV antenna with frequencies between 148-152 MHz (Wagner, Germany) and then by triangulation using compass bearings obtained from the signal directions (WHITE & GARROTT 1990) (Figure 3.13).

Three coordinates from three different positions were taken within an average time frame of 15 minutes and then digitised the location of all individuals by Universe Transverse Mercator coordinates. As far as possible, locations of individuals were taken twice a day, from a day time hour and a night time hour, so that finally every hour of a 24 hour day could have been covered. During the rainy season data could not be taken regularly.

For additional information regarding activity pattern every leopard was followed and tracked for 24 hours, apart from one male, which left the study area. Subsequently, not enough data was collected to develop a reliable activity pattern for this individual. Additional data (locations of the leopards) were taken by photo traps which captured all of the collared individuals.

3.2.3 Home ranges

In order to estimate home ranges of the collared individuals as well as overlaps between them I used ArcView GIS software (version 9.1) with the extension Animal Movements (Hawth tools). To calculate the home range estimates I used the 95% Minimum Convex Polygon (MCP) (Mohr 1947) as this is common to most felids studies published so far.

I used Kernel-method in order to quantify the relative space use within their home range estimates (Worton 1989). In order to determine the approximate usage within the home range I defined the 50% contour as the core area (Seaman & Powell 1996, Powell 2000, Kernohan et al. 2001).

Locatings which were temporarily too close to each other during the 24 hour follow periods were filtered to avoid autocorrelation. The time in which every leopard needed to cross its home range (White & Garrott 1990, Harris et al. 1990) was calculated to minimize dependence of data. Only data which lay below these time ranges were not included within the analysis.

M1 was tracked for around 12 months, from August 2007 until November 2008, with a break for around 2 months (July and August) after he had managed to destroy his collar.

In September he was re-collared. During these two months he was seen four times and he had been captured several times by camera traps.

M2 was tracked for around 9 months from September 2007 until June 2008, and then he left the area. Three months later he was seen in an area ca. 80 km away from the study area (South Luangwa National Park) directly bordered to a GMA. He settled there for around two and a half months until November. During this time he had several fights with a local resident female and ended up killing one of her cups. After that he left the area again.

3.2.4 Activity pattern

Every 15 minutes the activity of the leopards, and every solid hour the location was recorded; both by triangulation (Odden & Wegge 2005). Activity has been scaled into following categories depending on continuity and intensity of the radio signals (data taken by C. Stommel):

- *inactive (no activity and no location change)*
- *active (activity with or without location change)*
    - *activity (without location change, non-moving activity)*
    - *mobile (activity with location change)*

This classification has been already proven as reliable on wolves (Pahl 2004) and wild cats (Wittmer 1998). After one minute of observing the signal (the activity) was evaluated. If during this minute the signal strength remained unchanged the animal was considered to be "inactive". Variation in signal strength and pulse frequency (52-75 pulse/minute) was considered as "non-moving active" (Pahl 2004). If it was proved that a leopard was moving away during observation, e.g. by an angular change of the location direction, it was categorized as "mobile". The classification of these signals cannot be associated with certain behaviour because it was impossible to discriminate between an animal which was resting or one lying in wait for prey. This imprecision could be qualified by the length of observations and the numbers of location points (Wittmer 1998). For a most reliable statement about the activity pattern every hour needed to be covered by the same volume of recorded readings. A procedure of a 24 hour observation period for every leopard was carried out. For the determination of the activity pattern, four of the collared leopards (2 female, 2 male) have been followed for 24 hours over different time periods (3-13 weeks) between the months June to October 2008.

The animals were located every hour, and controlled additionally every 15 minutes. Due to this the number of locating points for the activity pattern is equivalent to the hours of observation. For every observing hour the activity pattern has been recorded.

Nevertheless, a gapless data acquisition was not always possible in some cases as very mobile animals moved out of the reception area. For one leopard not all 24 hours of a day could be covered. Thus, a clear statement about the missing hours cannot be made.

Gaps emerged due to signal losses. Therefore we averaged the results of activity of an hour over the number of observing days which included this hour. Data was collected in accordance with Zambia's time zone, GMT+2 hours. Day time has been defined as the hours between 6.01 h-18:00 h and as night time the hours between 18:01h-6:00h.

3.2.5 Analysis of habitat use

In order to proof if certain habitats are preferred or avoided by leopards I conducted an analysis of habitat use following Jacobs (1974). By this calculation it is possible to get a "negative" and "positive" habitat preference from the observed and expected frequency of use. Only vegetation types which cover a 5% minimum of the study area can be considered.

Formula according to Jacob (1974):

$$\text{Jacob-Index} = (p(\text{obs})-p(\text{exp})) / (p(\text{obs})+p(\text{exp}) - 2p(\text{obs})p(\text{exp}))$$

The frequency of use (amount of location points) is defined by p(obs) and percentage of the surface area by p(exp). Is the observed use similar or the same to the expected frequency of use, then the index is = 0 or close to zero. If a habitat is used higher than in relation to its occurrence the index goes to +1. If a habitat type is avoided the observed frequency of use is less than the expected. Apart from the fact that by this way also small samples sizes can be analysed, it is possible to signify differences in references between single habitat types.

3.2.5.1 Comparison of habitat availability and habitat use

Habitat use (*locating points of the leopards within the actual vegetation type*) and availability (*percentage of vegetation types within the 95% MCP polygons*) were compared. Every leopard was studied individually to find out differences between the animals. Therefore, locatings of females with a minimum error of 100 metres have been used. Finally, a range difference according to Jacobs (1974) was generated for every leopard, and the average value calculated to qualify a general statement.

3.2.6 Statistical methods

For statistical analysis non parametric statistical hypothesis tests were used such as the chi^2-test and the Mann-Withney-U Test (SPSS 13.0). The Mann-Whitney-U test is used for assessing whether two independent samples of observation have equally large values (Wilcoxon 1945, Mann & Withney 1947, Mühlenberg 1993). The chi^2-test is applied to see if the sampling distribution of the test statistics is a chi^2 - distribution when the null hypothesis is true (Mühlenberg 1993).

3.3 Results

3.3.1 Baiting and information collected during collaring procedure

The average responding time to baits was 2 days for the LNP and 4.6 days for GMA-A. Discriminating between sexes gave an average of 1.5 days for females and 2.6 days for males in LNP, and 2.4 days for females and 6 days for males in the GMA (Table 3.1).

Table 3.1: Average responding time to baits inside LNP and GMA-A

Sex of leopards	Responding time (days) in LNP	Responding time (days) in GMA-A	In total
♀	1.5	2.4	2
♂	2.6	6	4.6

In 2007 I collared three adult leopards F1, M1 and M2 inside the LNP. F1 was pregnant at this time, I estimated her age at about 6 years (according to Stander (1997) and to further characteristics of own experiences, see methods and Table 3.2). M1 was about 5-6 years and M2 about 4 years. Adult male leopards are larger and more muscular than female leopards, which is indicated by the different body weights of female (30-33 kg) and male leopards (48-58 kg) captured (see Table 3.2). Leopards were tracked from August to December 2007. In July and August 2008 two further leopards were collared, a female F2, and a male M3 outside of the LNP in the GMA-A (see Figure 3.16 and Figure 3.17).

I estimated the females age at about 6 years according to Stander (1997) and to further characteristics of own experiences, (see methods and Table 3.2), and the age of M3 at about 8 years.

Table 3.2: Overview of the five collared leopards

Collared leopards	Year of collaring	Sex	Age in years	Weight (kg)
F1	2007	♀	6-7	33
F2	2008	♀	5-6	30
M1	2007	♂	6-7	52
M2	2007	♂	4-5	48
M3	2008	♂	8-9	58

3.3.2 Home ranges

For every leopard individual time interval was calculated in which it can manage to cut across its home range. This was necessary to receive independent data. Only locating points are mentioned below (see Table 3.3) which were included in the home range calculations.

Table 3.3: Overview of the locating points of the five collared leopard

Collared leopards	Year of collaring	Sex	Number of locating points
F1	2007	♀	186
F2	2008	♀	182
M1	2007	♂	122
M2	2007	♂	55
M3	2008	♂	55

Three of the MCP-home ranges of all the leopards were larger than the home ranges calculated with Kernel method (see Table 3.4).

While the MCP home range of F1 (2007-2008) was about 42 km² and fell with 95% into the home range of M1 of about 56 km², the Kernel 95% home range embraced 15 km² and was with a maximum part of about 76% included in M1 home range. The females' 50% home range (2.8 km²) was included completely in M1's 95% home range (55 km²) and covered 68% of the southern 50% home range of M1 (3 km²). In total the 50% home ranges of M1 were about 4.5 km² (see Table 3.4).

MCP-Method

A	F1 (%)	F2 (%)	M1 (%)	M2 (%)	M3 (%)	MCP Home range size (km²)
F1	---------	------------	95.4	37	8	42 (3)*
F2	---------	------------	-------------	-------------	-------------	14
M1	72.5	------------	-------------	51.7	4.5	56
M2	44	------------	57.6	------------	-------------	50
M3	5.4	------------	2.3	------------	-------------	28

KERNEL Method

B	F1 (%)	F2 (%)	M1 (%)	M2 (%)	M3 (%)	KDE (95% / 50%) Home range size (km²)
F1	---------	------------	76 (68)[a]	56.7	0.5	15 / 2,8 (3/0.2)*
F2	---------	------------	-------------	-------------	-------------	17 / 2.3
M1	20.7 (63)[a]	------------	-------------	48.5	4.7 (4)[a]	55 / 4.5
M2	10.5	------------	33 (49)[a]	------------	-------------	81/8.1
M3	0.2	------------	7.9 (16)[a]	------------	-------------	33 / 3.1

Table 3.4: Percentages of overlaps within the home ranges of the different leopards collared, home range sizes of the leopards in km², calculated with A: Multi-Convex Polygon (MCP) and B: Kernel (KDE)-Method. *= F1 home range from 04-11.2008, [a] = overlap of the 50% home ranges

M2’s MCP-home range was of 50 km² and overlapped to ca. 44% and 51% of the home ranges of M1 and F1. This averaged 37% of M2’s home range. The Kernel home range embraced 81 km², and was overlapping the two other home ranges as well as with 10.5% and 33% of his range. M2’s 50% range is only partly included (49%) in M1’s 95% area and is found close to border between the LNP and GMA-B.

In 2008 the home range of M1 did not change and remained the same size as in 2007. From April to November 2008 the MCP-home range of F1 shrunk from 42 km² (MCP)/ 15 km² (KDE) to 3 km² (MCP)/ 3 km² (KDE) and was completely included in the home range of M1. There was also no change in M2’s home range until June 2008, but then he left the study area. At the end of October we managed to locate him approx. 80 km (linear distance) away from the actual study area. Then he left this area again.

The home range of F2 was about 14 km^2 (MCP)/17/2.3 km^2 (KDE 95%/ 50%). Her home range did not overlap with any of the other leopards collared in this study. The home range of M3 was about 28.4 km^2 (MCP)/33 /3 km^2 (KDE 95%/ 50%) and overlapped with 4.5% of his MCP-home range the home range of M1. One of M3's 95% KDE ranges was situated with 7.9% in M1's home range and one of M1's 95% KDE-occurrences was situated in M3's home range at 4.7% (see Table 3.4).

3.3.3 Home ranges in and outside the National Park

While the female F1 never left the LNP, the MCP-home ranges of the males M1 and M2 were situated at approximately 1.4% (KDE: 3%) and 16% (KDE: 29%) in the southern GMA (see Table 3.5 and Figure 3.14). But as Figure 3.15 indicates, the KDE-50% home ranges of M1 were entirely inside the LNP, whereas M2's 50% home range borders with the southern GMA-B. The MCP-home range of F2 remained mainly in the GMA-A (see Figure 3.16) and had a 12.8% (KDE: 14%) overlap with the area of the LNP. Her KDE-50% occurrences (2.3 km^2) were situated mainly in the GMA-A (see Figure 3.17) but overlapped the LNP with 22%. The MCP-home range of M3 was situated with 54.2% (KDE: 53%) in GMA-A and with 45.7% (KDE: 47%) in the LNP. His KDE-50% occurrence was located entirely in the LNP.

Table 3.5: Percentages of overlaps (based on A: MCP-home ranges, B: KDE-home ranges) between the home ranges of leopards collared with area of LNP and the northern GMA-A, home range sizes of the leopards in km^2, calculated with A: Multi-Convex Polygon (MCP) and B: Kernel (KDE)-Method. *= F1 home range from 04-11.2008, [a] = overlap of the 50% home ranges

A	**Overlaps of the home ranges with LNP or GMA-A**		**MCP-Home range sizes**
	LNP (%)	GMA (%)	MCP (km^2)
F1	100	---------	42(3)*
F2	12.8	87.2	14
M1	98.6	1.4	56
M2	84	16	50
M3	45.7	54.2	28

B	**Overlaps of the home ranges with LNP or GMA-A**		**KDE-Home ranges sizes**
	LNP (%)	GMA (%)	KDE (95%/ 50%) (km^2)
F1	100	---------	15/ 2,8(3/0.2)*
F2	14 (22)[a]	86	17/ 2.3
M1	97	3	55/ 4.5
M2	71	29	81/8.1
M3	53	47	33/ 3.1

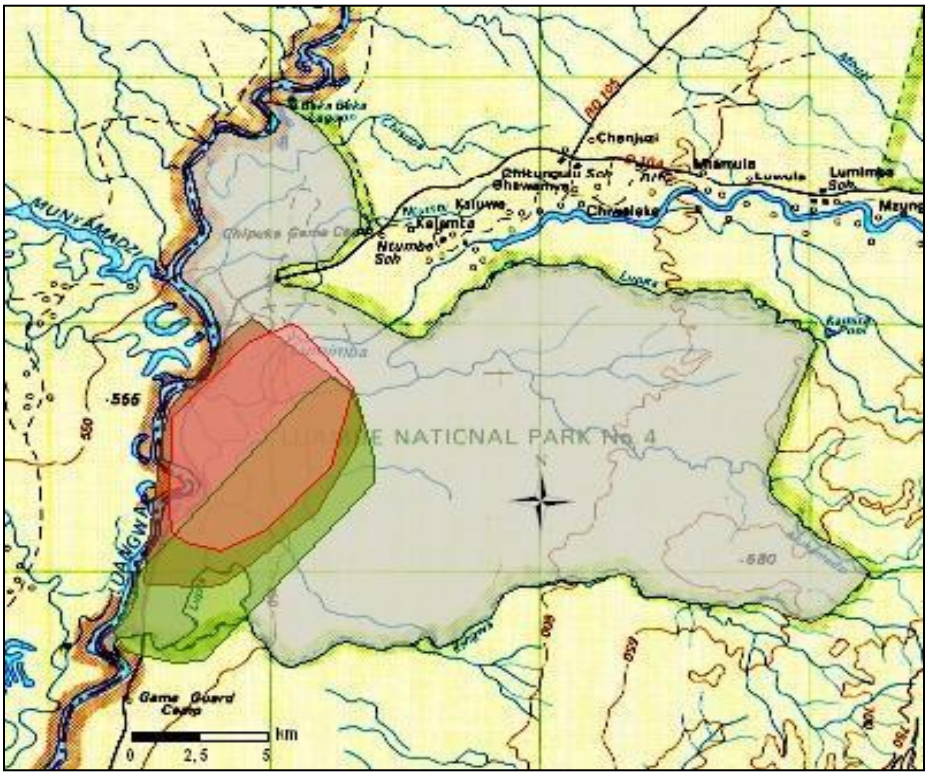


Figure 3.14: MCP-Home ranges of three leopards, 2007–2008, M1 (brown), M2 (green), F1 (08.2007-03.2008) (red)

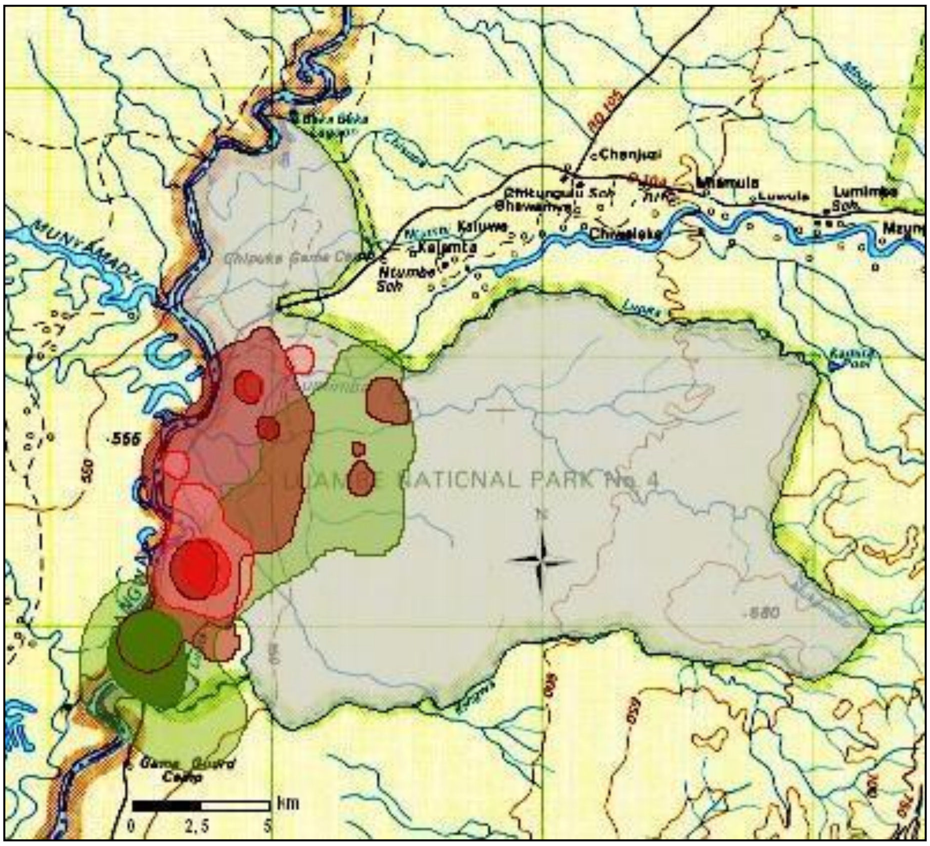


Figure 3.15: Kernel-Home ranges (95% & 50%) of three leopards, 2007-2008, M1 (brown)/ dark-brown), M2 (green/dark-green), F1 (08.2007-03.2008) (red)

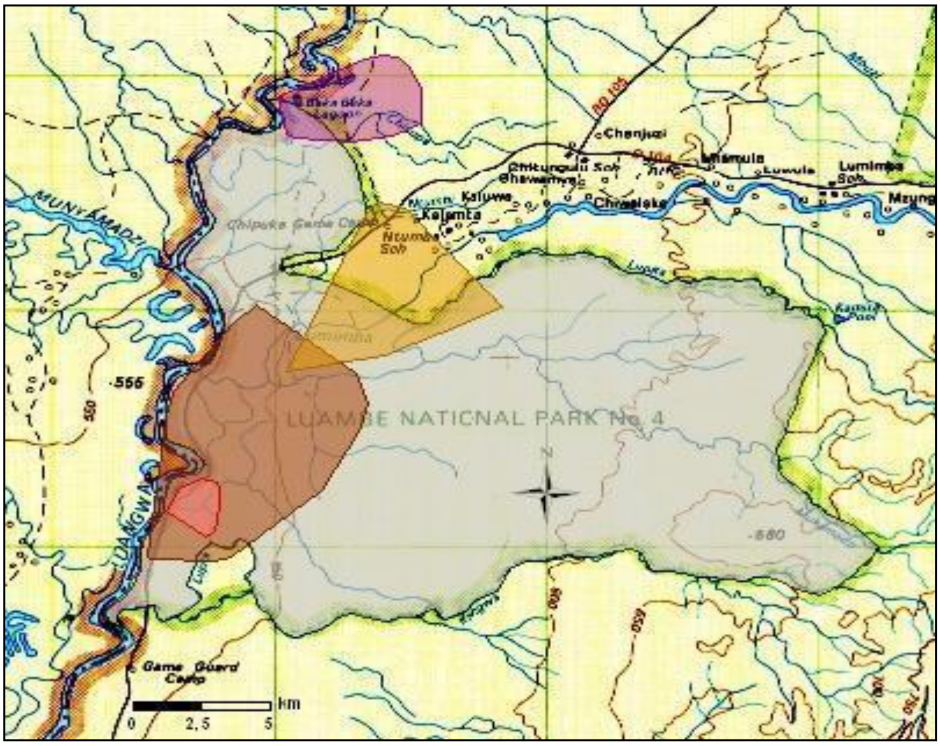


Figure 3.16: MCP-Home ranges (95%) of four leopards 2008, M1 (brown), M3 beige), F1 (light red), F2 (violet)

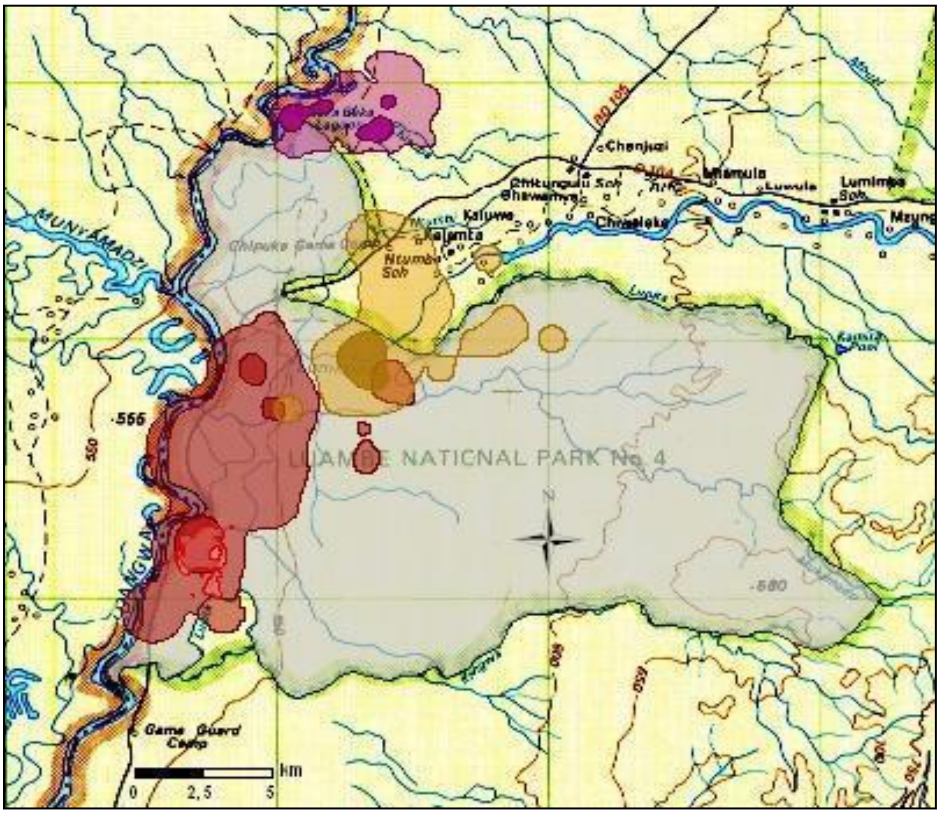


Figure 3.17: Kernel-Home ranges (95% & 50%) of four leopards 2008, M1 (brown/dark-brown), M3 (beige/light-brown), F1 (red/light red), F2 (violet/dark violet)

3.3.4 Tendencies of certain factors in relation to home range size

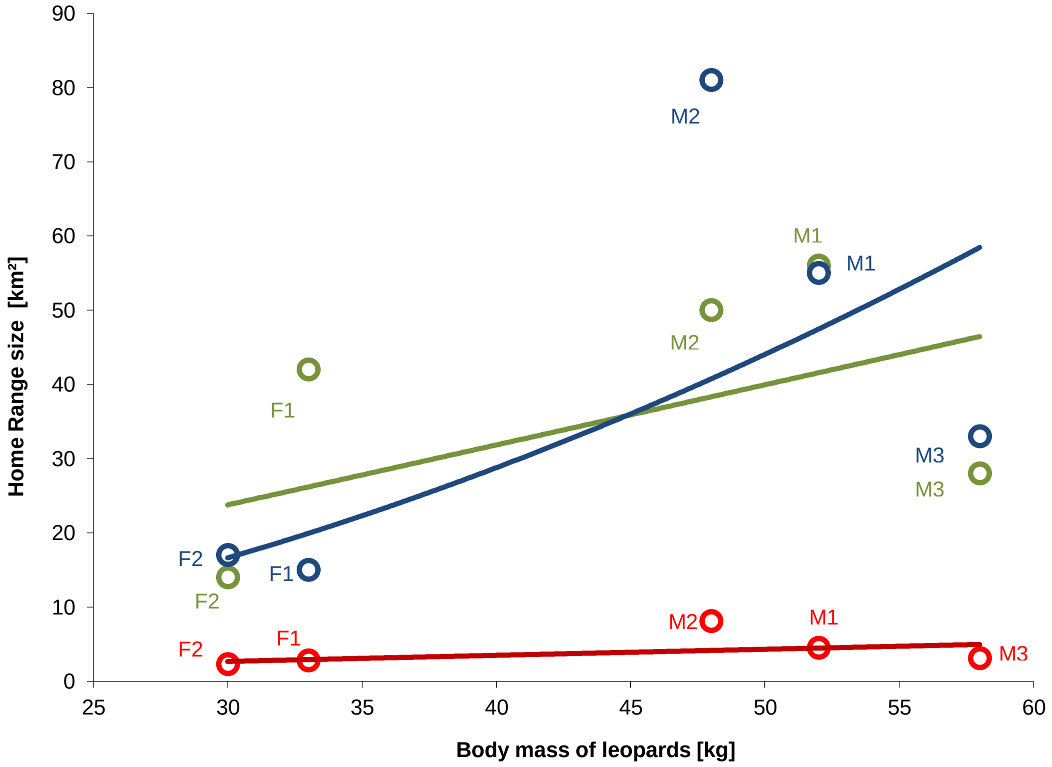


Figure 3.18: Relationships between body mass and home range sizes of the leopards, calculated with MCP-, KDE (95%) -and KDE (50%) home ranges. (Potential regressions, green= MCP, R^2=0.275; blue: KDE 95%, R^2= 0.576; red: KDE 50%, R^2= 0.299)

Regression analyses of the MCP-, KDE (95%) – and KDE (50%) home ranges differ from each other (Figure 3.18). While the regressions of the MCP-values and KDE 95%-values indicate that the size of a home range is depending on body mass of a leopard, the size of the KDE 50%-core area of the leopards is not related to body mass.

Figure 3.19 illustrates the relationship between the females' home range size and the age of the cubs. This indicates that the size of home ranges is not depending on body mass and age of adults, but other factors. During the time when F1 had no cub her home range size was about 42 km², but it shrunk to 3 km² while she had a cub < 1 year. F2 had an older cub > 1 year and her home range was with 14 km² larger than that of F1.

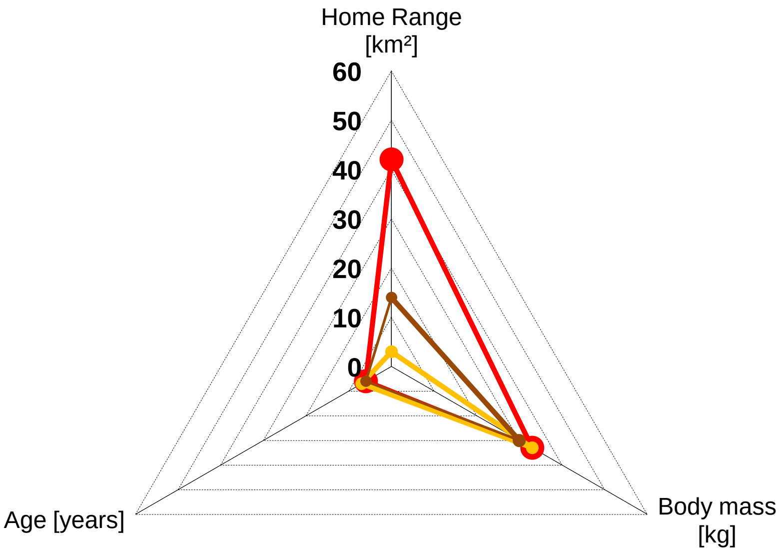


Figure 3.19: The relationship between home range size of the females (F1 and F2) and the age of the cubs, and without a cub. Red: F1 (no cubs); yellow: F1 (cub < 1 year); brown: F2 (cub > 1 year)

3.3.5 Activity pattern

Four of the collared leopards (2 female, 2 male) have been followed for 24 hours over different time periods (3-13 weeks) between the months June to October 2008 (Table 3.6). The number of locating points for the activity pattern is equivalent to the hours of observation.

Table 3.6: Overview of four leopards which were intensively followed for activity pattern analysis between the months June to October 2008

leopards	sex	Age in years	Number of locatings	observing hours	
				day	night
F1	♀	6-7	148	71	77
F2	♀	5-6	222	108	114
M1	♂	6-7	32	25	7
M3	♂	8-9	41	20	21

3.3.5.1 Comparison of mobility and immobility

Comparison between mobility and immobility (Figure 3.20) of day and night times showed differences. Data of mobility have been averaged over 12 hours for night and day times. The female leopards (F1 and F2) were mobile during 20-30% of daytime, which increased for both the cats up to 36% at night times. The mobility of the two male leopards M1 and M3 during day time was between 21-23% and increased during night to 41-52%. From day to night times mobility of the males were increasing on an average of 24.5% whereas the mobility of the females increased just on an average of 11%. Mobility of both sexes were significantly higher (p=0.002) during night hours, whereas males moved significantly more (p=0.009) than females (Figure 3.21).

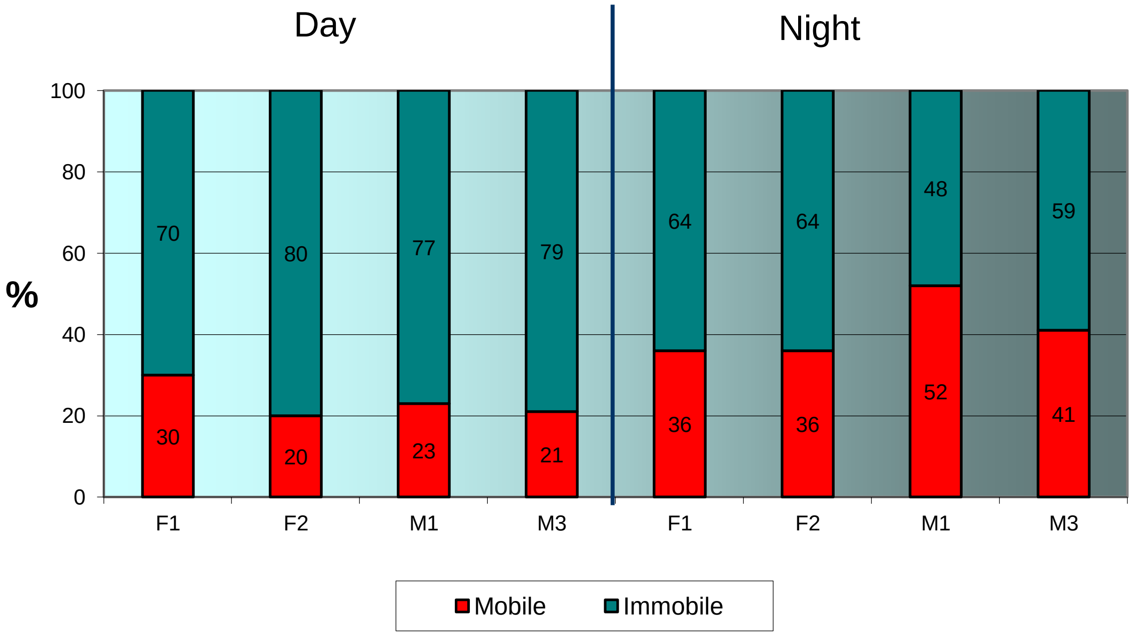


Figure 3.20: Overview of mobility and immobility over day and night hours of four leopards (F1, F2, M1, and M3) followed for 24 hours (in percentage)

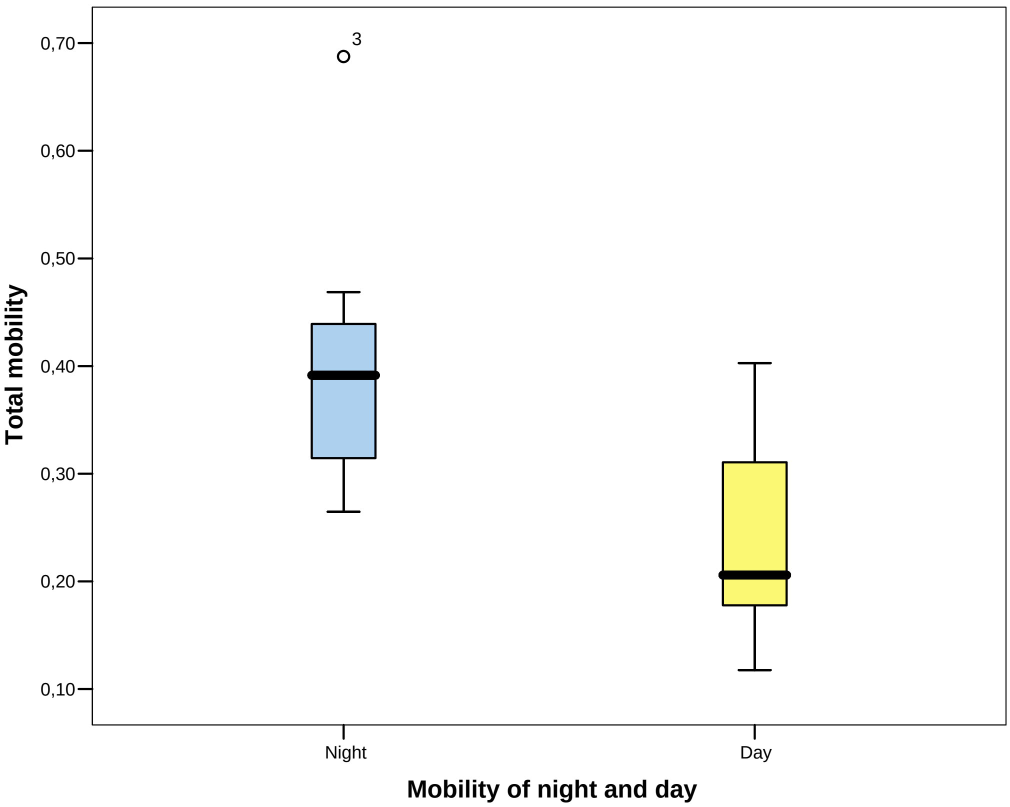


Figure 3.21: Difference between mobility at night (blue) - and day-time (yellow), Mann-Whitney-U-test (p=0.002)

3.3.5.2 Activity pattern in the course of the day

Movement and activity pattern of F1

148 (71 at day, 77 at night) observing hours have been analysed for the activity pattern of the female F1. Every hour of a day (0:01-23:01h) could be covered between five to nine times. The activity pattern in the course of the day shows between 10:01h-12:01h a decrease of mobility (11 and 10%) with a minimum of activity (35%) (Figure 3.22).

Within the hours 13:01-14:01h activity increased together with a slight increase of mobility and both decreased after that until to 15h. From 15:01h activity increased and reached its maximum of 100% around sunset (between 17:00-18:00h). The maximum mobility was reached around 20:01h. After that, mobility and activity decreased. From 22:01-04:01h the activity increased and showed a peak within 01:01-02:01h and decreased after that. The mobility remained almost constant low during these hours. In the course of the early morning hours, and sunrise, between 05:01-07:01h, activity and mobility increased again. After this, both values decreased until 11:01h.

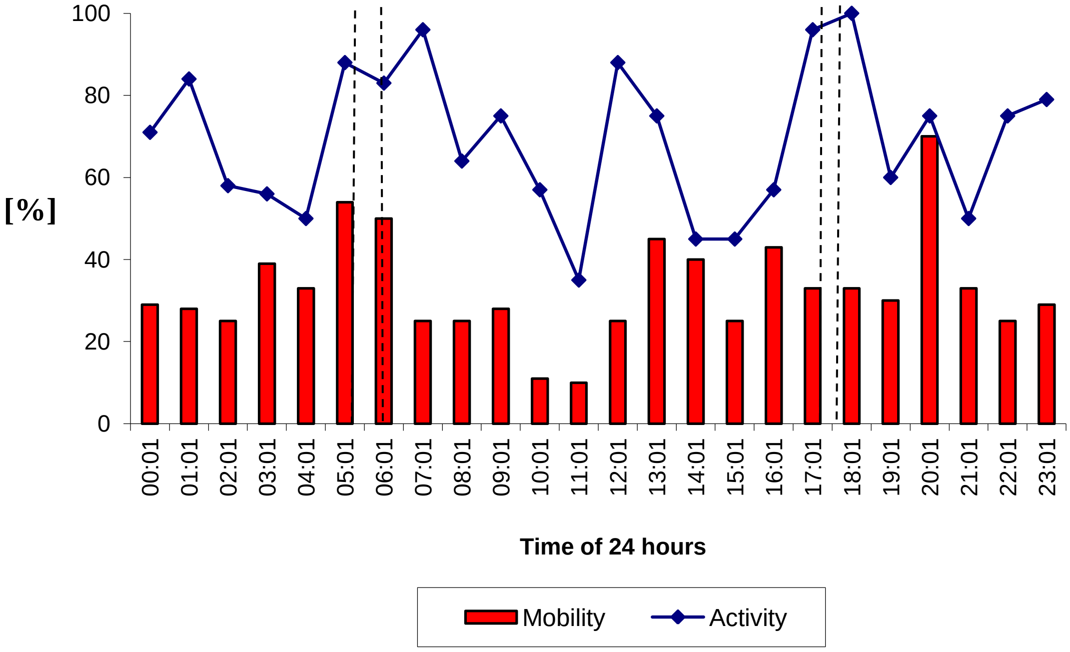


Figure 3.22: Representation of the activity pattern (%) of animal F1, observation over 24 hours time period. The dashed line indicates sunrise and sunset.
Activity = stationary activity; mobility = activity with movement

Movement and activity pattern of F2

Activity pattern has been analysed with 222 (108 at day, 114 at night) observing hours. With F2 it was possible to record every hour of a day at least eight times, sometimes twelve times. From midmorning until late afternoon (11:01-17:01h) the values of activity and mobility decreased (Figure 3.23), with a slight peak of activity between 14-15h. A mutual minimum was reached 13:01h. Both values increased with sunset and remained constantly high from 19:01h to 22:01h. The maximum of activity at 94% was achieved at 20:01h and the maximum of mobility at 56% around 21:01h. Mobility decreased between night hours 23:01-03:01h to 31-28%. Activity remained almost constantly high with a slight variation during night hours and decreased from 10:01h. Mobility lessened between 04:01-07:01h to 15%. Around 09:01h mobility values show a short time increase at 58% and decrease after that between 12:01h and 15:01h.

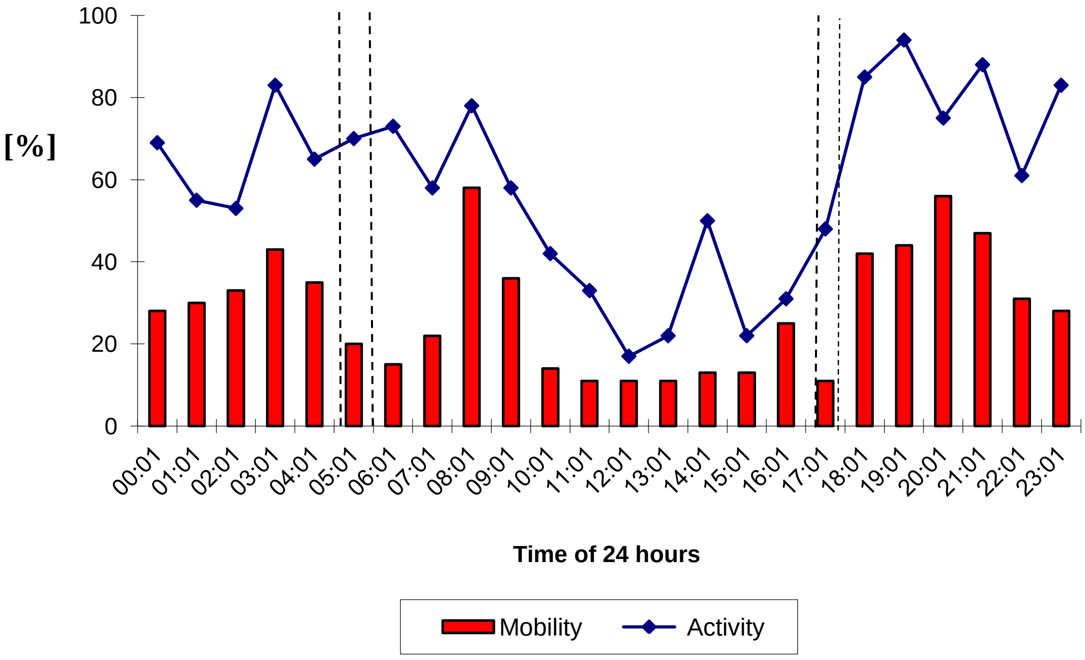


Figure 3.23: Representation of the activity pattern (%) of animal F2, observation over 24 hours time period. The dashed line indicates sunrise and sunset.
Activity = stationary activity; mobility = activity with movement

Movement and activity pattern of M1

The male leopard M1 destroyed his collar and could not be located for around three months via triangulation. In September, it was possible to trap and equip him again with a new collar. Due to this a much lower number of observation hours in contrast to the female leopards were recorded. However, the activity pattern of the male M1 could be analysed from the number of 41 observing hours (20 at day time, 21 at night time). It was possible to cover all 24 hours of a day (0:01-23:01h) one to three times. The activity showed a clear decrease in the 11th hour (11:01h), without notification of mobility. Between 07:01-15:00h mobility was about 33%, but increased after 15:01h and reached a maximum together with activity from 19:01-21:00h. While the activity remained constantly high, the mobility decreased until 22:00h. After 22:01-23:01h both the values achieved absolute zero, but increased after that again. During the 6th morning hour (06:01h) and sunrise, activity and mobility increased to maximum. Between 7:01-9:01h no mobility was observed. Activity declined continuously from 7:01h and reached the minimum between the 10th and 11th hour (Figure 3.24).

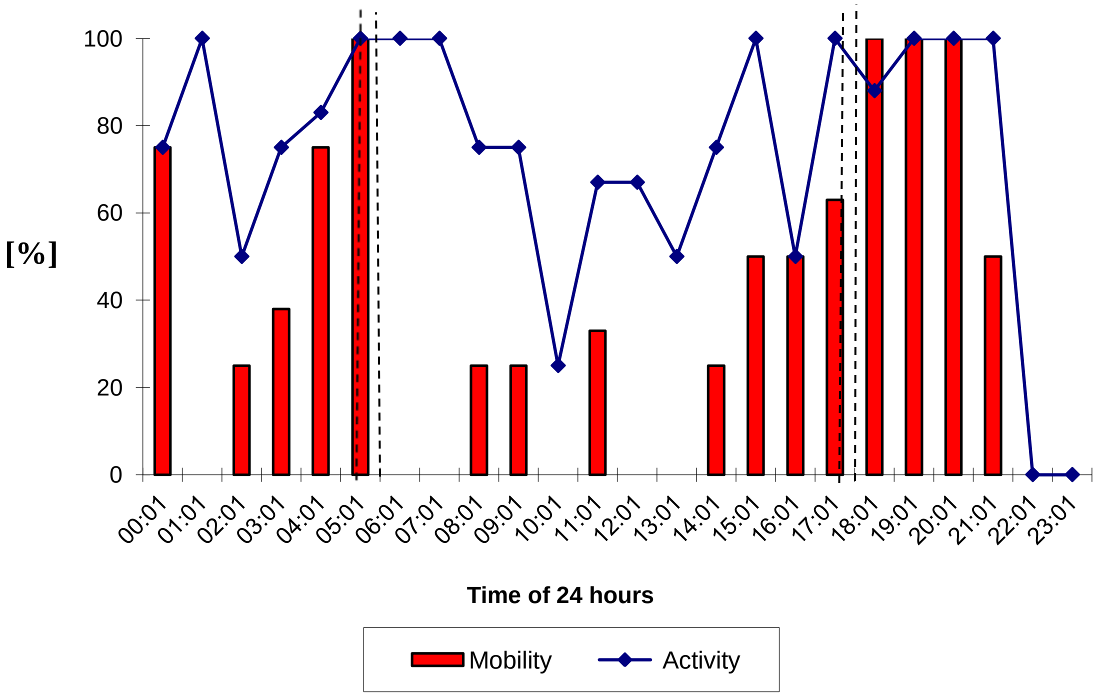


Figure 3.24: Representation of the activity pattern (%) of animal M1, observation over 24 hours time period. The dashed line indicates sunrise and sunset.
Activity = stationary activity; mobility = activity with movement

Movement and activity pattern of M3

I was aware about the presence of this male by camera-traps before, but M3 went into the live-trap late so that he could not get collared earlier during time of data acquisition. According to this a lesser number of 32 observing hours (25 at day time, 7 at night) in comparison to the females were taken. Not all hours of a day could be covered consistently. Data for following hours could not be recorded: 19:01-23:01h, 4:01h, 12:01h and 16:01h (Figure 3.25). Values of activity decreased from hours between midmorning to afternoon (no data for 12:01h) to 10%. No mobility between 11:01-15:01h was recognized. Between 15:01 and 16:01h both values increased, also in the hour of sunset from 17:01-18:01h. During night hours between 01:01-03:01h a maximum of mobility and activity was achieved as well as a slight increase of both values during sunrise and morning hours 05:01-07:01h and 09:01-10:01h. A maximum of activity in the morning hours was reached within the 11th hour of midmorning.

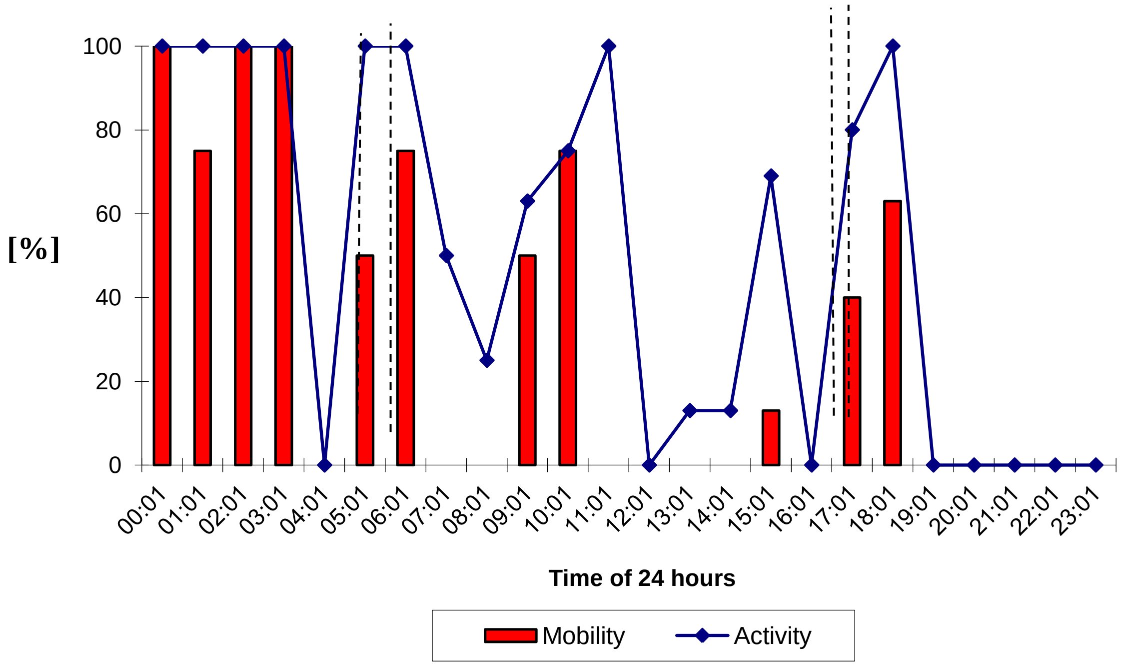


Figure 3.25: Representation of the activity pattern (%) of animal M3, observation over 24 hours time period. The dashed line indicates sunrise and sunset.
Activity = stationary activity; mobility = activity with movement

3.3.6 Habitat composition of the different leopard home ranges

To represent the habitat prevalence and preferences of the radio-tracked leopards I used the MCP-home ranges in order to see which categories of habitat were accessible and used by the animals (see Figure 3.26 und Figure 3.27).

The dominating habitat type for the home range of female F1 (Figure 3.28) was grassland with 51% followed by Combretum-Terminalia woodland (18%), semi permanent water and riverine woodland (7%). Vegetation such as thickets, acacia woodland and mopane scrubland were represented by a lesser amount (4%, 3%) and water occurred at 1%.

From April to November 2008 the females F1 home range shrunk to a much smaller size to what it was before and due to that habitat composition changed within these months. The dominating habitat type at this time was Combretum-Terminalia woodland (29%), followed by riverine woodland (17%), semi permanent water (14%) and grassland (11%). Mopane scrubland and Mopane woodland made up 8% and 7%, while thicket and acacia woodland covered 6%. Pure water occurrences represented 3% (Figure 3.29).

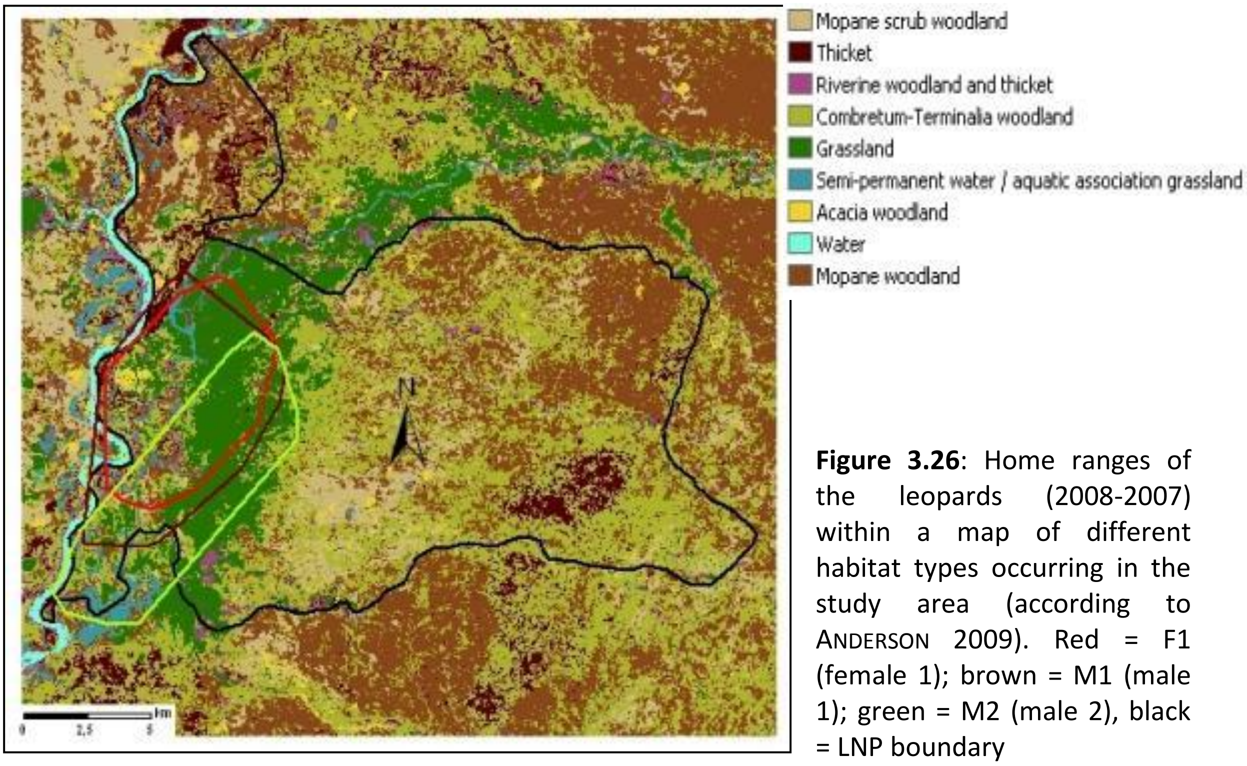


Figure 3.26: Home ranges of the leopards (2008-2007) within a map of different habitat types occurring in the study area (according to ANDERSON 2009). Red = F1 (female 1); brown = M1 (male 1); green = M2 (male 2), black = LNP boundary

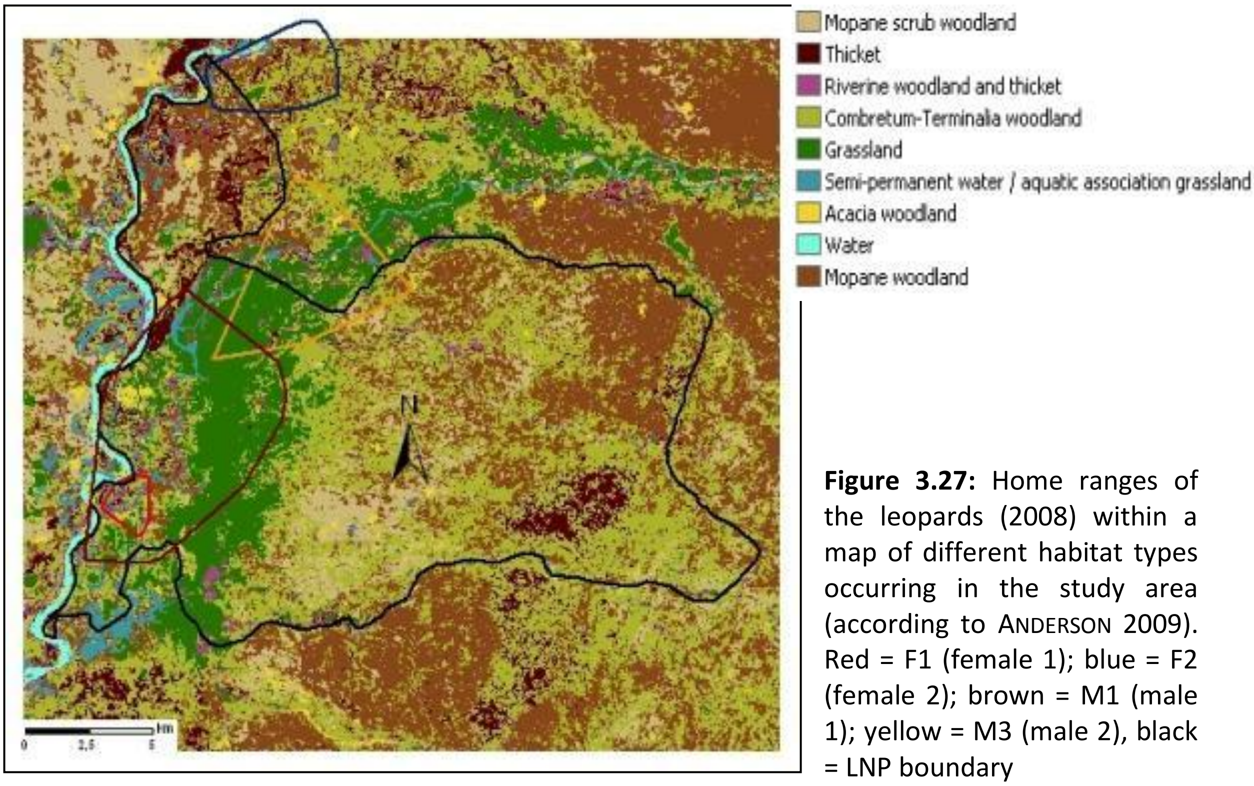


Figure 3.27: Home ranges of the leopards (2008) within a map of different habitat types occurring in the study area (according to ANDERSON 2009). Red = F1 (female 1); blue = F2 (female 2); brown = M1 (male 1); yellow = M3 (male 2), black = LNP boundary

Habitat compositions within the home ranges of collared leopards

🟥 Mopane woodland
🟩 Thicket
🟫 Combretum-Terminalia woodland
🟨 Mopane Scrubland
🟦 Riverine woodland and thicket
🟩 Grassland
⬜ Semi permanent water/acquatic association grass
⬛ Acacia woodland
⬜ Water

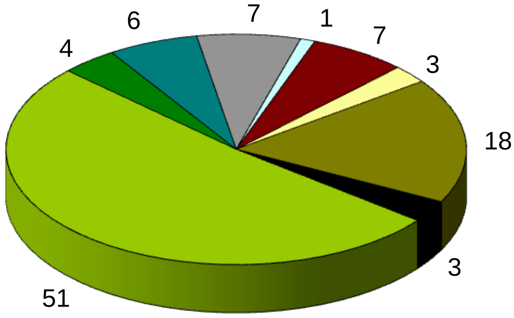


Figure 3.28: Habitat types within the home range of F1 (female 1) 08.2007-03.2008

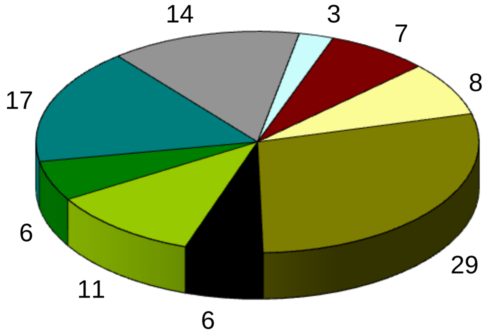


Figure 3.29: Habitat types within the home range of F1 (female 1) 04-11.2008

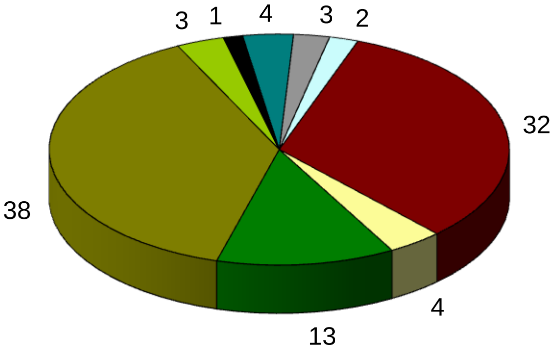


Figure 3.30: Habitat types within the home range of F2 (female 2) 2008

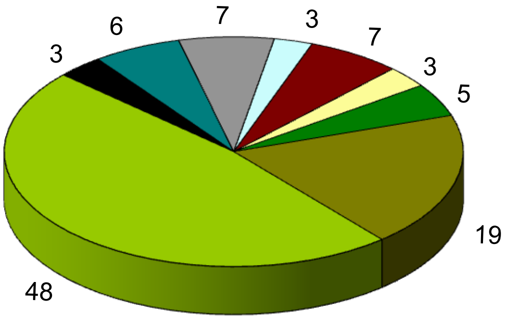


Figure 3.31: Habitat types within the home range of M1 (male 1) 2007-2008

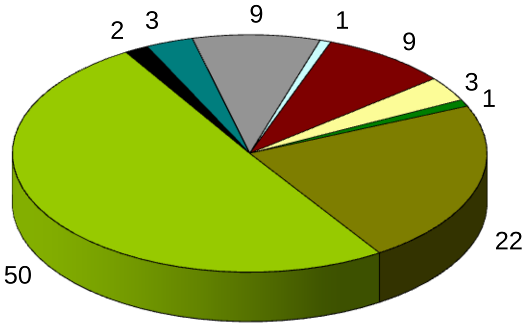


Figure 3.32: Habitat types within the home range of M2 (male 2) 2007-2008

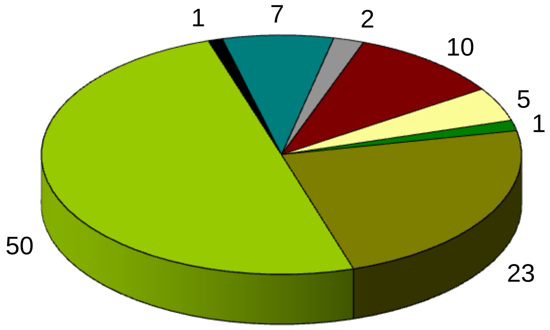


Figure 3.33: Habitat types within the home range of M3 (male 3) 2008

The dominating habitat type in F2’s home range was Combretum-Terminalia woodland (38%) followed by Mopane woodland (32%) and thicket (13%). Further habitat types ranged from 4-1% (Figure 3.30).

The home range of M1 was dominated by grassland (48%). The second most frequently occurring habitat type was Combretum-Terminalia woodland (19%). Habitat types such as semi permanent water/aquatic association grass, riverine woodland, and thicket were represented at 7%, 6% and 5%. Acacia woodland, Mopane scrubland, and water occurred at 3% in his home range (Figure 3.31).

Grassland (51%) was the most frequently represented habitat type in M2’s home range. The second most frequent was Combretum-Terminalia woodland (22%). Semi permanent water/aquatic association grass and Mopane woodland embraced 9% whereas habitat types like Mopane scrubland and riverine woodland covered 3%. Less represented habitat types were Acacia woodland (2%) and water (1%) and thicket (1%) (Figure 3.32).

In M3’s home range grassland (50%) was the dominating habitat type and the second most occurring habitat type was Combretum-Terminalia woodland (23%). Mopane woodland covered 10% and riverine woodland 7%. Mopane scrubland, semi permanent water / aquatic association grass, thicket and Acacia woodland comprised 2%, 1%, 1% and 1% of his home range. Water such as parts of the Luangwa River did not occur in M3 home range (Figure 3.33).

3.3.7 Habitat availability versus habitat use

In F1's home range from August 2007 to March 2008 habitat types such as Combretum-Terminalia woodland, Mopane woodland, Mopane scrubland were used more frequently (22.1% 18.2%, 6.5%) than their coverage availability (17.6 %, 6.9%, 2.5%) would have suggested (Figure 3.34). Habitat types like thicket, riverine woodland, semi permanent water/aquatic association grass and water were also strongly used (7.8%, 11.7%, 15.6% and 2.6%) in relation to the availability (4%, 6.4%, 7.3% and 1%). Although the availability of grassland was very high (51.3%), it was hardly used (13%). The use and availability of Acacia woodland (2.6% and 3.1%) was almost conforming.

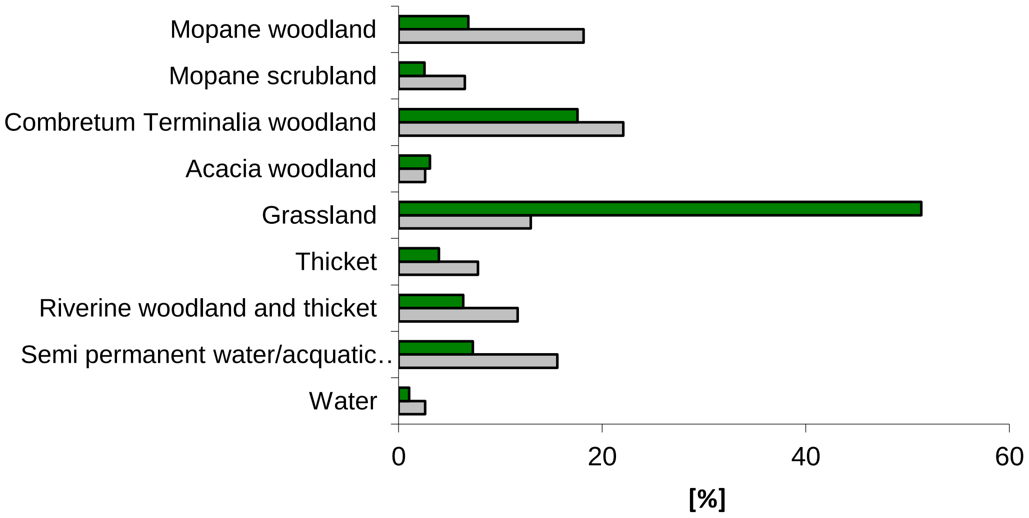


Figure 3.34: Habitat availability v.s. habitat use of F1 (female 1) from 08. 2007-03.2008. Y: habitat types, X: ratio, green = habitat prevalence, grey = habitat use (locatings)

From April to November 2008 the female's F1 home range shrunk to a much smaller size with Combretum-Terminalia woodland as the most available (28.7 %) and most used habitat (38.5 %) (Figure 3.35). Mopane woodland and thicket was also more frequently used (11 %, 7.3 %) as expected by their occurrence (7.4%, 5.3%). The use of Mopane scrubland (8.3 %) and its availability (7.9 %) were almost the same. The use of further habitats such as riverine woodland, semi permanent water, grassland, Acacia woodland and water (14.7%, 8.3%, 8.3%, 2.8%, 0.9%) was less in comparison to their higher availability (17%, 13.9%, 11%, 5.7%, 2,5%).

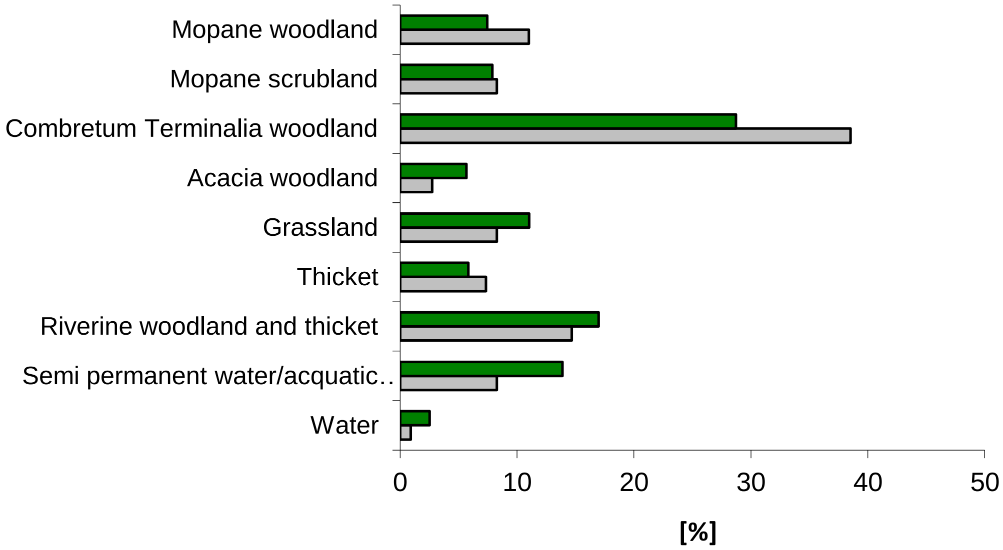


Figure 3.35: Habitat availability v.s. habitat use of F1 (Female 1) from 04-11.2008
Y: habitat types, X: ratio. green = habitat prevalence, grey = habitat use (locatings)

In F2's home range (Figure 3.36) Mopane woodland, thicket, riverine woodland and semi permanent water were more often used (38%, 14.6%, 5.3% and 4.1%) than their availability would have suggested (32.4%, 12.5%, 3.5%, and 2.5%). Use and availability of acacia woodland was almost the same (1.2%/ 1.4%).

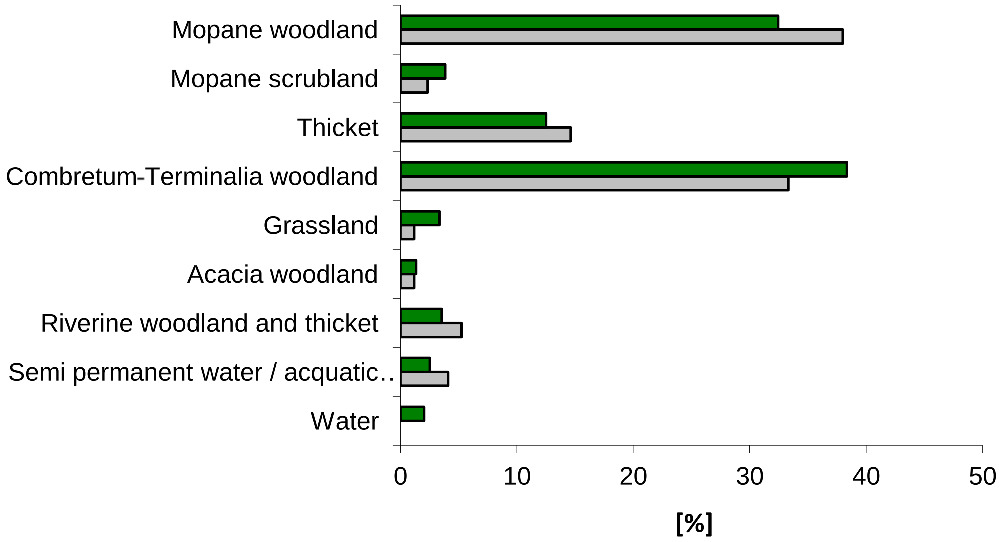


Figure 3.36: Habitat availability v.s. habitat use of F2 (female 2) 2008;
Y: habitat types, X: ratio. green = habitat prevalence, grey = habitat use (locatings)

F2’s use of Combretum-Terminalia woodland was (33.3%) although it was the most available habitat type (38%). Further habitat types such as Mopane scrubland, grassland and water have been less used (2.3%, 3.4%, 0%) than their availability (3.9%, 3.4%, 2%) would have suggested (Figure 3.36).

The male M1 (Figure 3.37) used the habitat type Combretum Termialia woodland also much more (23%) than it was available (19%), followed by Mopane woodland, thicket and riverine woodland (10.7%, 9.8%, 8.2%). The occurrence of those three was less (6.6%, 4.7%, 6.2%). Mopane scrubland, semi permanent water /aquatic association grass and water were almost similar in usage (3.3%, 6.6%, and 3.3%) and availability (3%, 6.7%, and 2.7%).
Grassland was the only habitat which has been less frequently used (32.8%) than its availability (47.8%) would have suggested. However it was the most used vegetation type.

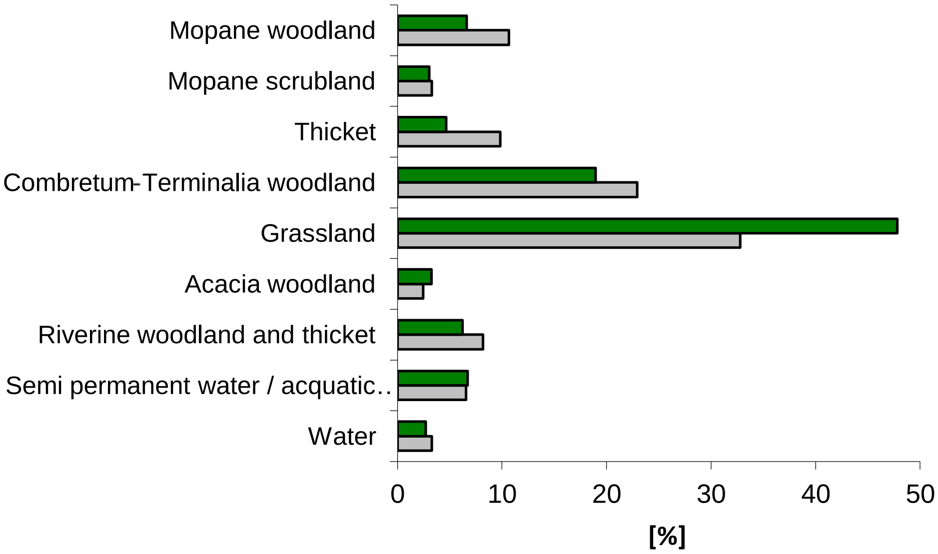


Figure 3.37: Habitat availability v.s. habitat use of M1 (male 1) 2007-2008
Y: habitat types, X: ratio. green = habitat prevalence, grey = habitat use (locatings)

In M2’s home range (Figure 3.38) the use of Mopane woodland, mopane scrubland, Combretum-Terminalia woodland, riverine woodland and water (14.5%, 5.5%, 23.6%, 5.5%, 1.8%) was in relation to their availability (8.6%, 3.4%, 23.6%, 3.2 %, 0.8%) higher. Use and availability of acacia woodland were nearly the same (1.8%, 1.6%). Grassland and semi permanent water/ aquatic grass association were less used (41.8%, 5.5%) in contrast to their availability (50.5 %, 8.7%) while thicket with an availability of 0.9% was not used.

M3 (Figure 3.39) used riverine woodland, semi aquatic association grass more frequently (18.2%, 3.6%) than their availability (7.5%, 2.1%) would have suspected.

Grassland and thicket were used (50.9%, 1.8%) almost as much as they were available (49.9%, 1.4%). Mopane woodland, mopane scrubland and Combretum-Terminalia woodland were used lesser (5.5%, 3.6%, 16.4%) than their availability (10.2%, 4.6%, 23.4%) would have assumed. Acacia woodland occurred at 1% but was not used. Water such as river parts or lakes did not occur in M3 home range.

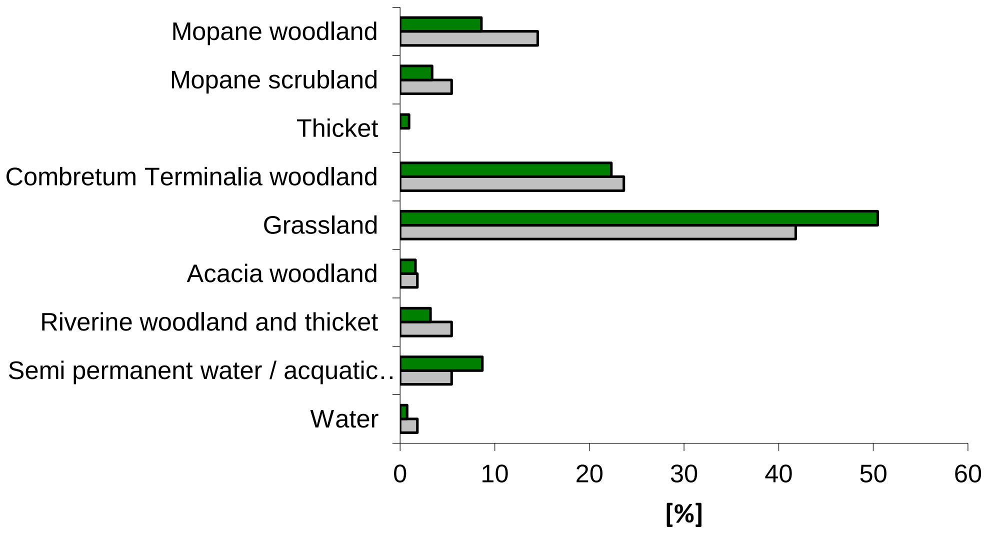


Figure 3.38: Habitat availability v.s. habitat use of M2 (male 2) 2007-2008
Y: habitat types, X: ratio. green = habitat prevalence, grey = habitat use (locatings)

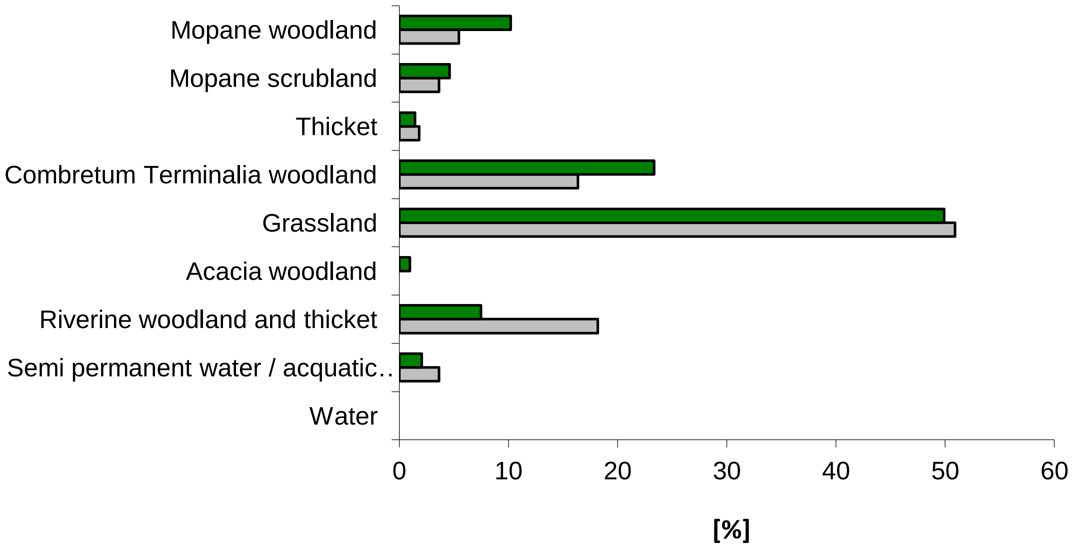


Figure 3.39: Habitat availability v.s. habitat use of M3 (male 3) 2008
Y: habitat types, X: ratio. green = habitat prevalence, grey = habitat use (locatings)

3.3.8 Habitat preferences according to Jacobs (1974)

From August 2007 to March 2008 F1 (Figure 3.40) showed a preference for Mopane woodland, semi permanent water/ aquatic association grass and riverine woodland but strongly avoided grassland (-0.75). Thicket, Acacia woodland, Mopane scrubland and water could not be considered in this case (Jacobs 1974), due to their occurrence under 5%.

In F1's home range after March 2008 (Figure 3.41), a preference for Mopane woodland, thicket, riverine woodland and Combretum-Terminalia woodland can be recognized, although lesser values are represented as in Figure 3.40. Further habitat types are avoided by F1, especially Acacia woodland, with a value of - 0.36.

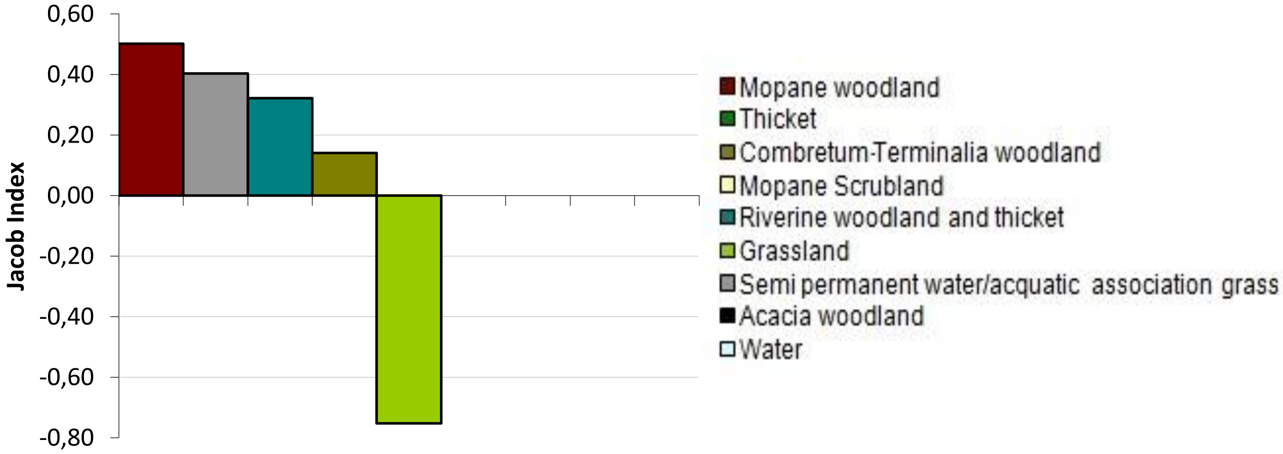


Figure 3.40: Habitat preferences of F1 (2007-2008), according to Jacobs (1974), positive values show preferences, negative values show avoidances. Habitat types that occurred below 5% were not included in this calculation (Jacobs 1974)

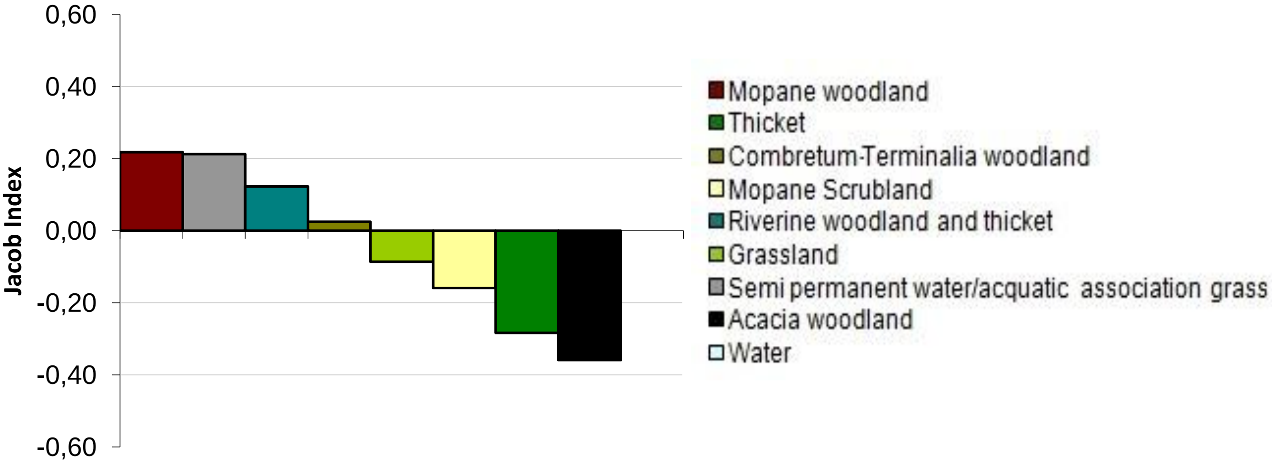


Figure 3.41: Habitat preferences of F1 (April-November 2008), according to Jacobs (1974), positive values show preferences, negative values show avoidances. Habitat types that occurred below 5% were not included in this calculation (Jacobs 1974)

F2 showed (Figure 3.42) preferences for Mopane woodland and thicket. The avoiding of grassland (-0.11) is also supported by the Figures 3.30 and 3.36. Other habitat types occurred in F2's home range below 5% could not be included in this calculation (JACOB 1974).

In M1's home range (Figure 3.43) preferences for thicket, Mopane woodland, riverine woodland and Combretum-Terminalia woodland are indicated. A slight avoidance for semi permanent water/ aquatic association grass (-0.01) as well as an avoidance of grassland (-0.31) is indicated.

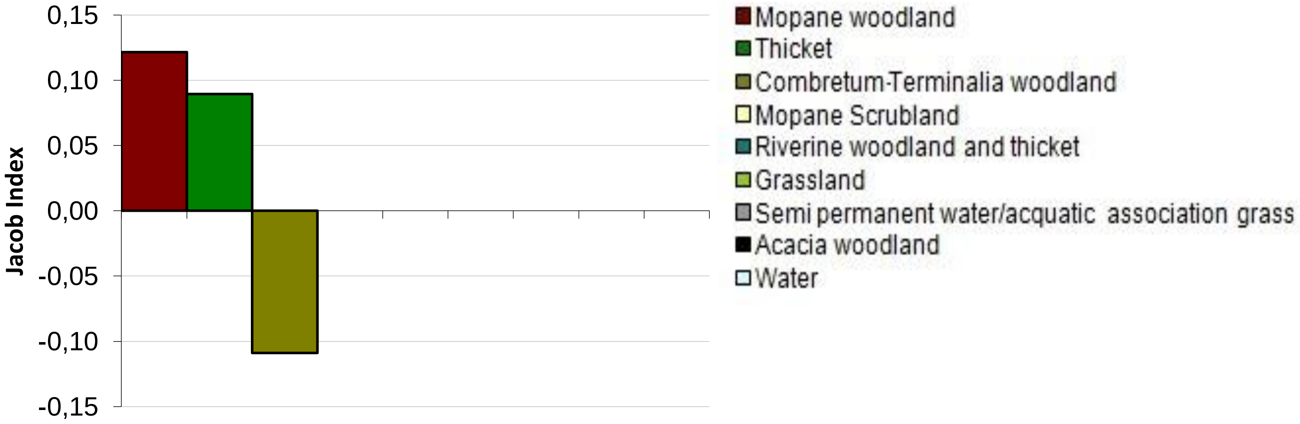


Figure 3.42: Habitat range preferences of F2 (2008) according to JACOBS (1974), positive values show preferences, negative values show avoidances. Habitat types that occurred below 5% were not included in this calculation (JACOBS 1974)

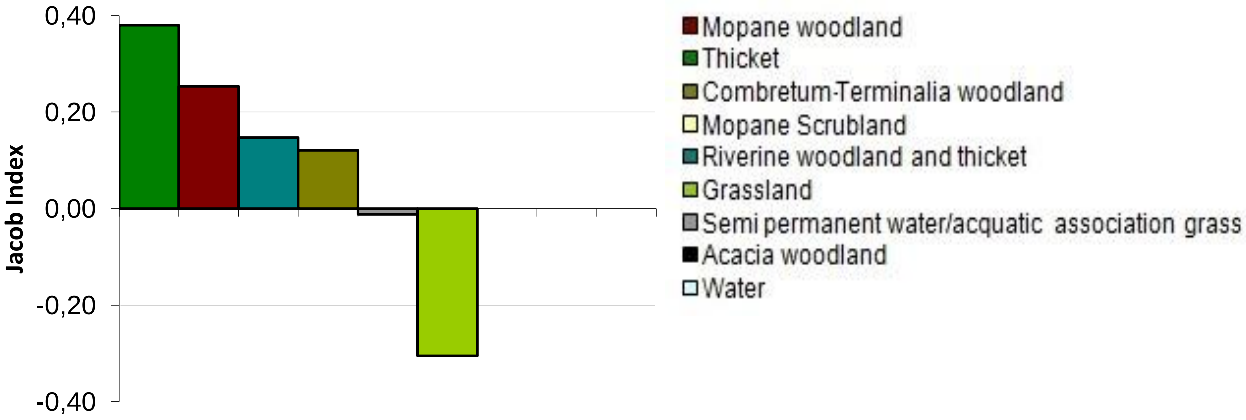


Figure 3.43: Habitat range preferences of M1 (2007-2008) according to JACOBS (1974), positive values show preferences, negative values show avoidances. Habitat types that occurred below 5% were not included in this calculation (JACOBS 1974)

M2 shows (Figure 3.44) a strong preference for Mopane woodland (0.29) and a slight preference for Combretum-Terminalia woodland (0.04), but the low value (very close to zero) rather indicates that he used habitat adequate to its availability which is also supported by Figure 3.38.

M3 (Figure 3.45) indicates a strong preference for riverine woodland and thicket (0.47). Grassland shows a positive value of 0.02. The negative value for Mopane woodland (-0.33), Combretum-Terminalia woodland (-0.22) and Mopane scrubland (-0.12) would indicate avoidances.

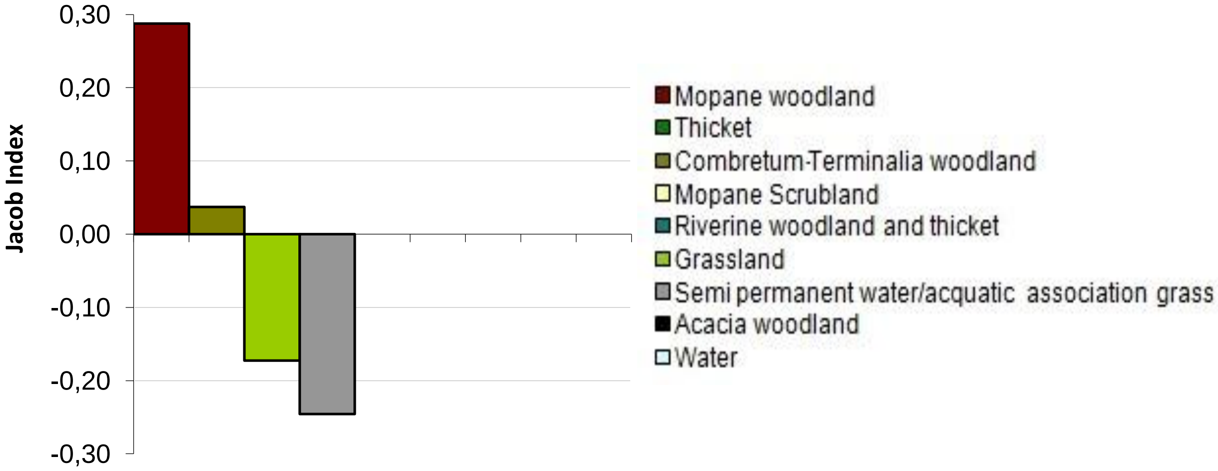


Figure 3.44: Habitat range preferences of M2 (2007-2008) according to JACOBS (1974), positive values show preferences, negative values show avoidances. Habitat types that occurred below 5% were not included in this calculation (JACOBS 1974)

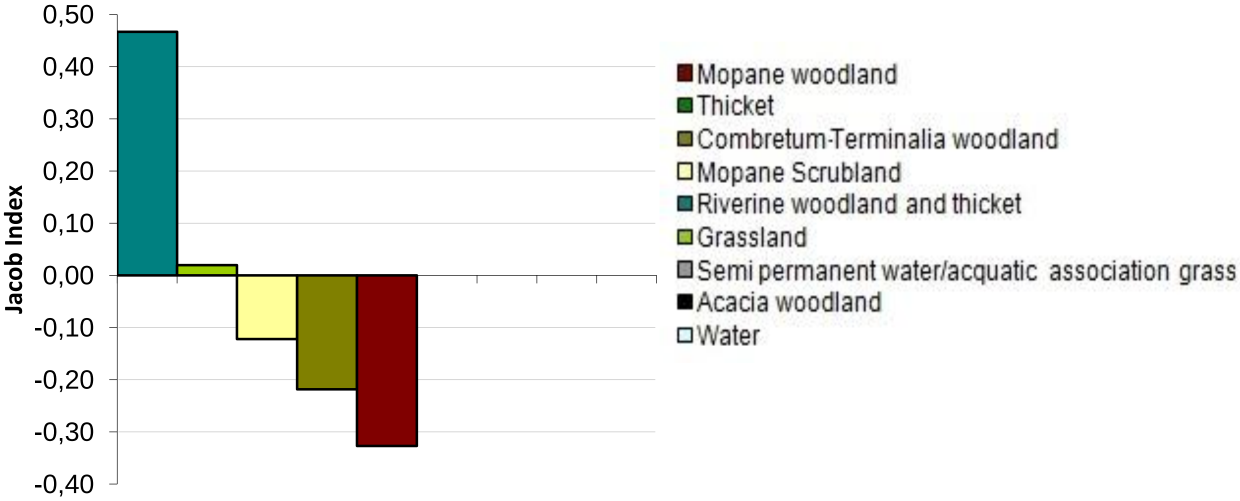


Figure 3.45: Habitat range preferences of M3 (2008) according to JACOBS (1974), positive values show preferences, negative values show avoidances. Habitat types that occurred below 5% were not included in this calculation (JACOBS 1974)

The values averaged over the females and the males (Figures 3.46 and 3.47) show slight differences between the preferences of males and females. Females (0.28; 0.08) show a stronger preference for Mopane woodland and Combretum-Terminalia woodland than males (0.07; -0.02) and also a stronger avoidance (-0.31) of grassland than males (-0.15).

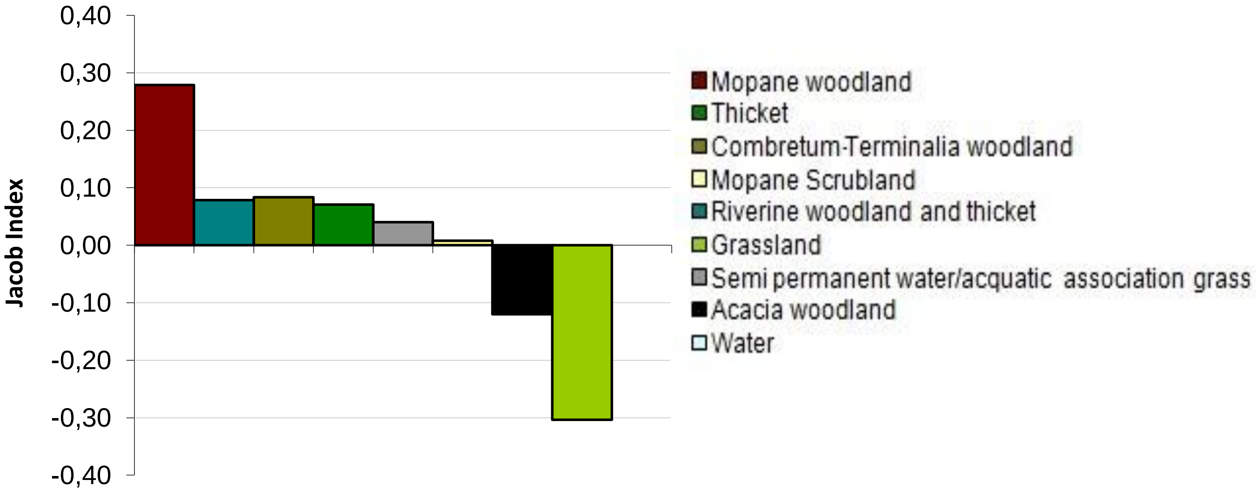


Figure 3.46: Habitat preferences averaged over the females, according to Jacobs (1974), positive values show preferences, negative values show avoidances. Habitat types that occurred below 5% were not included in this calculation (Jacobs 1974)

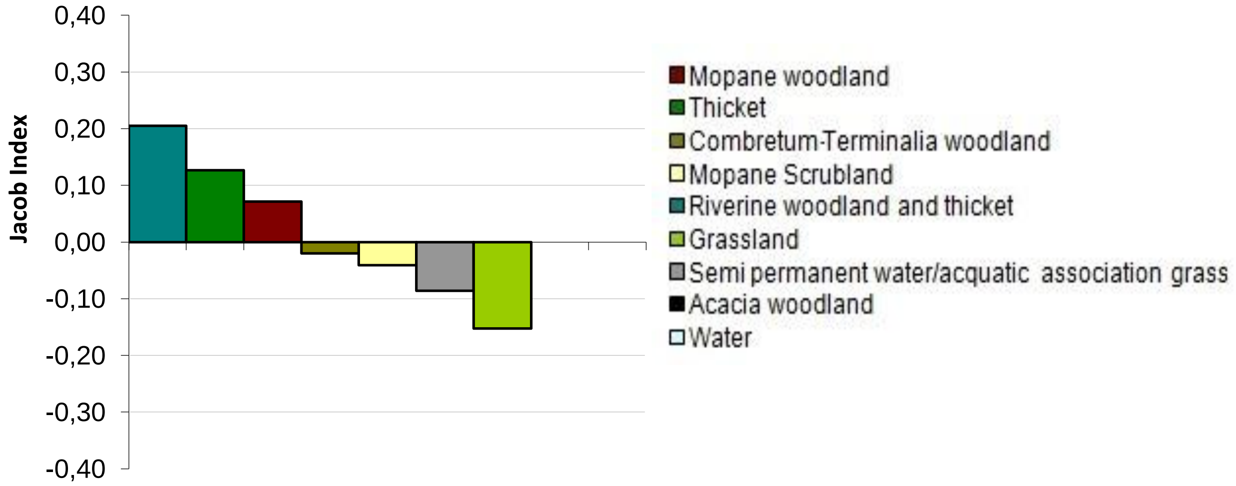
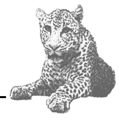


Figure 3.47: Habitat preferences averaged over the males, according to Jacobs (1974), positive values show preferences, negative values show avoidances. Habitat types that occurred below 5% were not included in this calculation (Jacobs 1974)



3.4 Discussion

3.4.1 Baiting and information collected during collaring procedure

The observation that leopards of LNP responded earlier to the baits than leopards within the GMA-A could indicate that leopards are aware of the disturbed situation in the GMA. Therefore, leopards living in the GMA are probably more timid than leopards living in the LNP.

All the collared leopards were weighed and showed as in other studies and observations (Bailey 1993, Meinertzhagen 1938, Wilson 1968) a sexual dimorphism (♀: 30-33 kg; ♂: 48 -58 kg, see Table 3.2). Comments of several trophy hunters implied that the leopards of the Luangwa Valley are in general of small size and definitely much smaller than those occurring for example inside the Kafue National Park region in the west of Zambia. Further, I was told that although the collared male leopards would be very good trophies for this area, many leopards were shot during hunting safaris in the surrounding GMA's that have been much heavier at about 70-80 kg. These, however, are weights based on visual observations and estimates, and not by weighing those hunted individuals. Weights of leopards seem to be very variable across their range. Other studies and observations report about males that weighed for example 35.5 kg (Schaller 1972) or 44.1 kg in India (Schaller 1972). Pienaar (1969) reported that leopards in the Kruger Park seldom exceeded 59.1 kg and Bailey (2005) accounts in the early 1970s weights averaged 63 kg from 5 male leopards and 37.2 kg from 6 female leopards inside Kruger Park. 63 kg as an average weight for males was also reported in Kenya (Meinertzhagen 1938).

In Zambia the heaviest male weighed by Robinette (1963) was about 56 kg and by Wilson (1968) about 59.9 kg. The latter noted an average weight of 33.6 kg from six females. My sample size is possibly too small to give reliable statements, but the recorded weights in my study do not differ much from these previous reports from Zambia. The collared male leopards appeared due to visual observations huge and heavy and were sometimes also mistaken at night with lionesses. M1 was visual estimated at first to be 70 kg, before it was weighed. The fur also made them appear much bigger as they really were. According to these experiences I assume that professional hunters were probably also mistaken by just visual estimating the leopards' weights.

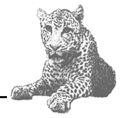
The theory about huge differences in size between leopards of the Luangwa Valley and those of the Kafue region is lacking scientific data to support it. They could be of interest for further studies to determine actual weights. Interviews with Zambian hunters indicated that massive leopards estimated between 70 – 90 kg were shot in the hilly regions of the valley. STEVENSON-HAMILTON (1947) also described two leopard types inside the Kruger National Park region: a small leopard occurring in the hot lowlands and a larger leopard living in the hilly, high country.

3.4.2 Home ranges in and outside the National Park

I used two home range calculation methods to get a more detailed analysis. Both methods have pro's and con's: The MCP-method connects the external locations points with each other and shows a good overview of the possible home ranges, but it does not focus on an area of main occurrences. The 50% Kernel polygons focus on an area of main occurrrence. However, the home ranges calculated with Kernel, get larger the less locating points you put into calculation.

The comparison between the Kernel and the MCP home ranges indicate that the home ranges calculated by Kernel are probably not reliable in this case, because the number of locatings differed strongly between the individuals (as tested). Therefore the premise for every calculation by Kernel is different. Due to this for example the home range of M2 calculated with Kernel reached a much larger size than calculated with the MCP-method. Consequently, using the MCP-method for comparing the home range sizes with each other is more convenient in this case. Nevertheless, the 50% Kernel polygons give an insight in which area the core occurrence of the home range is located. In consideration, if GMA's have an impact on leopard home ranges this information might be important.

The home range (KDE and MCP) of female F1 is smaller and included inside the larger home range of M1. This is not surprising since it is assumed that this male is the father of her cub. The shrinkage of F1's home range from April 2008 can be explained due to her motherhood. According to photo trap pictures she had a cub which was already old enough to accompany the mother (approx. 4-6 months), but not for long distances. It was likely born at the beginning of or during the rainy season. Leopards are considered capable of giving birth at any time of the year, however, cub survival are probably related to births being



timed for a particular period in the year. In East Africa for example, where two rainy seasons occur, carnivores like cheetahs (EATON 1974), hyenas (KRUUK 1972), wild dogs, and perhaps lions (SCHALLER 1972) are born in the early long rainy season. SCHALLER 1972 documented in the Serengeti National Park the birth of leopard litters at the beginning and one near the end of the dry season, which could confirm my assumption.

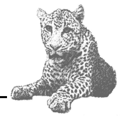
The home range of male M2 overlapped both these home ranges but due to the fact that he left the area be a sign that he was chased away by the older and bigger male M1. Months later I managed to locate him ca. 80 km south of the study area, where he tried to take up residence by killing one of two cubs of a female in this area.

Sexual selective infanticide seems to be a reproductive strategy by male carnivores (HRDY 1974, BERTRAM 1975a). Females which loose cubs resume their mating activities much quicker than females with surviving offspring (PACKER & PUSEY 1983, PACKER & PUSEY 1984).

Since this area (a part of South Luangwa NP) was directly bordered to a GMA, it could be possible that the previous male who fathered the cubs had been shot. During the time M2 was observed in this area I found no evidence or signs of any other male leopard which could have led M2 to take over this home range. Nevertheless, it seemed that he did not succeed because he left the area again and I lost signs of him.

The home range of the female F2 overlapped with none of the other collared leopards. She also had at least one male cub (evidence from a photo trap picture) which was already about 12 months old.

M3's home range was the smallest among the three home ranges of the males, but this was more likely caused by the short tracking period. M3 got captured and collared very late during data acquisition and therefore the study period was much shorter in comparison to the other four leopards. M3 was older and bigger than M1, and due to this his home range is probably much larger than it was shown during the tracking period. M3 overlapped the home range of M1 to a small degree. Assuming that his home range is much larger and by that embracing a larger part of the LNP, both the home ranges of the two male leopards would necessarily overlap with each other to a much greater extent. The overlapping of males home ranges is not unusual and has been also experienced in prior studies (BAILEY 2005, ODDEN & WEGGE 2005). In this case they seem to tolerate and avoid each other which may support the "dear enemy effect" (YDENBERG et al. 1988) where familiar neighbours are rather accepted than unknown individuals.



None of the home ranges of the leopards was exclusively inside the GMA. M2 and M3 both visited the GMA's much more than M1 but their main home range areas were clearly inside the LNP.

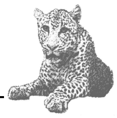
F1 never left the LNP while M1's home range bordered onto the southern GMA-B. However, M1 hardly overstepped the border. M2 also moved into the GMA-B but the larger part of his home range was inside the LNP. His 50% home range only bordered onto the GMA-B but was completely inside the LNP. M3 was captured inside the GMA-A, but he also frequented the same parts inside the GMA-A and in the LNP. His core area (50% home range) was inside the LNP. F2's home range (KDE & MCP) was the only range primarily distributed in the northern GMA-A, and with a smaller part occurring inside the LNP.

It is representative that all the home ranges are settled close to the Luangwa River. None of those moved deep into the eastern part of the LNP. Apart from the Luangwa River, which only partly dried out with preceding dry season, there were also lagoons which carried permanent water in the western part. Thus, this was a center of attraction for many species, including prey species. I noticed in the eastern areas that there were no lagoons and waterholes holding permanent water throughout the dry period. The farther east the dryer it got. Hardly any antelope species were seen. In view of these circumstances I assume that this area did not attract leopards.

3.4.3 Factors in relation to home range size

Home range sizes seem to be dependent on body mass as Figure 3.18 imply. This can be only hold true for the 95% (MCP & KDE) home ranges, because the regressions calculated with the values of both the methods show the same tendencies. The coefficient of determination for MCP-values is lower than 0.5 which is probably reasoned in the change of F1 home range size from 42 km^2 to 3 km^2. The 50% core area of the leopards in contrast does not appear to be dependent upon the body mass. But as soon as the leopards leave their core area for patrols the distance of those wanderings perhaps becomes dependent on their body mass (and perhaps also to their age).

In females the home range size seems to be dependent on additional factors (Figure 3.19). F2 was not anymore like F1, accompanied by a very young cub. But I assume a certain young male of older than 12 months to be her cub because he occurred in F2's home range



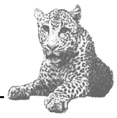
and sometimes he was captured together with F2 by a camera trap. Therefore, there is a relation between the age of the cub and the size of the home range. As Figure 3.19 shows, there are increases in the size of a female's home range with corresponding increase in the age of her cub. The older the cub the more independent it is. A cub of older than 12 months is perhaps not as much exposed to infanticide as a cub of six months. These observations described are also in accordance to the studies conducted in the Kruger National Park (Bailey 2005) and Nepal (Odden & Wegge 2005).

3.4.4 Activity pattern

3.4.4.1 Comparison of mobility and immobility

Both sexes were significantly more mobile during night than daytime hours. Mobility data for all leopards averaged at 41% during the night and 24% during the day. This is supported by Bailey (2005) where he observed in South Africa a mobility of leopards of 65% during night time and 42% during day time. A reason for the lower mobility during day times could be attributed to the very high temperatures encountered in the Luangwa Valley. The temperature reach 30°C between June and July and during summer months between August and November often rises above 40°C (see climate diagram, Figure 1.2). Further, mobility of leopards could be influenced by the mobility of prey species (Sunquist & Sunquist 2002, Jenny & Zuberbühler 2005) which will be looked at in more details in Chapter 3.4.4.2.

F1 showed a higher mobility during day times than the others. This could be explained by the existence of a very young cub (Bailey 1993). It is possibly safer to move around with a young cub during day time than at night times when more predators (such as lions and hyenas) are active. Male leopards may be more capable of defending themselves than females (Bailey 2005), especially when they have cubs. An additional reason for the higher mobility of F1 during day time could be that motherhood required feeding on a kill more often than usual.



3.4.4.2 Activity pattern in the course of the day

The mobility of males in the course of a 24 hour day was significantly higher than those of the females. Most of the possible reasons have already been discussed above. A further reason could be the distinctive territorial behaviour of males who have to patrol a larger home range.

Females with cubs possess smaller home ranges and cover shorter hunting distances (Bailey 1993, Sunquist & Sunquist 2002) which can be confirmed in this study. The mobility of females and males increased during night hours at 11% and 24% respectively. The higher mobility by males compared to females during the night were also observed in the only few studies about the activity pattern of leopards (Bailey 1993, Odden & Wegge 2005). It has also already been proven in other felids (Schmidt 1999, Wassmer et. al. 1988) like lynx's (*Lynx lynx*) and mountain lions (*Puma concolor*). Because males tend to cover longer distances than females during a 24 hours day the temperature might influence their movement (Bailey 2005). In order to avoid the heat of the day they might use the night hours for wandering longer distances.

The most widely documented intra-specific mortality for felids is infanticide, recorded for most pantherines (Davies & boersma 1984; Bailey 1993; Smith 1993). The higher mobility of males at night could be another reason for females with cubs to be less mobile at the same time avoiding infanticide (apart from other predators) by unrelated male leopards. This was also assumed by Odden & Wegge (2005).

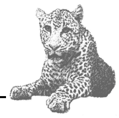
All observed animals showed a minimum of activity and mobility during 11:01-13:01h which leads to the conclusion that the cats avoided being active during the hottest hours of the day (Hamilton 1976, Bailey 2005). All the leopards showed an increase of activity and mobility before or during sunrise and sunset, which could be related to the activity of prey species. Sharpe's grysbok (*Raphicerus sharpei*) and bushbuck (*Tragelaphus scriptus*), two of the chief prey species for leopards in this area (see chapter 4) show their main activity during sunset and night time (Wronski et al. 2006, Kingdon 2007). Further important prey species in this study such as puku (*Kobus vardoni*) and impala (*Aepyceros melampus*) showed the highest activity during early morning (6:00h) and evening (16:00-16:30h) hours (Rduch 2008, Simon 2008, Skinner & Chimimba 2005).

The mobility before or during sunrise and sunset can be also confirmed by the observations at bait stations where all leopards were captured by photo traps chiefly during early morning and evening hours. This knowledge was also used by trophy hunters who are not allowed to hunt animals after sunset.

The activity of all leopards shows only between 11:01-13:01h a significant minimum. This might imply that they were resting. Bailey (1993) substantiated that leopards very seldom are entirely immobile, even if they lie or rest they change their posture periodically, or raise their head as soon as they notice noises or warning calls of any animals. These observations could explain why the cats in the average 24 hour day were mostly active, apart from at noon time.

Although the acquisition of radio data was taken in a vehicle, it cannot be excluded that the observed leopards did not get disturbed in their natural activity behaviour by proximity and sound of the motorcar. However, it seems to be that wild animals are less disturbed by detection from a car than by humans moving on foot (Pohlmeyer 1991). Apart from that the animals in this region were used to vehicles because of photographic safaris. As annotated a leopard was radio tracked every 15 minutes for a minimum of 1 minute. A stationary activity was noted when the fluctuation of signals and frequency (according to Pahl 2004) was strong. But we cannot rule out the possibility that atmospheric fluctuations or strong moving branches caused similar fluctuations of signals. The mobility which was used as an indicator of location change was not subjected to this error and can be considered as the most reliable data in this case.

The number of locatings for analyzing the activity pattern is very heterogenic among the four leopards. The facts that M3 was captured much later than the other leopards and that M1 destroyed his collar resulted in a shorter observation period. According to this activity data of the males showed observation gaps. Despite these restraints the collected data represent clear tendencies of the observed leopards, as an example the higher activity of males during night hours.



3.4.5 Habitat composition of the different leopard home ranges and comparison of availability and use

The habitat compositions of all the leopards observed apart from F2 were similar to each other since they partly overlapped each other. Only F2’s home range differed from the others by a minor percentage of grassland but included the highest amount of Mopane woodland. F1, M1, M2 and M3 included in their home ranges grassland as the largest part followed by Combretum-Terminalia woodland.

Although the percentages varied individually, the home ranges of all leopards comprised the same habitat types. Just M3 ‘s home ranges was lacking of “water”, because the term “water “ in our case was only used for parts of the Luangwa River. Apart from M3, the other four leopards were settled along the Luangwa River, but nevertheless in M3’s home range water certainly occurred in form of waterholes or lagoons which held permanent water.

The comparison between habitat availability and use shows that the leopards’ use of grassland in most cases (apart from M3) is much lower with regards to its availability. This definitely indicates that for both sexes dense habitat types are very important. Nevertheless, males generally tend to use grassland to a much higher extent than females. The high occurrence of grassland in the home ranges could be explained by the distribution of grazing antelopes such as pukus (*Kobus vardoni*) which are also one of the most consumed prey species by leopards in the LNP, but not in the GMA-A (see Chapter 4). Antelopes like impala (*Aepyceros melampus*) were found also in grassland, but mostly in dense vegetation (Simon 2008, Stuart & Stuart 1997, Kingdon 1997). Thus, grassland offers an important hunting opportunity. This can perhaps hold true especial for males, which are more mobile (see Chapter 3.4.4) than females and more defensive towards competitors such as lions (Bailey 2005). The latter also use grassland as an important hunting habitat in this region (personal observation).

Only M3’s use is appropriated to the availability of grassland in his home range. But here I have to debate that it could be possible that his home range - if I had time to observe M3 longer than three months- would have reached a larger size and then the use of grassland towards its availability would be reduced. Possible reasons, why M3 was more often located in the grassland of the LNP than of the GMA could be that the prey species occurred mostly inside the LNP due to the undisturbed situation (no people and no hunting allowed). The leopard also might have preferred the undisturbed LNP in order to avoid the villages and hunting activities in the GMA-. The assumption that leopards are capable of knowing the difference between a disturbed and undisturbed area could be supported by the different time periods between LNP and GMA-A when leopards were observed feeding on a bait.

The percentage of the habitat composition changed with F1's smaller home range in 2008. Instead of grassland, Combretum-Terminalia woodland comprised the highest amount followed by riverine woodland and thicket and semi permanent water/aquatic association grass. Furthermore, F1's use towards the availability of especially Combretum-Terminalia woodland and also Mopane woodland was very high. This is likely associated with her having a few months old cub and hence the need to be better concealed: The need to avoid competitors and foreign male leopards and thus reduce the risk of possible infanticide is a reason to use denser vegetation. It also provides a higher hunting success rate by eliminating the discovery by prey species. Grassland does not provide enough cover and an adequate number of trees for caching kills, which is important in order to avoid scavengers like lions, hyenas and wild dogs (Bailey 1993, Sunquist & Sunquist 2002). This fact is probably more relevant for females when they have cubs.

The same applies to F2 which also used riverine woodland, semi permanent water / aquatic association grass, acacia woodland and Combretum-Terminalia woodland more frequently or according their availability. The cub of F2 was not very young anymore but still immature.

All these assumptions also imply a sex-specific choice of prey (Bailey 2005), especially if females have cubs.

3.4.6 Habitat preferences

None of the values of Jacob Index reached the maximum avoidance (-1) or preference (+1), so the results can be considered as tendencies.

Due to the shrinkage of F1's home range in 2008 the composition of habitat types within her home range changed considerably. Consequently, none of the habitat types reached values below 5 % and all types could be by that included inside the Jacob-Index calculation. Despite the shrinkage F1's preferences for Mopane woodland, semi permanent water/ aquatic association grass and riverine woodland remained the same as it was in her previous home range.

F2's preferences for Mopane woodland and thicket can be confirmed with the Jacob Index. F2's preferences for habitat types like riverine woodland, semi permanent water/ aquatic association grass, acacia woodland and Combretum-Terminalia woodland cannot be confirmed by Jacobs-Index due to their occurrence below 5% in her home range. However, it is obvious that she used those habitat types more or according their availability.

Studies so far showed that home ranges of females included mostly important resources like habitat of prey richness and watering places (Bailey 2005, Bothma 1997, Mizutani & Jewell 1998, Kruuk 1986). This can be confirmed in this study. Vegetations types like riverine woodland, thicket and Mopane woodland are preferred by the chief prey of leopards in this study (see chapter 4) such as grysbok, bushbuck and impalas.

According to the Jacob-Index all the leopards (apart from M3) tend to prefer denser vegetation types and rather avoid grassland although it comprises the largest part of most of their home ranges (F1(2007-2008), M1, M2, M3). Nevertheless, males used grassland much more than females which imply that males rather show a preference for grassland than females.

3.5 Summary

In this study, home range sizes, activity patterns and habitat use of leopards (*Panthera pardus*) were studied in Luambe National Park (LNP) and a bordering Game Management Area (GMA-A) in Zambia. Therefore, two female and three male leopards were radio tracked to answer these questions.

Home range sizes calculated with MCP-95% resulted in 28 - 56 km² for males and 3 - 42 km² in females; Kernel calculations resulted in 33 - 81 km² in males and 3 -17 km² females. In this context the home range of one female did shrink due to motherhood.

Analysis of habitat use and activity pattern of the leopards showed differences between males and females. Although all observed leopards moved significantly more during night than they did in day times, movement of females during the night times was less than movement of males. In total males were moving much longer distances than females.

During 24 hour observations all observed leopards showed a minimum activity and movement during hours around noon whereas maximum movement and activity were documented before sunrise and before sunset.

In contrast to the male leopards, females are mainly distributed in dense forested areas, possibly due to a higher safety factor for cubs. Generally, according to the Jacob-Index, most of the leopards tend to prefer denser vegetation types and rather avoid grassland although it comprises the largest part of their home ranges. This is likely correlated with the fact that certain dense vegetation types are preferred by the chief prey of leopards such as grysbok, bushbuck and impalas. Nevertheless, grassland may offers also an important hunting habitat that more likely is used predominantly by male leopards.

4 The leopard’s prey spectrum and preferences in the Luambe National Park and the surrounding Game Management Areas (GMA’s)

This chapter deals with the leopard’s diet and questions to be answered here are:

- What is the leopard’s prey spectrum in both the area types?
- Are there any differences in the leopard’s diet composition between a protected area (Luambe National Park) and an area where the impact of humans is obvious (Game Management Area)?

4.1 Introduction

Due to their extremely catholic diet, leopards are known to be very adaptable. Alone in Sub-Saharan Africa 92 prey species of leopard have been recorded, varying from small arthropods (Fey 1964) to adult male eland (Bailey 2005). However, it has been shown that the generally held view that the leopard as a supergeneralist predator under the existing easy to deal with conservation measures can no longer be considered as adequate (Ray et al. 2005, Spong et al. 2000, Balme et al. 2007).

Leopards have preferences for certain prey and if it is available in their habitat their diet is dominated by ungulates between 20-80 kg (Stander et al. 1997a). Thereby, leopards show some specialization in their choice of preferred hunting habitat (Balme et al. 2007). The leopards’ preferred habitat is certainly related to the abundance of prey but it has been also proved that the catchabilty of prey plays the same or depending on the circumstances an even more important role (Balme et. al 2007). One of the main important characteristics of a habitat preferred by a leopard is for example intermediate cover for the strategy of stalk-hunt. For a successful attack it needs to get as close as possible to the prey without getting perceived by it. Too much cover can be a problem as well and hinders catchability (Balme et al. 2007). Thus, there are certain factors that influence leopards’ prey choice.

The more we know we can work out commonalities and differences to develop an efficient conservation management plan. Results of diet analyses could have a useful impact on the development of carnivore management plans, especially if economic important species are involved (Klare et al. 2011).

There are varied reasons why large felids can come into conflict with men over competition for wild prey species. Predators were persecuted as vermin in some national parks until as late as the 1950s, because they were thought to suppress "game" numbers (Davison 1967, Smuts 1976). Wherever the human spreads out and shares habitat with predators, conflicts due to attacks on livestock are pre-programmed (Treves & Karanth 2003, Frank, Woodroffe & Ogada 2005, Miquelle et al. 2005, Rabinowitz 2005). There are diverse reports about leopard's attacks on livestock in African countries (Schiess-Meier et al. 2007, Frank, Woodroffe & Ogada 2005, Ogada et al. 2003, Kolowski & Holecamp 2006, Mizutani 1999, Stander 1997a,b, Butler 2000). In the part of the Luangwa Valley, where the study area, the Luambe National Park (LNP) and its surrounding Game Management Areas (GMA's), are located, the tsetse fly exists which broadcasts the sleeping sickness for animals. According to this, keeping of livestock is senseless and conflicts between human and leopard due to livestock losses do not play any role.

However, something which has not been proven is the impact of trophy hunting on the leopard' prey spectrum and diet composition in the area. While the LNP is assumed to be undisturbed, in the surrounding GMA's villages exist and commercial trophy hunting is allowed. This also could lead to a competition between large predators and game users. Every year following ungulates and primates which are probably relevant for the leopard, can be hunted there (Table 4.1).

Depending on species' size it is assumed that a few species are more relevant than others as leopard prey (Mills & Hes 1997) in this region, as follows:

Table 4.1: List of prey taxa probably relevant for leopards, and trophy hunted in the GMA's

Relevant prey taxa	**Less relevant prey taxa (assumed)**
Puku (*Kobus vardoni*)	Eland (*Taurotragus oryx*)
Impala (*Aepyceros melampus)*	Greater kudu (*Tragelaphus strepsiceros)*
Reedbuck (*Redunca arundinum*)	Waterbuck (*Kobus ellipsiprymnus*)
Bushbuck (*Tragelaphus scriptus*)	Buffalo *(Syncerus caffer)*
Oribi (*Ourebia ourebi*)	
Sharpe's grysbok (*Raphicerus sharpei*)	
Warthog (*Phacochoerus africanus*)	
Baboon (*Papio cynocephalus)*	
Vervet monkey (*Cercopithecus aethiops*)	

4.2 Methods

4.2.1. Collecting of feces

Between 2006 and 2008 leopard feces were collected inside the LNP, Chanjuzi-GMA (GMA-A), Nyampala-GMA (GMA-C) and Luawata-GMA (GMA-D) (Figure 4.1). The bulk of the feces which were found in the GMA's came from GMA-A. This borders directly onto the LNP and due to this fact, this GMA was compared with the LNP (see chapter 1, the characteristics of each study site is described in Table 1.1 and Table 1.2.).

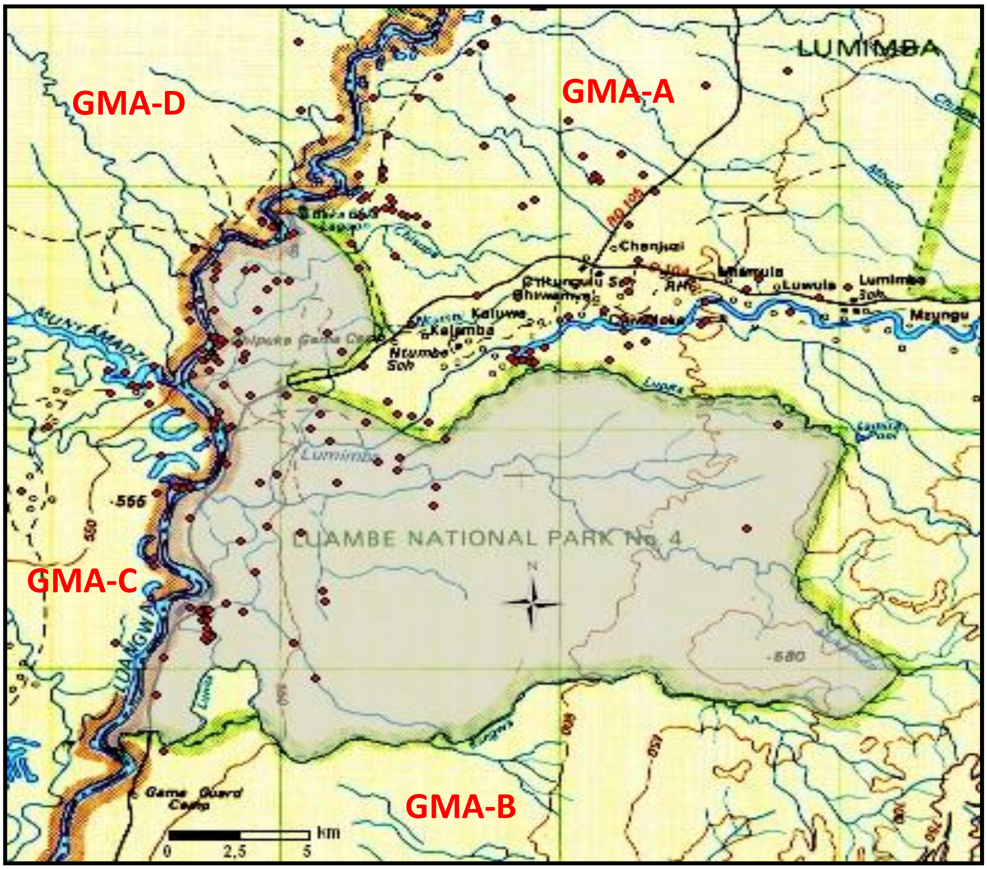


Figure 4.1: GPS-points of the feces samples found in the study area LNP (grey) surrounded by Game Management Areas (GMA's) A-C-D, with GMA-A being the second main study site

416 feces samples have been used in total, 187 from the LNP (data taken from C. Stommel) and 188 from the GMA-A have been examined and compared for their content. The remaining feces samples were collected in the two other GMA's, C and D. The other two GMA's are separated from the LNP through the natural border of the Luangwa River. GPS-

coordinates could not be recorded from all feces samples, because many of the collectors were village scouts (extra paid for this purpose) who did not possess a GPS. In our research camp three GPS devices were available and used for this task. Most feces from GMA-C and GMA-D were collected during the months when the Luangwa carried enough water to minimize an easy interchanging of leopards from both sides. GMA-C and GMA-D are not the main study areas, but due to their location at the opposite banks of the Luangwa River it was interesting to note if there are any differences of prey composition across this natural border. Feces were either collected along prominent game trails and vehicle tracks or along the Luangwa River, as well as along small tributaries, which were regularly patrolled for inspection. Camera traps were set and distributed along the sides of these locations to determine leopard population density. This ensured that all domains of LNP could be covered, as well as the parts of GMA-A that were compared with the LNP.

Leopard feces could be readily discerned from feces left by other species according to size, shape, consistency (Stuart & Stuart 2000), odor and visible adjacent tracks.

Confusing leopard feces with feces of other animals occurring in the research area such as civet cat and spotted hyena was very unlikely. During the period of data acquisition it was possible to see enough feces of these other species’ to distinguish them easily from the leopard feces. Feces of spotted hyena and civet in this region differ completely from leopard scats in shape, size and colour. Feces of both those species are much larger in diameter than those of leopards. Civets, defecate usually in latrines (Walker 1996, Stuart & Stuart 1998), their scats constitute a big heap, the consistency is fluffy and the color is much lighter in color than leopard scats. In addition to that, it was found that civet scats were characterized by a content of fruit seeds.

Figure 4.2: Leopard feces, air dried

Hyena scats are not only much harder in comparison to leopard scats but they are also white in colour caused by a high ratio of calcium residue of digested bones (Chame et al. 1991, Walker 1996). A possible confusion persisted with feces of lion, wild dog and serval. By definition of a diameter of 2 - 3.2 cm for leopard feces, confusion with those species could be minimized. Leopard feces of 2 - 3.2 cm were collected regularly at the live-trap (see chapter 3) and by that of doubtless origin (feces found close to the live-trap were not included within this analysis). Additionally, we found in many cases tracks of leopards close to the feces while collecting them in the field. Therefore, we believe that the definition of this size diameter is reliable as a reference point.

Lion feces were in general bigger in diameter and the serval feces were smaller. The shape of serval feces was furthermore observed to be somewhat different from those of leopard, as was experienced by a parallel ongoing study on the diet of the serval by C. Thiel in the LNP. Wild dog feces are much similar in size to leopard feces but can also be distinguished by a stronger necking (Dickmann & Msigwa 2007) and an obvious unmistakable odor. For each sample of feces collected, the GPS-position, the date of collection along with the size (length and diameter) was recorded. The feces were then air dried (Figure 4.2) and stored in plastic bags with silica gel until further examination.

4.2.2 Analyses of feces

The dried feces were soaked and inlaid with 99% ethanol for a few hours, for the purpose of germ killing on one hand and to facilitate the further washing on the other.
The feces were then dissolved in water and carefully rinsed through a 1 mm sieve, and all the solid contents of the feces such as hair, bone fragments, hooves, toe nails, teeth and grass retained were sorted out and air dried (Figure 4.3). The content was compared with a reference hair catalogue that was generated by us for this issue.

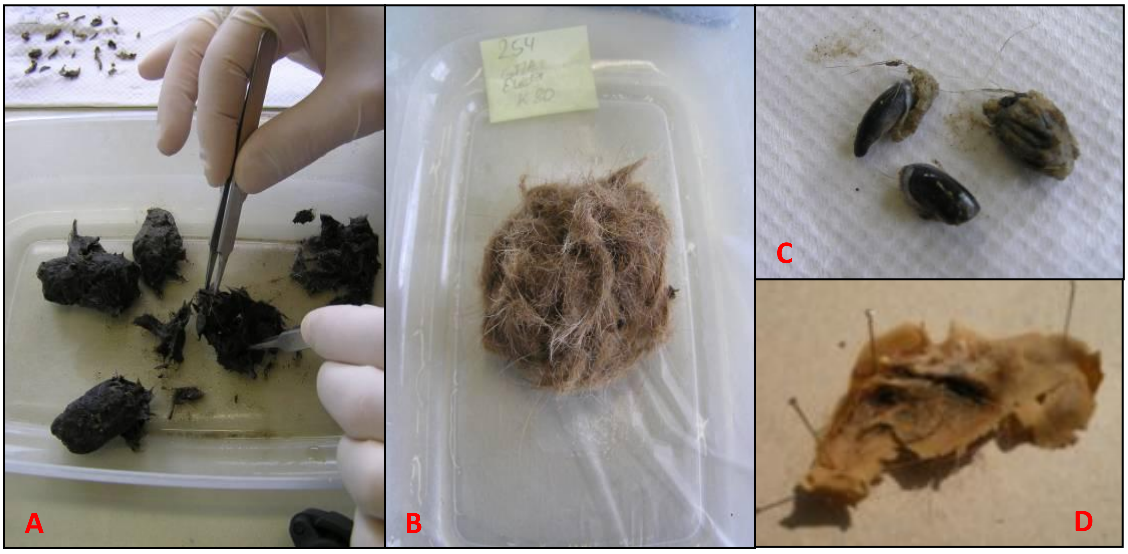


Figure 4.3: A= preparation of soaked feces; example for contents of faeces: B=hairs; C = finger nails (primates), D=skin with hairs

Hair samples from different possible prey species have been collected during data acquisition in the field (from kill remains, dead animals that died a natural death, diverse trophies from professional hunters, mice traps) and from specimens of the Zoological Research Museum A. Koenig (ZFMK) and the Livingstone Museum collection.

Samples from all ungulates (large, medium sized and small) which were noticed by us in the research area have been added to our hair catalogue, to exclude implausible cases.

Prey hair was examined macroscopically, for shape, coloration, size and thickness and microscopically for complexion and structure of medulla and cuticula.

For the microscopic examination of medulla analysis, 3 to 6 hairs were pasted with Euparal on an object slide, and pictures were taken with a photographic microscope. For cuticula analysis negative prints were made following methods described by Perrin & Campbell (1980) and Wachter et al. (2006), and photographed.

Further, the contents of feces like bone fragments, hooves, toe nails, skin and teeth were used to support the results gleaned from hair analysis.

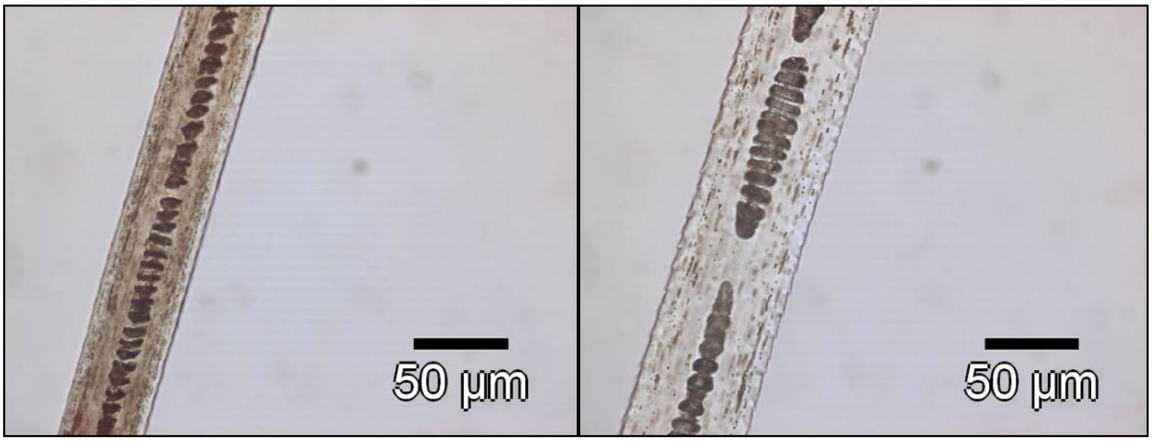


Figure 4.4: Medulla structure from a hair of baboon (left) and vervet monkey (right)

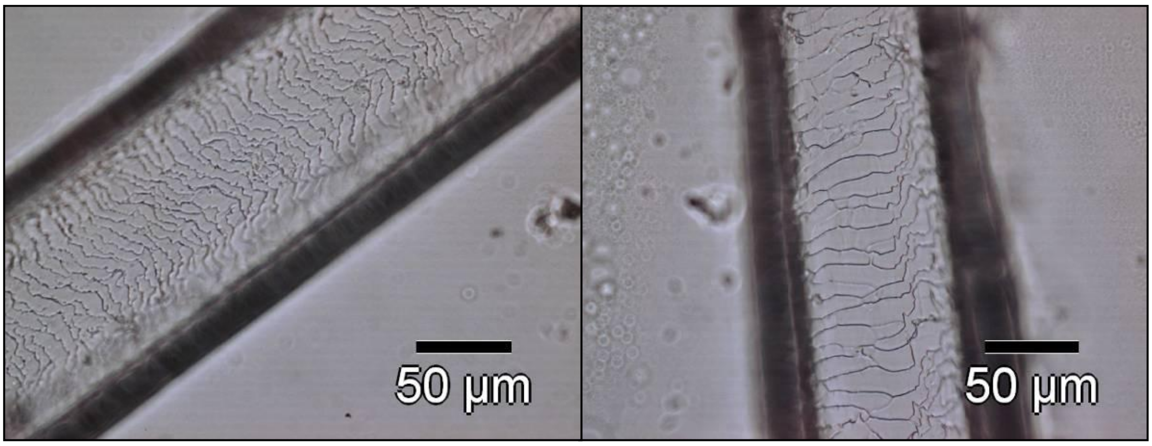


Figure 4.5: Cuticula structure from a hair of impala (left) and puku (right)

In order to get an idea about the prey choice of leopards within the research areas it was necessary to reconstruct the relative number of individuals eaten. To avoid making mistakes regarding the significance of various species (Ackermann et al. 1984), which is attributed to differences in digestion times (Mills 1996), the relative biomass and the relative number of eaten individuals were calculated (Hart et al. 1996, Karanth & Sunquist 1995). For the calculation of the biomass per feces we used the formula developed by Ackermann et al.1984 for pumas (*Puma concolor*):

$$Y = 1.98 + 0.035\ X$$

In so doing Ackermann et al. 1984 proved through feeding experiments a linear relationship of consumed biomass per excreted feces (Y) and the weight of the prey species (X). The resulting relationship was used as a correction factor, to convert frequency of occurrence to relative consumed biomass (Ackermann et al. 1994).

Emanating from a comparable digestive system of leopard and puma, we used the relative frequency of occurrence to calculate the relative biomass consumed (Hart et al. 1996; Karanth & Sunquist 1995, Henschel 2001). Species with a live weight < 2 kg were not considered within this calculation, but every prey item was considered as a whole individual (Ackermann et al. 1984). In these cases the live weight was simply multiplied by the frequency of occurrence.

All live weights for the identified prey species were taken from Hayward et al. 2006; live weights for birds and mice were taken from Dunning (1993) and Bowland & Bowland (1991).

4.2.3 Analysis of prey choice and comparisons between study areas

For the calculation of existing biomass of three antelope species such as puku, impala and bushbuck I used abundance data (density/km²) for Puku according to Rduch (2008), for impala according to Simon (2008), and bushbuck according to Van den Elzen and Rduch (unpublished data) within the LNP. Similar data do not exist for the GMA-A. In assumption of a habitat composition similar to the LNP I projected abundance data to the part within GMA-A where leopard feces were found.

For a better comparison and to minimize the error between the areas I calculated biomass abundance and consumption per km^2. Therefore, I broadly defined by GIS 9.1 the area size within the GMA-A which roughly encompassed the feces found (204 km^2). Feces that were collected very far in the east of GMA-A were not included in this area calculation. The abundance data for the three antelope species were mainly extended to the western part of the LNP. In addition to that, I was insecure about the habitat composition and following this I intended to minimize errors. For the LNP I used the area size of the western part (145 km^2) because first this was used to determine the abundance data and second it included most of the fecal samples found in LNP. The only two samples found in the east of LNP were excluded.

4.2.4 Statistical analyses

To determine if the prey choice differed significantly between the research areas the proportion of prey species found in feces was compared between the study sites using the chi^2-test (non-parametric test) from SPSS 13.0 for Windows. For a better comparison all diagrams shown in this work represent percentage data. To guarantee the significance of the data I used raw data (in kg, frequency of occurrence) for the chi^2-test. Further an exponential regression analyses was compiled by SPSS 13.0 for Windows. In so doing I divided the absolute number of individuals consumed by leopards by the number of individuals shot by hunters to get the prey index and plotted it against prey body mass.

4.3 Results

4.3.1 Leopard prey spectrum at the study sites

From 203 examined feces of the LNP, prey items of 15 faecal samples could not be identified. For further analyses a number of 187 and 188 feces were examined in the main study areas, LNP and GMA-A, and 194 and 225 prey items were detected. From samples taken in the remaining areas GMA-C 40 feces samples contained 49 prey items, while in GMA-D with 32 feces included 40 prey items. 8-18 taxa were recognized in all areas where scats have been collected.

97.3% could be determined to species level and 2.6% to only genus level. The latter are rodents which will not be considered further according to the low percentage. The biggest part of prey items, found in scats belong to ungulates in the LNP (83.6%) and in the GMA-A (81%) (see Table 4.2).

Small antelopes like Sharpe's grysbok represented 9.8% in LNP, whereas larger species such as puku and impala comprise a greater part (21% and 24.2% respectively), directly followed by the bushbuck (17%). Reedbuck was found to be 5.7%, and the last represented antelopes were oribi and waterbuck at 2.6%. Warthog was not detected.

In the GMA-A small antelopes like Sharpe's grysbok comprised 18.2% of the diet, directly followed by impala (17.3%), puku and bushbuck at 15.1%. Oribi and waterbuck represented 6.2% and 3.1% and reedbuck 0.4%. Other ungulate species like warthog represented 5.8% (see Table 4.2).

Primates as baboons and vervet monkeys comprised 5.7% in the LNP (2.1% and 3.6%) and 13.3% in the GMA-A (7.6% and 5.6%). In both these areas baboons constitute the largest amount of primates. The hairs of baboon *(Papio cynocephalus)* and vervet monkey *(Cercopithecus aethiops)* look very similar in their macroscopic appearance, but could be distinguished microscopically based on the structure of their medulla (Figure 4.4).

Rodents covered 7.2% in the LNP, whereof porcupine represented the greatest part at 3.1%. The minority were represented by carnivores (2.1%) and birds (1.5%) (Table 4.2 and Figure 4.6). In GMA-A the minority of prey was represented by rodents (4.4%) and carnivores at (1.3%), no prey items of birds could be found (Table 4.2 and Figure 4.6).

The largest part of prey items found in scats of the study sites GMA-C and GMA-D belong to ungulates (71% (C), and 81.8% (D)), (Figure 4.7). Sharpe's grysbok (25.8%) was the prevalent antelope in C, followed by impala and puku (12.9), while bushbuck, oribi and waterbuck substituted the minority. Warthog was determined at 3.2%. In study site D, the majority was represented by bushbuck (36.4%), followed by impala, oribi and waterbuck while Sharpe's grysbok substituted the minority. Warthog was found at 4.5%. Primates comprised 29% (baboon 19.4%, vervet monkey 9.7%) in area C and in D 13.6% for only baboon (Table 4.2 and Figure 4.7).

Prey items of rodents and birds were not found in feces of study sites C and D. In all study sites ungulates covered the main portion of prey items in scats.

4.3.2 Comparison of biomass in the study sites LNP and GMA-A, -C and -D

In terms of relative biomass consumed, antelopes like puku and impala were the most important prey taxa in LNP and GMA-A, followed by bushbuck and Sharpe's grysbok. Warthog was not consumed in the LNP but it represented 7.59% of the diet in GMA-A. Beyond ungulates, vervet monkeys and baboons were the second most important prey taxa at study site A, accounting for 4.17% and 6.22%, while at study site LNP, the diurnal primates were consumed to a much lesser extent (4.3%) (Figure 4.8).

In all study sites ungulates comprised the main part of the biomass consumed, comprising 88.12%-90.67% of the overall biomass consumed (Table 4.3).

Grysbok was the most commonly consumed prey species in study site C, followed by puku and impala, whereas in study site D, bushbuck was the most consumed antelope, followed by impala and waterbuck. Warthog was consumed in both sites in the same quantity. Beyond ungulates baboons were the second most important prey species in area C (16.23%) followed by vervet monkey (7.11%), but not in D, where only baboons covered 10% (see Table 4.3). In both the study sites ungulates made up the main part of the biomass consumed, comprising 76.66%–89.99% of the overall biomass consumed (Table 4.3).

Table 4.2: Prey composition of leopard in LNP, GMA–A, GMA-C & GMA-D

	Relative frequency of occurrence (%)			
	LNP n = 187	**GMA-A n = 188**	**GMA-C n = 25**	**GMA-D n = 16**
Ungulates				
Sharpe's Greysbock *(Raphicerus sharpei)*	9.8	18.2	25.8	4.5
Impala *(Aepyceros melampus)*	24.2	17.3	12.9	18.2
Bushbuck (*Tragelaphus scriptus)*	17	15.1	9.7	36.4
Puku *(Kobus vardoni)*	21.7	15.1	12.9	9.1
Waterbuck *(Kobus ellipsiprymnus*)	2.6	3.1	3.2	9.1
Oribi (*Ourebia ourebi)*	2.6	6.2	3.2	-
Reedbuck (*Redunca arundinum*)	5.7	0.4	-	-
Warthog *(Phacochoerus africanus)*	0.0	5.8	3.2	4.5
Total	***83.51***	***81.33***	***71***	***81.8***
Primates				
Baboon *(Papio cynocephalus)*	3.6	7.6	19.4	13.6
Vervet monkey *(Cercopithecus aethiops)*	2.1	5.78	9.7	-
Total	***5.67***	***13.33***	***29***	***13.6***
Rodents				
Porcupine *(Hystrix africaeaustralis)*	3.1	1.3	-	4.5
Rat *(Pellomys* spec.*)*	2.1	0.9	-	-
Mouse 1 *(Gerbilliscus* spec.*)*	2.1	1.3	-	-
Mouse 2 *(Mastomys* spec.)	0.00	0.4	-	-
Total	***7.22***	***4***		***4.5***
Carnivores				
Genet *(Genetta tigrina)*	2.1	0.4	-	-
Civet (*Civettitis civetta)*		0.9	-	
Total	***2.06***	***1.33***		
Birds				
Helemted guineafowl (*Numida melagris*)	0.5			
Grey Crowned crane (*Balearica regulorum*)	1		-	-
Total	***1.55***			

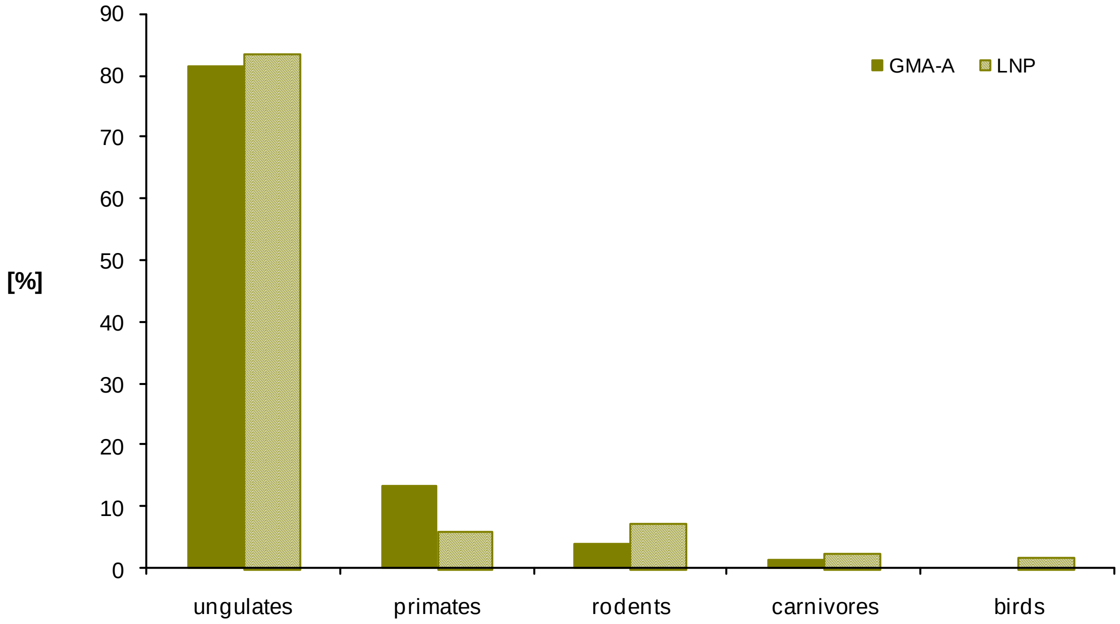


Figure 4.6: Representation of the percental diet composition of the two main study sites (LNP & GMA-A)

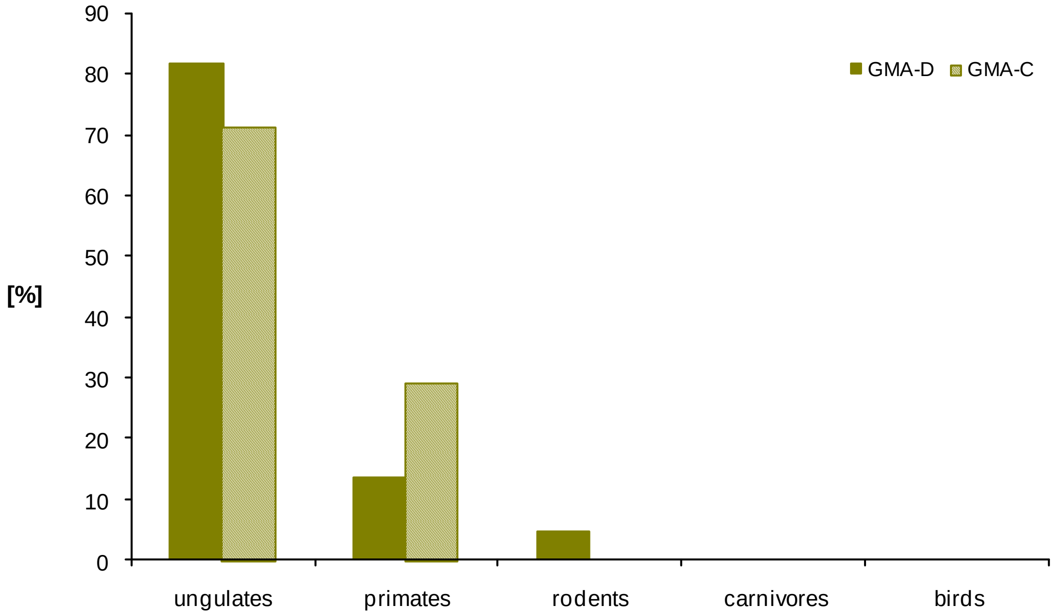


Figure 4.7: Representation of the percental diet composition of the two study sites GMA-C & GMA-D, across the Luangwa River

Table 4.3: Estimated relative biomass consumed by leopards in Luambe NP and all GMA – study sites

			Biomass consumed (%)			
	Body weight (kg)[a]	**Correction factor (kg/feces)**[b]	**LNP n=188**	**GMA-A n=187**	**GMA-C n=25**	**GMA-D n=16**
Ungulates						
Sharpe's Grysbock *(Raphicerus sharpei)*	7	2.23	7.29	13.92	20.06	3.09
Impala *(Aepyceros melampus)*	30	3.03	24.57	18.03	13.66	16.84
Bushbuck (*Tragelaphus scriptus)*	22,5	2.77	15.76	14.35	9.36	30.77
Puku *(Kobus vardoni)*	52	3.80	*27.45*	19.71	17.13	10.56
Waterbuck *(Kobus ellipsiprymnus*)	188	8.56	7.39	9.14	9.65	23.79
Oribi (*Ourebia ourebi)*	14	2.47	2.13	4.90	2.78	-
Reedbuck (*Redunca arundinum*)	32	3.21	6.08	0.49	-	-
Warthog *(Phacochoerus africanus)*	45	3.56	-	7.59	4.01	4.94
Total biomass			***90.67***	***88.12***	***76.65***	***89.99***
Primates						
Baboon *(Papio cynocephalus)*	12	2.40	2.90	6.22	16.23	10.01
Vervet monkey *(Cercopithecus aethiops)*	3.5	2.10	1.45	4.17	7.11	-
Total biomass			***4.3***	***10.39***	***23.34***	***10.01***
Rodents						
Porcupine *(Hystrix africaeaustralis)*	10	2,33	2.41	1.07	-	-
Muridae species	0.06-0.13	0.06-0.13[c]	*0.83*	0.08	-	-
Total biomass			***3.24***	***1.15***	-	-
Carnivores						
Genet *(Genetta tigrina)*	1	1.00	0.69	0.15	-	-
Civet (*Civettitis civetta)*	7	2.23	-	0.68	-	-
Total biomass			***0.69***	***0.83***	-	-
Birds						
Helmeted guineafowl (*Numida melagris*)	1.3	1.3	0.22	-	-	-
Grey crowned crane (*Balearica regulorum)*	3.6	2.11	0.73	-	-	-
Total biomass			***0.95***	-	-	-

[a] Live weight according to HAYWARD et al. 2006

[b] Correction factor following ACKERMANN et al. 1984

[c] No correction factor, prey species < 2kg were not included in the calculation with the formula (see text)

4.3.3 Comparison of leopards prey selection across sites

The prey selection of leopards differed significantly between study sites in terms of frequency of occurrence as well as in biomass. Shape’s grysbok were consumed at a significantly higher rate in GMA-A than in LNP ($p = 0.005$, chi^2-test). The consumption of impala, puku, bushbuck and waterbuck did not differ significantly, but in consumption of oribi ($p=0.059$) and reedbuck ($p = 0.004$) between the two study sites. The coverage of warthog was significantly different ($p < 0.001$) as it was not detected in scats collected in LNP. The next significant difference indicates the consumption of primates. Baboon ($p = 0.041$) and vervet monkey ($p = 0.029$) were more often consumed in GMA-A than in LNP, while baboon was the most preferred primate species (see Figure 4.8).

No significant differences were found in rodents, small carnivores and birds, since these groups were hardly consumed in both of the study sites.

Leopard’s prey selection at area C and D differed significantly in terms of biomass and frequency of occurrence. Grysbok was significantly more often consumed at GMA-C ($p<0.001$), whereas the consumption of bushbuck was significantly higher in GMA-D ($p=0.011$). The consumption of primates ($p = 0.028$) differed significantly between sites (Figure 4.9).

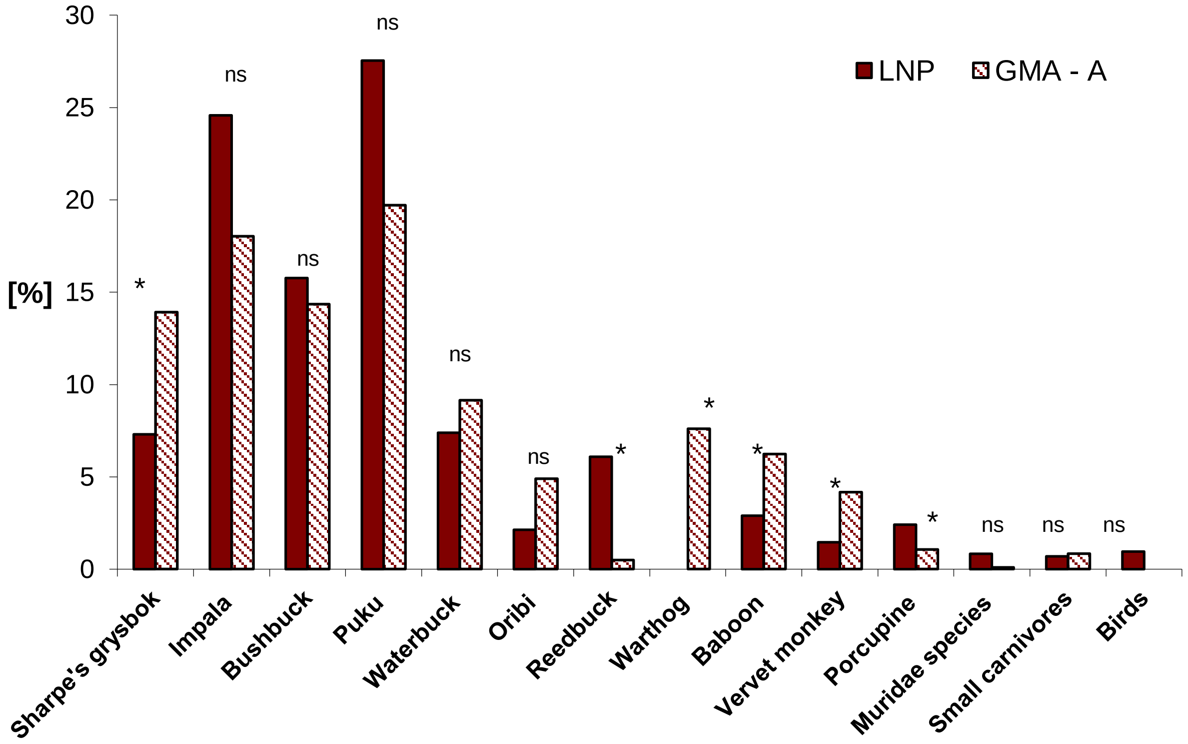


Figure 4.8: Representation of different prey composition of consumed biomass in the two main study sites LNP & GMA-A, brown: LNP; striped: GMA-A; ns= not significant; *:p < 0.05; For the Ch² test, raw data were used (see Chapter 4.2)

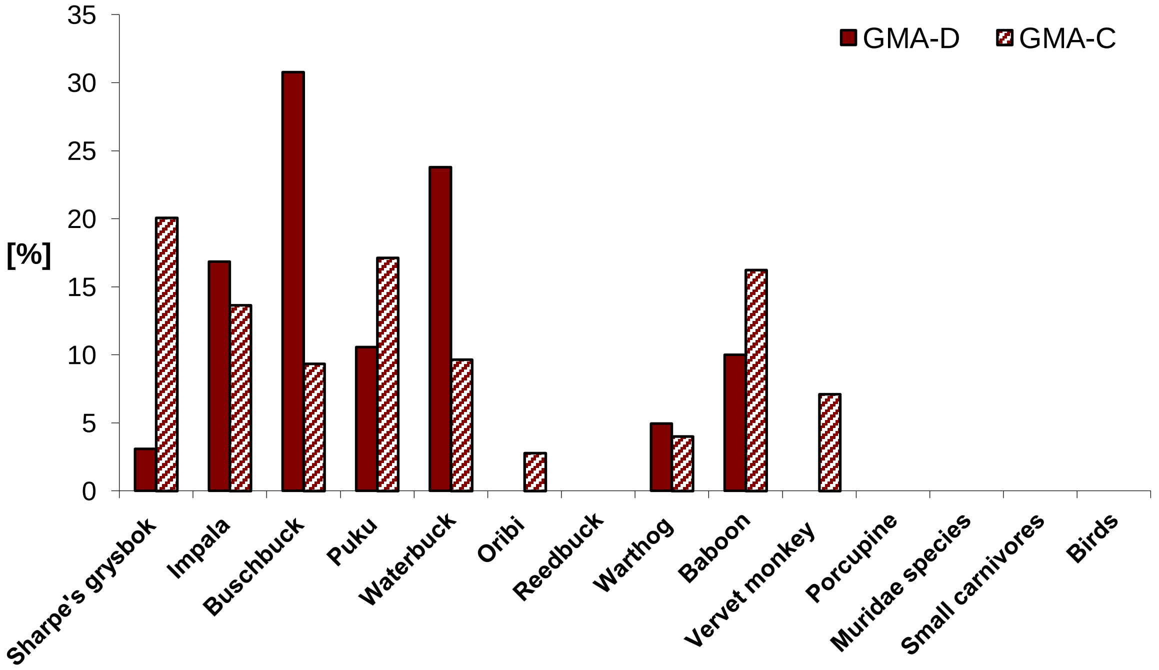


Figure 4.9: Representation of different prey composition of consumed biomass in the two study sites across the Luangwa GMA -C & GMA-D, brown: GMA-D; striped: GMA-C

4.3.4 Preference for prey body mass

The preferences in body mass of prey in the LNP lay between 15-30 kg (45%) and in GMA-A between 1-15 kg (41%). The second most preferred prey body mass class in area A was 15-30 kg (34%) followed by prey between 45-60 kg, whereas the second most preferred body mass classes of GMA-A were from 45-60 kg and 1-15 kg. In both the sites class of 30-45 kg have been consumed to the almost same low amount (6-7%) and the last preferred prey class was above 60 kg with ca. 3% (Figure 4.10).

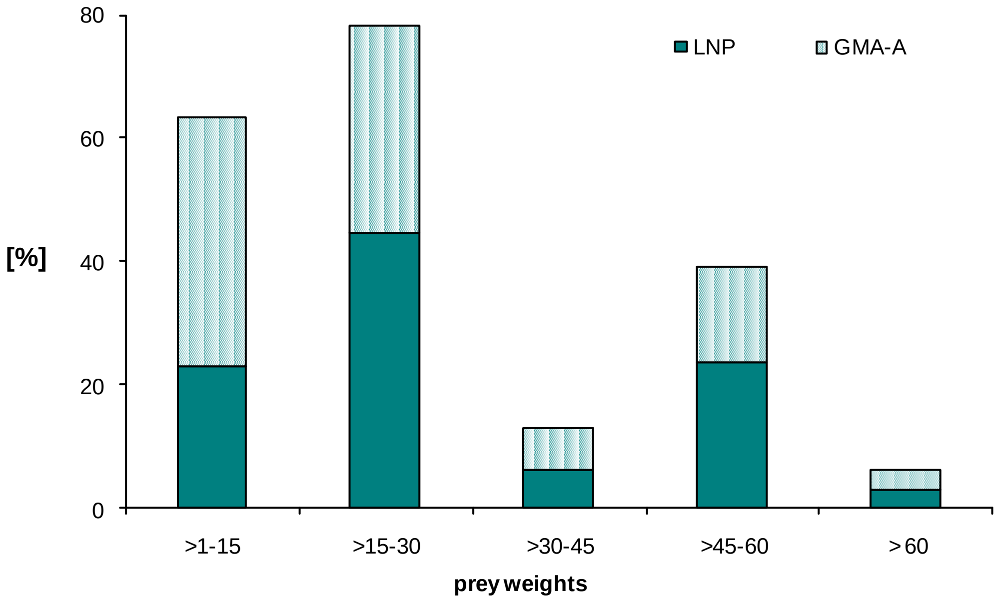


Figure 4.10: Percental representation of preferred prey body mass classes of the two main study sites (LNP & GMA-A)

In GMA-C the most important prey body mass class was 1-15 kg (58%). Prey between 15-30 kg (23%) was the second most preferred body mass class. In contrast, in GMA-D body mass between 15-30 kg (52%) was the most important and prey from 1-15 kg (24%) was the second most preferred. Body mass class from 45-60 kg was the next preferred in GMA-C at 13% and in D at 10% only In both these study sides prey between 30 - 45 kg and > 60 kg have been consumed to the lowest extent (see Figure 4.11).

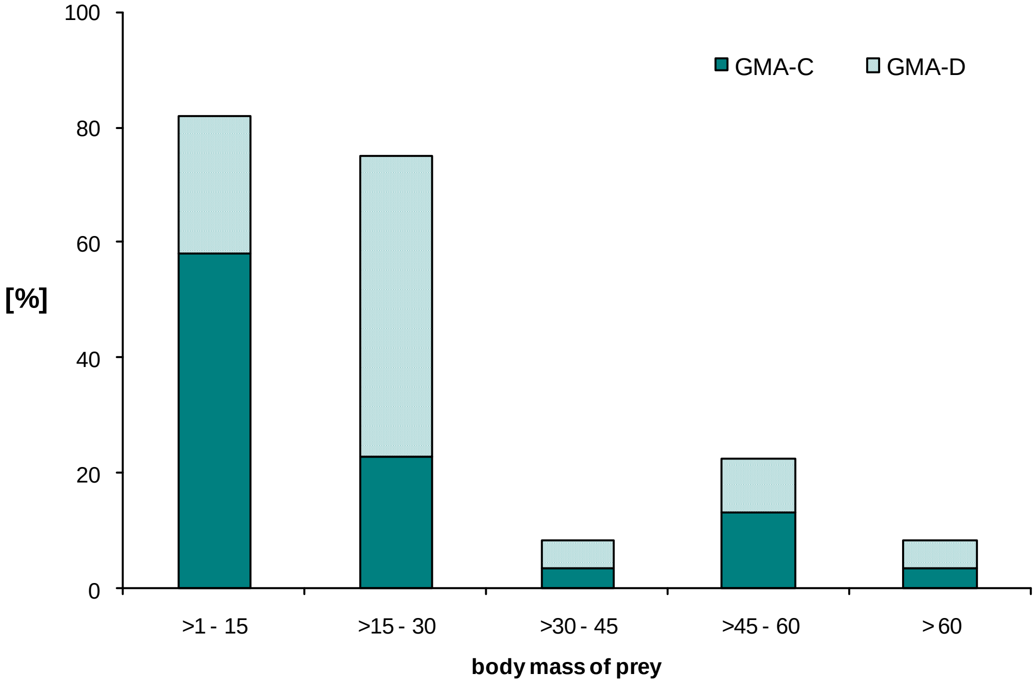


Figure 4.11: Percental representation of preferred prey body mass classes of the study sites GMA-C (blue) and GMA-D (patterned).

4.3.5 Comparison of biomass consumption between the areas LNP and GMA-A

The data presented below (Table 4.4) show the biomass abundance and biomass consumed per km^2 of puku, impala and bushbuck. Puku (541.4 kg) and impala (524.1 kg) constitute the largest part of biomass abundant per km^2 in contrast to bushbuck (23.4 kg) but also the largest part of biomass consumed in the LNP (1.1 kg/ 0.98 kg) and also in the GMA-A (0.63 kg/ 0.58 kg). Biomass of bushbuck consumed per km^2 was lower in LNP (0.63 kg) and GMA-A (0.46 kg). It however indicates that puku and impala, and also bushbuck were consumed more often per km^2 in LNP than in GMA-A.

Table 4.4: Comparison between abundant biomass and consumed biomass per km^2 as well as the proportion of abundant biomass and consumed biomass of important prey species within the study areas Luambe National Park (LNP) and Game Management Area-A (GMA-A).

Luambe National Park

	biomass abundance per km^2		**biomass consumption per km^2**		**proportion of consumed/abundant biomass**
	(kg)	**(%)**	**(kg)**	**(%)**	**(%)**
Puku *(Kobus vardonii)*	541.4	49.72	1.1	40.6	0.2
Impala *(Aepyceros melampus)*	524.1	48.13	0.98	36. 1	0.2
Bushbuck *(Tragelaphus scriptus)*	23.4	2.15	0.63	23.2	2.7
Total	***1,089***	***100***	***2.71***	***100***	▨

Game Management Area-A

	biomass abundance per km^2		**biomass consumption per km^2**		**proportion of consumed/abundant biomass**
	(kg)	**(%)**	**(kg)**	**(%)**	**(%)**
Puku *(Kobus vardoni)*	541.4	49.72	0.63	37.8	0.1
Impala *(Aepyceros melampus)*	524.1	48.13	0.58	34.6	0.1
Bushbuck *(Tragelaphus scriptus)*	23.4	2.15	0.46	27.6	1,9
Total	***1,089***	***100***	***1.67***	***100***	▨

The proportion of consumed biomass against abundant biomass shows (Table 4.4), that although bushbuck (2.15%) does not occur in comparable abundant numbers like puku (49.72%) and impala (48.13%) the demand for bushbuck is relative high (2.7%) in contrast to both the other antelopes (0.2%).

4.3.6 Is the leopard in competition with trophy hunting?

Every year a certain number of antelopes are allowed to be hunted in Game Management Areas however the hunting quotas differ from species to species. According to the Zambia Wildlife Authority (ZAWA) a certain number of the following species are allowed to be trophy hunted every season inside the studied GMA's: puku, impala, bushbuck, grysbok, waterbuck, oribi, reedbuck, warthog and baboon (see Table 4.5). Those quotas can change annually depending on the demand for these species.

Table 4.5: Hunting quotas of following species for 2008 (according to ZAWA Off Take Quota 2008):

Species	GMA-A	GMA-C	GMA-D
Grysbok (*Raphicerus sharpei*)	8	3	3
Impala (*Aepyceros melampus*)	27	20	18
Bushbuck (*Tragelaphus scriptus*)	13	7	5
Puku (*Kobus vardoni*)	22	10	8
Waterbuck (*Kobus ellipsiprymnus)*	9	4	2
Oribi (*Ourebia ourebi*)	2	0	0
Reedbuck (*Redunca arundinum*)	1	0	0
Warthog (*Phacochoerus africanus*)	16	8	9
Baboon (*Papio cynocephalus*)	16	3	2
Total	***114***	***55***	***47***

In 2008, diverse relevant prey species for the leopard have been shot in varying numbers by commercial trophy hunting in all the Game Management Areas mentioned in this study (see Table 4.5 and Figure 4.12).

In general, it is conspicuous that the amount of hunted individuals does not differ much between GMA-C and D. However, the comparison between the areas shows, that prey species important to the leopard were hunted in a higher amount in GMA-A than in the two other sites. Figure 4.12 shows the percentage of hunted individuals (trophy and resident hunting) of all studied Game Management Areas (100% = total number of shot individuals including different species). The species hunted in largest numbers in 2008 was the impala in all the three areas. In GMA-A impala was less hunted at 24% than in GMA-C (36%) and GMA-D (38%).

The second most hunted antelope is the puku at 19% in GMA-A, 18% in GMA-C and 17% in GMA-D. The third most hunted antelope is bushbuck at 11% in GMA-A and D and at 13% in GMA-C. Waterbuck was hunted at 8% in GMA-A and GMA C (7%), and in GMA-D at 4%. Grysbok was less frequently hunted (6%) in GMA-C and -D than in GMA-A, it comprised together with oribi and reedbuck the least hunted species. Other taxa like warthog and baboon were hunted in the same quantity in GMA-A (14%), and at 15% and 5% in GMA-C. In contrast to these areas, the highest quantity of warthogs (19%) and lowest quantity of baboons (4%) was hunted in GMA-D.

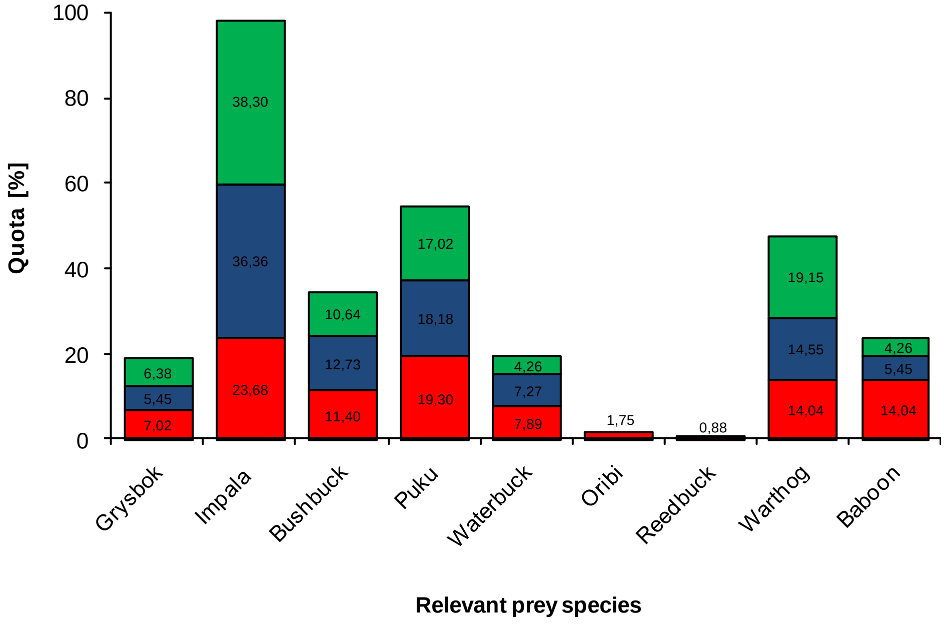


Figure 4.12: Representation of commercially trophy hunted species (%) in the Game Management Areas A-C-D, red=GMA-A; blue=C; green=GMA-D for the year 2008

The comparison between individuals harvested by commercial hunters and by leopard in GMA-A (see Figure 4.13) shows that antelopes like waterbuck, puku, impala, and bushbuck were less consumed by leopard (1-9 %) than those shot by commercial hunting (8-24 %). Puku and impala are the most preferred hunting game (19% and 24%). Antelopes like oribi and grysbok have been hunted at a low extent (2%, 7%) but were consumed by leopard at 5% and 28%.

Warthogs and baboons were hunted at 14% and consumed by leopards at 2% and 7%, whereas in the LNP warthogs were not consumed, but baboons at 4%.

Species that are trophy hunted in high quantities in the GMA-A are consumed in lower quantities by leopards in this area, but in higher quantities in the LNP (see also Figure 4.14).

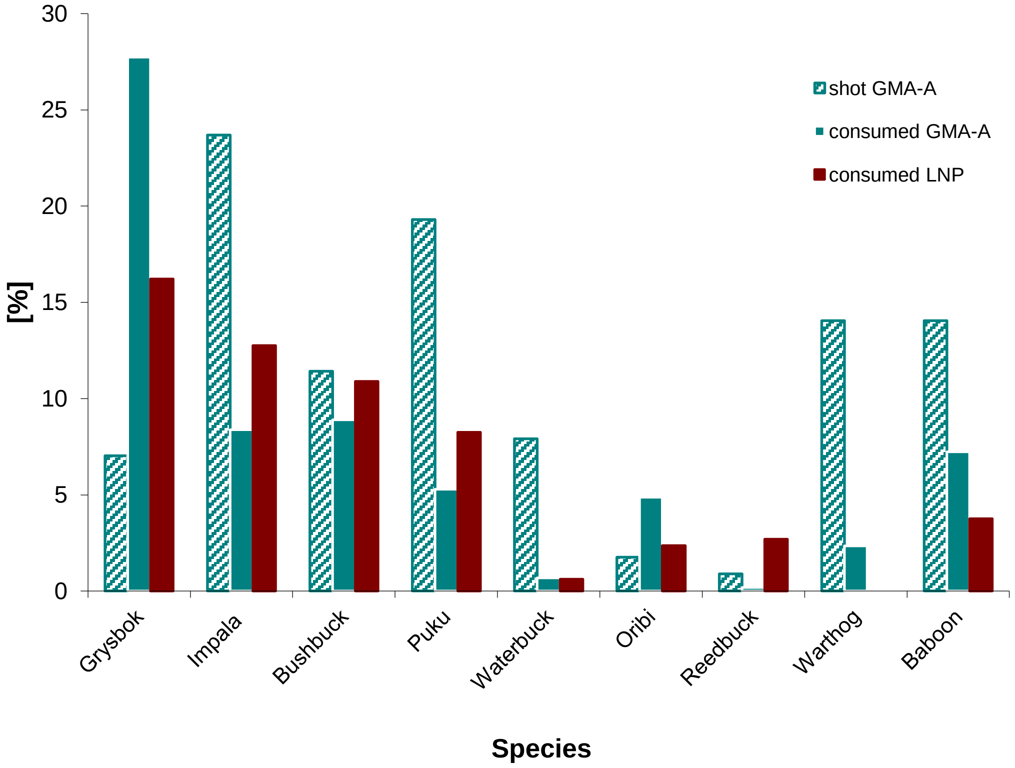


Figure 4.13: Percental representation of hunted individuals versus consumed individuals in GMA–A and consumed individuals in LNP

In the GMA-A, potential prey is either consumed by leopards or shot by hunters. The ratio of consumed to trophy-hunted prey will be greater 1 if more prey was consumed than trophy-hunted, and lower than 1 if more prey was trophy-hunted than consumed (e.g. if 6 animals were consumed and 4 were trophy-hunted, the resulting ratio would be 1.5. (consumed/hunted = prey-index). Plotting the prey index against prey body mass (Figure 4.14) shows that species up to a weight of 15 kg were more frequently consumed by leopards than killed by trophy hunters. By contrast, species heavier than 15 kg were trophy-hunted more often than consumed by leopards ($p=0,012$, $r^2=0,678$).

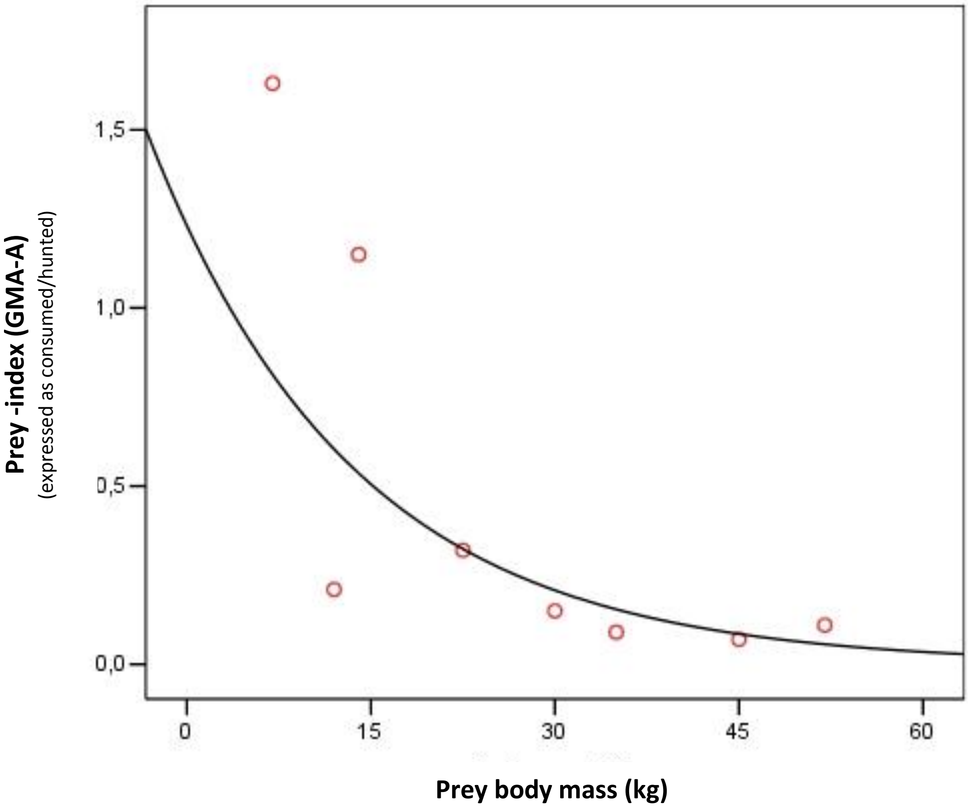


Figure 4.14: Relationship of the prey index (species consumed/ trophy-hunted) and live body mass of the different prey taxa in GMA-A, $p = 0,012$, $r^2=0,678$.

4.4 Discussion

4.4.1 Leopard prey spectrum at the study sites and comparison of prey selection across sites

Ungulates are the most preferred prey in all study sites. In this context we need to discriminate between small and middle sized antelopes, because they were consumed in different percentages across the different study sites.

In the LNP the leopard showed great preference for the middle sized antelopes such as impala and puku. The preference for impala can be explained due to the heavier weight and the life style of puku. Grazers such as pukus prefer the open savannah grassland (de Vos & Downsett 1964, de Vos 1965, Jenkins et al. 2002, Rduch 2008) whereas impalas mainly prefer the denser habitat (Averbeck 2002; Oboussier 1965; Simon 2008) like forest. The forest is the leopard's preferred hunting habitat (see Chapter 3). Although leopards use different hunting strategies' varying with the prey species, they almost always rely on the habitat type (Hunter et al. in press). Therefore, it is obvious: to approach the prey closely for a successful hunt, the leopard needs the cover for concealment.

Significant is that in terms of frequency of occurrence Sharpe's grysbok represent the most consumed antelope in GMA-A directly followed by impala. In the LNP the impala comprises the biggest part of the leopard's diet. Larger antelopes which include puku were less consumed in the GMA-A than in the LNP. One reason could be that middle sized antelopes are hunted in a higher quantity by trophy hunters than small sized antelopes in the GMA-A. In this case the big cat is competing with human hunters in the GMA. That is why the leopard perhaps shifts to smaller sized antelopes which are a) either more available than middle sized antelopes due to hunting, or b) the leopard is more careful in hunting middle sized antelopes because it combines it with trophy hunting activities in open woodland. During the study period I observed that it took longer to get a leopard feeding at a bait in the GMA than in the LNP (average 2 days in LNP/average 4.6 days in GMA) (see Chapter 3, Table 3.1). According to this observation I assume that leopards of the GMA's are more timid than they are in the LNP due to the hunting pressure.

The question here is whether it is the abundance of prey or its catchability that is of higher significance in driving decisions such as where and what to hunt: In this context Balme et al. (2007) reported from the Phinda Game Reserve in South Africa, that leopards hunt where their prey is easier to catch rather than where prey is more abundant. These findings in Phinda imply that leopards are not the "supergeneralists" as has been always assumed so far and that they show in their choice of hunting-habitat a certain degree of specialization (Balme et al. 2007).

I suggest that leopards prefer to hunt in GMA's in a denser habitat where middle sized antelopes like impala and puku are less available than grysbok, although the abundance of impala and puku could be higher in the GMA-A than in the LNP due to the larger size of the area.

The region of the LNP is more undisturbed, and being aware of that, leopards also hunt in open habitat. In so doing they hunt middle sized prey species which provide meat for a longer time period. Baboons are also consumed more frequently in GMA-A than in the LNP, which supports the theory that leopards switch to smaller prey whenever their favourite prey is hunted (Bodendorfer et al. 2006, Weckel et al. 2006). Baboons are trophy hunted as well but also, not in the quantities the middle and large sized antelopes are. Most of the baboons are probably killed by leopards while they sleep on trees at night time (Busse 1980, Brain 1981, Cavallo & Blumenschine 1989, Cavallo 1990a, 1990b and 1991, Cowlishaw 1994). Trees also create denser habitats in comparison to grassland and therefore the leopards prefer hunting on them in "disturbed" areas more than in open habitats.

Warthogs are also lesser trophy hunted than middle sized antelopes in the GMA-A. Warthog was not designated as a prey species in the LNP. Reasons could be, a) a lower density of warthogs in the LNP than in the GMA-A. b) In the LNP there are enough preferred prey species available for the leopard and easy to catch without being in competition with trophy hunters. This means it does not need to risk a fight with a defensive warthog that would be a powerful opponent. If it only catches the young, the risk of a fight with the mother-warthog would also exist. c) In the GMA, favourite prey species such as antelopes, like the impala are hunted, so it is in competition with human hunters. Thus, it switches to warthog, which is not as frequently hunted as middle sized antelopes are (ZAWA-Offtake quotas 2004-2008). Accessory warthogs are slower and have less endurance than most of the savannah ungulates (Estes 1991).

On the other hand warthogs prefer open habitat (Hirst 1975, Nowak 1999, Wilson & Reeder 2005) that leopards perhaps avoid in areas disturbed by trophy hunting. In addition to that warthogs generally sleep in dugouts or abandoned aardvark holes at night (Frädrich 1974, NOWAK 1999; Wilson & REEDER 2005) when leopards usual hunt (see activity pattern, chapter 3). This is not an immaterial obstacle for a leopard which requires exhaustive effort to get hold of this kind of prey. Although it has been determined that warthogs belong to the diet of leopards in areas of their abundance (BAILEY 2005, HAYWARD et al. 2006), this cannot be supported in the LNP. HAYWARD et al. 2006 also mentioned that Suidae species were less frequently killed by leopards than expected on the basis of their abundance. Also MITCHELL (1965) recorded only two warthogs attained by leopards, when he studied the kills of predators in Kafue National Park. In LNP, the energy requirements may not meet the minimum energy expenditure combined with least risk (ELLIOTT et al. 1977, HAYWARD & KERLEY 2005) for the predator.

It is difficult to make a reliable statement about GMA-C and GMA-D because the sample sizes were much smaller than the sample sizes of the LNP and the GMA-A. Thus, I cannot conclude with certainty that the leopard's prey composition is different from the areas across the Luangwa River.

I can recognize that weight class >1-15 kg is preferred slightly more in GMA-C than in GMA-D, which could also be due to the smaller sample size in GMA-D. Interviews with local people and professional trophy hunters implied that grysbok and puku do not occur in a high number in the region of GMA-D compared to GMA-C and the other study sites across the river. Conspicuous is that in these GMA's the ungulates relevant for leopard were hunted in lesser quantities than in GMA-A (see Figure 4.6).

4.4.2 Body mass of preferred prey

In the LNP leopards prefer prey species of >15-30 kg which include impala and bushbuck. In the GMA-A >1-15 kg comprises the largest quantity grysbok, baboon, vervet monkey, oribi and young warthogs. Nevertheless, this is followed directly by the body mass class >15-30 kg. This supports the theory explained above (Chapter 4.4.1).

The difference in consumption between the prey body mass class >15-30 kg (45%) and >1-15 kg (23%) in the LNP is much higher and significant than the difference in consumption of these two body mass classes in the GMA-A with 34% of >15-30 kg and 41% of >1-15 kg.

This could imply that leopards if they have the choice without disturbance and competition by human hunters would choose the middle sized antelope species.

In order to minimize kleptoparasitism leopards use trees or dense vegetation to hide their kills (Sunquist & Sunquist 2002). Explanation why they consumed species of body mass classes above 30-45 kg (which includes reedbuck, adult puku and warthog) less than the lighter species could be that an adult puku of 52 kg, for example, is more difficult to carry into a tree than an impala of 30 kg. If, in this case a tree as a caching possibility gets lost, the kill needs to be hidden somewhere at the ground. Here, depending on vegetation cover, the risk of discovery by scavengers such as lion and hyena is high.

The same is true for warthogs (45 kg) but these animals are also very defensive and serious opponents and energy requirements towards high energy input in association with a high risk of getting injured might be weighted by the predator (e.g. Hayward & Kerley 2005, Krebs & Davies 1993).

The reedbuck density in all the study areas seems to be low, definitely much lower than these of impalas, puku and bushbuck without scientific studies to confirm this, because it was rarely seen. According to the assumed low density of this antelope species it is not surprising that leopards in GMA's and LNP do not hunt this species in high quantity. It also was not much trophy hunted (ZAWA-Off-Take quota 2006-2008), which could support the suggestion, that reedbuck density could be low in comparison to other antelope species in the area.

4.4.3 Biomass abundant and consumed at the study sites LNP and GMA-A

A comparison of the biomass consumption per km² of puku, impala and bushbuck between the two main study areas supports the assumption that middle sized antelopes were generally more often taken in LNP than in GMA-A. Reasons for that could be either that the density/km² of these three species is lower in the GMA-A than in LNP due to hunting, or the leopard is evading the competition by human hunters and switches to smaller prey as alternative. In both cases it addresses with an impact of hunting.

The comparison also shows for both areas a higher preference by leopards of bushbuck by leopards in relation to the abundance of these three antelope species. Due to its body mass of 22.5 kg, the bushbuck is included inside the preferred body mass class of > 15-30 kg described above (Chapter 4.4.2). Bushbucks occur more frequently in denser woodland than

in open woodland (Stuart & Stuart 2002) and savannah as for example, the puku (Jenkins 2002; Rduch 2008). This might be the explanation why this species is preferred by leopard which favors to hunt in areas with a specific cover.

4.4.4 The leopard in competition with trophy hunting

Population densities of large felids are positively correlated to the biomass of their prey (Van Orsdol et al. 1985, Stander et al. 1997, Karanth et al. 2004b). Bodendorfer et al. 2006 documented for leopards' diet in the Comoe' NP, Ivory Coast, predominately prey species' of medium sized (5-20 kg) to large (> 20 kg) ungulates over a three year period. When those populations became reduced due to heavy poaching, leopards' predation on large rodents, birds and reptiles increased significantly.

In the Cockscomb Basin in Belize, after this area experienced protection from hunting, the consumption of larger ungulates by jaguars increased significantly (Weckel et al. 2006).

The recently reanalysed relationship between the population densities of large African predators and the biomass of their prey (Hayward et al. 2007) presented that the relationships are more robust if only preferred prey species or species within the predators preferred weight range are considered. Hereby, the leopard showed the highest significance between abundance of prey and predator density among the large African predators which explained the great amount of variability in the density estimates of this predator species (Hayward et al. 2007).

All this indicates that the leopard is heavily dependent on prey species of its preferred weight range and a depletion of species within this body mass range could inevitably lead to a decrease of leopard population density.

Although scientific based population density counts of most of the prey taxa have not taken place in the region of the GMA's, I assume according to our observations that the relative abundance of the impala, bushbuck and puku is very likely not lower in the GMA-A than in the LNP, but perhaps the density per km².

Nevertheless, the findings of the prey choice analyses show, in facts, that the leopard shifts to smaller prey in the GMA-A than it does in the LNP.

4.5 Summary

In this study the diet of leopards (*Panthera pardus*) was determined in Luambe National Park (LNP) and surrounding Game Management Areas (GMA's) in Zambia, with the primary focus of a direct bordering GMA-A. Therefore, 416 fecal samples of leopards collected inside LNP and surrounding GMA's were analyzed to investigate prey spectrum of leopards and biomass consumed by leopards.

8-18 taxa were recognized. Ungulates represented the majority of prey items found in all study sites (e.g LNP=83.6%; GMA-A=81%) and also comprised the largest portion of the biomass consumed (LNP: 90.67%; GMA-A: 88.12%).

In terms of frequency of occurrence Sharpe's grysbok constituted the most frequently consumed antelope (18.2%) in the primary considered GMA-A but only 9.8% in the National Park. Larger antelopes such as impala (17.3%) pukus and bushbuck (15.1%) were less consumed in GMA-A than in the LNP in which impala (24.2%), puku (21%) and bushbuck (17%) comprised the largest part of the leopards' diet.

In terms of body mass, in the LNP, leopards preferred prey species' of >15-30 kg (43%) which include impala and bushbuck and in the GMA-A species of >1-15 kg (41%) comprising in largest quantities grysbok, primates and young warthogs. Puku (52 kg) was more consumed in LNP than in the GMA-A.

One reason could be that middle sized antelopes are trophy hunted in a higher quantity than smaller sized antelopes in the GMA-A. In this case the leopard is in competition with human hunters in the GMA-A. Therefore, it perhaps shifts to smaller sized antelopes which are more available than middle sized antelopes due to hunting, or the leopard is capable to discriminate between a disturbed area (GMA) and an undisturbed area (LNP). Thus, it is probably careful in hunting middle sized antelopes because it combines it with disturbance in open habitat. The findings showed that leopards prey choice inside the GMA-A is more likely influenced by hunting.

5 The possible impact of trophy hunting on the leopard (*Panthera pardus*) in Zambia, especially in a selected region in the Luangwa Valley

This chapter deals with the conclusions regarding the impact of hunting, drawn from the hunting harvests of leopards and from the results described in Chapter 2-4 and concerning following questions:

- What are the annual offtake quotas of the four Game Management Areas around Luambe National Park and how many leopards have been hunted in these Game Management Areas?
- What is the hunting intensity of leopards in Game Management Area-A?
- Is there any indication of a high hunting pressure?

5.1 Introduction

The African leopard (*Panthera pardus*) is one of the most demanded trophies in Africa. Until the 1980s the leopard belonged to one of the most threatened species listed by IUCN due to the international trade in the skins and other products. A modelling study in which a population of leopards of about 700,000 in Africa was suggested (Martin & De Meulenar 1988), resulted in an increase of hunting quotas of leopards by CITES. Although the mentioned study was critized as overestimated from many experts (Martin & De Meulenar 1989, Norton 1990, Nowell & Jackson 1996), it is still widely used as it represents the most practical and quantitative attempt to estimate potential leopard numbers across a large geographic area (Nowell & Jackson 1996). Nevertheless, there are still no reliable continent wide estimates of leopard population size in Africa. According to the progressing habitat loss and fragmentation leopards are declining in their range aggravated by hunting for trade and pest control. The African leopard (*Panthera p. pardus*) has recently been uplisted by IUCN from “least concern” to “near threatened” (IUCN 2008).

The impact of trophy hunting on the leopard population is unclear (IUCN 2010) and should not be underestimated. Demographic side effects on carnivore and ungulate populations caused by selective hunting (concerning age, sex, size, etc.) received far less

attention than direct overharvesting although these effects exist even when the overall offtake is not regarded as excessively high (Milner et al. 2007).

Hunting in general could play an important role in depleting a population (e.g. Milner-Gulland et al. 2003, Fryxell et al. 2010), especially true in species, where infanticide is common (e.g. Whitman et al. 2004, Caro et. al. 2009, Swenson 2003). Large-scale declines in the African lion (*Panthera leo*) and possibly in leopards were probably caused by excessive trophy hunting activities (Packer et al. 2009, Packer et al. 2010).

In several countries, where leopards are available for trophy hunting such as Zambia, the status of the leopard population is not clear and no research regarding this has taken place. Declining leopard harvests as for example in Zimbabwe and gaps in the knowledge of leopards in Zambia have raised concerns about leopard management and trophy hunting (Balme 2009, Packer et al. 2009, Balme et al. 2010a, Purchase & Mateke 2008).

This implies that the country wide quotas are probably too high or too easy to allocate and the need for an effective and sustainable leopard management.

At the moment (2011) in twelve African countries, that include Zambia, international quotas for the export of leopard trophies were set (CITES 2011, Zeet 2011) (Table 5.1):

Table 5.1: Countries and their international CITES quotas set for leopards

Name of the country / Number of individuals allowed on quota			
Botswana	130	South Africa	150
Central African Republic	40	Tanzania	500
Democratic Republic of the Congo	5	Uganda	28
Ethiopia	500	**Zambia**	**300**
Malawi	50	Zimbabwe	500
Mozambique	120		
Namibia	250		

The international quotas represent a number of leopards allowed to be trophy hunted in the respective countries and also permitted to export the trophies from these countries.

Records provided by ZAWA indicate that the quotas of 300 leopards did not fulfill the approved quota (offtake quotas 2004-2010). Zambia has 43 hunting blocks (excluding game ranges) across the country from which 13 can be classified as “prime”. Five categories of hunting blocks exist in Zambia which are defined according to ZAWA 2004-2010 in Chapter 1 (see Table 1.1 and Table 1.2): “prime” hunting areas are slowly degenerating to “secondary” if not “under stocked” status, especially in the Kafue and Luangwa ecosystem. In a hunting block which is qualified as “prime” usually four to five male leopards are allowed to be harvested per hunting season.

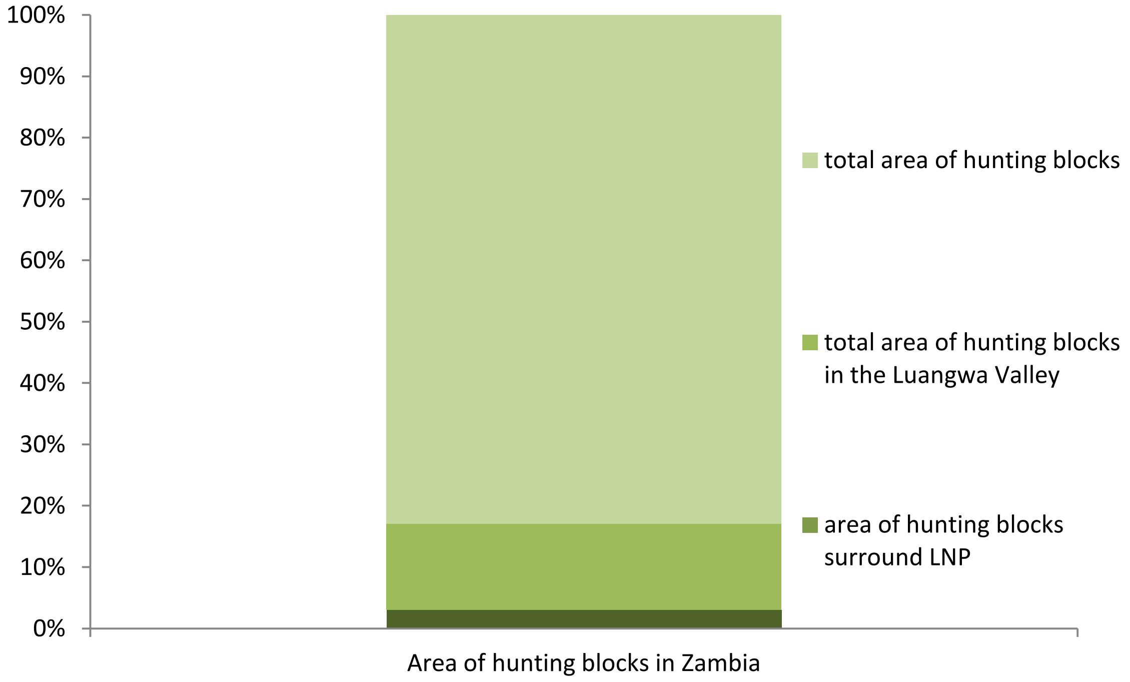


Figure 5.1: Representation of the percentual area covered by hunting blocks in Zambia

One third (28.6%) of Zambia’s area encompasses hunting blocks; 17% are situated in the Luangwa Valley, and the Game Management Areas that are surrounding the Luambe National Park account for 3.6% (see Figure 5.1). The latter represents the focus area of this study described in the following.

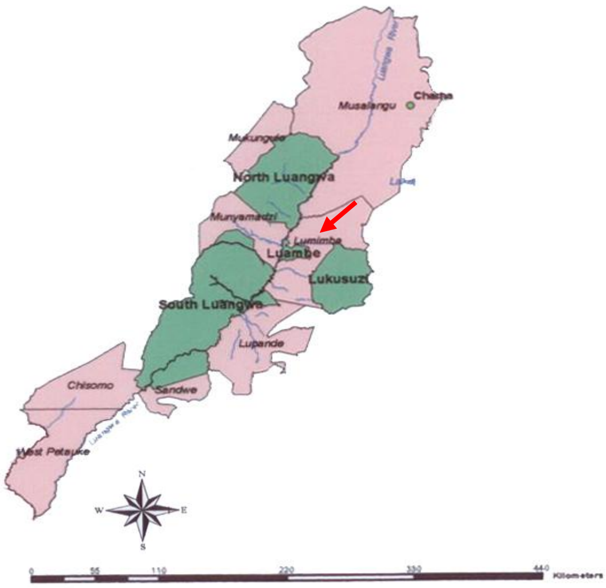


Figure 5.2: Map of the Luangwa Valley, in Zambia, showing the National Parks/ green), GMA's (pink), and rivers (blue), red arrow: LNP
Modified from original map. Source: ZAWA (Zambia Wildlife Authority)

5.1.1 Investigation area

The Luangwa Valley in the East of Zambia in historical times was already famous for the high game abundance but also notorious for excessive poaching which apparently caused depletion in the once richness of game abundance. However, the Luangwa Valley is still a popular hot spot for hunting safaris. Nine Game Management Areas (GMA's) which include thirteen hunting blocks occur in the area where controlled hunting is allowed, following the quota given by the Zambia Wildlife Authority (ZAWA). Four National Parks are located there to leave parts of the area undisturbed (Figure 5.2).

The area of main focus within the Luangwa Valley comprises the Luambe National Park (LNP) (encompassing 338 km²) and a GMA that borders directly onto it. The LNP is surrounded by four GMA's in total, in the north by the GMA-A, which is the main considered GMA in this study, and in the south by GMA-B. In the west it is flanked by two GMA's, C and D, both of which are separated from the LNP by a natural border of the Luangwa River. Human habitation and settlements are prohibited within the boundaries of the LNP. In contrast, villages and agricultural activities occur in the GMA's and sustainable hunting for game meat as a source of food, as well as trophy hunting is allowed. All GMA's which are

surrounding the LNP are “prime” areas according to the categories by ZAWA (see Table 1.1 and Table 1.2).

The GMA-A actually consists of two hunting blocks from which the part bordering directly against the LNP is categorized as “prime” and the part further in the North as “secondary” (ZAWA 2004-2008), see Table 1.2.

5.2 Methods

Data of hunting quotas (2004-2008), provided by the Zambia Wildlife Authority (ZAWA) were rehashed and analyzed. Country wide findings were compared with those only concerning the Luangwa Valley with special focus on the four GMA’s around LNP. Quotas were set in relation to the area covered by hunting blocks.

Results of the precedent studies that were described in Chapter 2-4, regarding population size, home ranges, habitat preferences and activity pattern as well as the leopard’s prey choice in the area of focus were included.

I calculated the hunting intensity as the average annual number of animals harvested (Packer et al. 2010) per 100 km^2 from 2004 to 2010 for the whole of Zambia, for only the Luangwa Valley and only the four GMS’s in focus. In order to calculate the density of males I used the sex ratios according to numbers of identified leopards in the GMA 2008 and the density of 4.79 leopards determined per 100 km^2 (Chapter 2). In addition, I also used a sex ratio of 1.1 females/males according to Bailey 2005 for comparison, to get an idea which sex ratio is more reliable. The percentage of hunting intensity on the density was calculated by hunting intensity/density (100 km^{-2}) *100.

Three skeletons of leopards trophy hunted in the Luangwa Valley in one season (2006) were roughly analyzed for age, only concerning if “juvenile” or “adult”. Measurements of femur and tibia were compared with skeletons of African leopards that died in zoos to see if any size differences exist.

5.3 Results

5.3.1 Quotas of leopards between 2004 and 2010

Figure 5.3 shows the quotas allocated and the actual harvest (real utilization) for leopards within the years 2004 to 2010 across Zambia. Not all allocated quotas are always utilized. In 2006 and 2008, 55% and 54% of the allocated quotas could not be utilized (ZAWA 2008, ZAWA 2006). In 2009 and 2010, 58% and 74% of the allocated quotas were utilized.

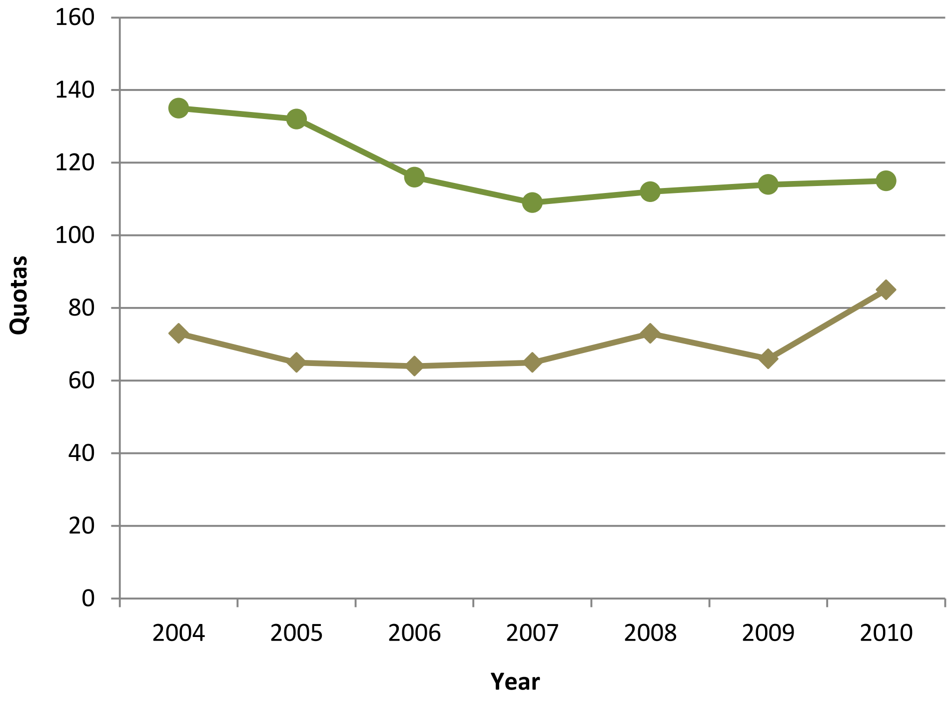


Figure 5.3: Comparison between allocated quotas (green) of leopard and the real utilization (brown).

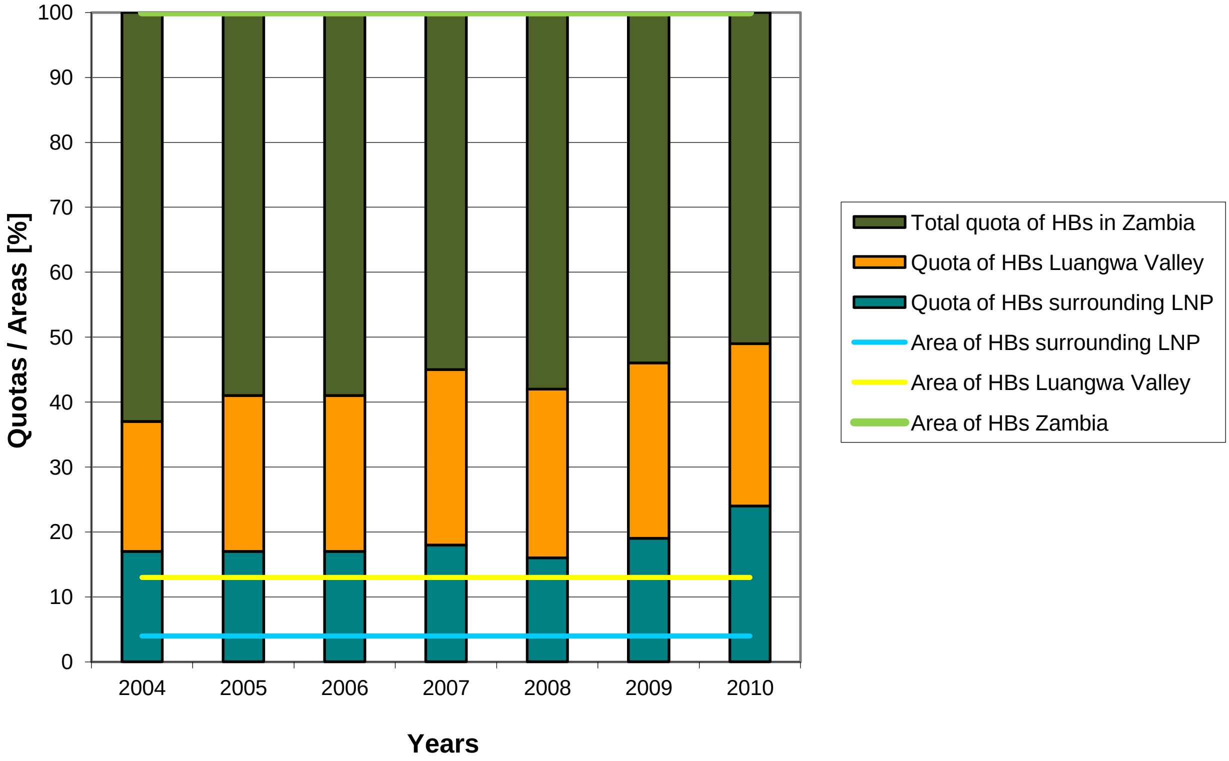


Figure 5.4: Representation of leopard quotas from 2004-2010, dark green: total leopard quota of Zambia; orange: total leopard quota of all hunting blocks (HBs) within the Luangwa Valley; dark-blue: quota of only the hunting blocks surrounding the Luambe National Park

The hunting block area in the Luangwa Valley and the area of the GMA's surrounding LNP encompass 17% and 3.6%, respectively, of the total area of hunting blocks in Zambia (Figure 5.4). The view of the leopard quotas from 2004 to 2010 indicates an average 43% of the country wide quotas covered by hunting blocks (HBs) occurring in the Luangwa Valley. An average of 18% of the country wide quotas is comprised by the four GMAs surrounding LNP (Figure 5.4).

Furthermore, 43% of the hunting quotas from hunting blocks located in the Luangwa Valley are brought out from the four GMA's surrounding the LNP.

In the area surrounding the LNP from 2004 to 2008, 23/23/20/20/18 individuals were allocated and also mainly utilized (ranging from 16-18%); resulting in 104 leopards hunted within five years. In 2009 and 2010 the allocated quotas increased (22/27 individuals) and were also fully utilized (19 and 23%), resulting in 49 leopards hunted (Table 5.2). The largest amount of leopards was hunted in GMA-A.

Table 5.2: Allocated hunting quotas from 2004-2010 for the leopard from Zambia in total, from hunting blocks (HBs) only occurring in the Luangwa Valley (game farms are not included), and from only the hunting blocks surrounding the LNP

Year	Total quotas Zambia	Quotas of all HBs in the Luangwa Valley	Quotas of HBs surround LNP
2010	115	56	27 (23%)
2009	114	52	22 (19%)
2008	112	47	18 (16%)
2007	109	49	20 (18%)
2006	116	47	20 (17%)
2005	132	54	23 (17%)
2004	135	50	23 (17%)

5.3.1.1 Density of males and hunting intensity

Table 5.3 show the sex ratio of leopards indentified in the GMA-A 2008 (Chapter 2). Since I found nine individuals with one of unknown sex, I calculated different possible sex ratios. One was calculated with only the identified sexes resulting in 1.0 female/males. The further sex ratios were calculated with assuming either the unknown individual as female and male, respectively, resulting in 1.3 females/males and 0.8 females/males. Bailey 2005 shows a sex ratio of 1.1 females/males.

Table 5.3: Sex ratio of leopards indentified in GMA-A (2008), and sex ratio according to BAILEY (2005), and density of females and males per 100 km² calculated with the leopard density of 4.79/100 km² of GMA-A (Chapter 2).

	absolute	**sex ratio (female/males)**	**density females/100 km²**	**density males/100 km²**
identified sex	4 females/4males	1.0 (50%)	2.4	2.4
unknown sex, assigned to ♀	5 females/4 males	1.3 (55%)	2.6	2.2
unknown sex, assigned to ♂	4 females/5 males	0.8 (44%)	2.1	2.7
according to BAILEY (2005)	//////////////	1.1 (52%)	2.5	2.3

With a sex ratio of 1.0 the density of females and males are the same (2.4 individuals/100 km²). The lowest density of males (2.2 males/100 km²) is shown with a sex ratio of 1.3 (females/males). The highest density of males (2.7 males/100 km²) is resulting from the sex ratio 0.8 (females/males). With a sex ratio of 1.1 (females/males) the density of males would be 2.3 (males/100 km²).

Figure 5.5 shows the hunting intensity (quota/100 km²) of male leopards per 100 km² for the country Zambia (average 0.05 quota/100 km²), for the hunting blocks occurring in the Luangwa Valley (average 0.13 quota/100 km²), for only the four hunting blocks around LNP (average 0.28 quota/100 km²) and for only the GMA-A (average 0.32 quota/100 km²) that was compared with the LNP. The four hunting blocks hold country wide the annual highest hunting intensity of leopards per 100 km². This is five times higher than the hunting intensity country wide (see Figure 5.5).

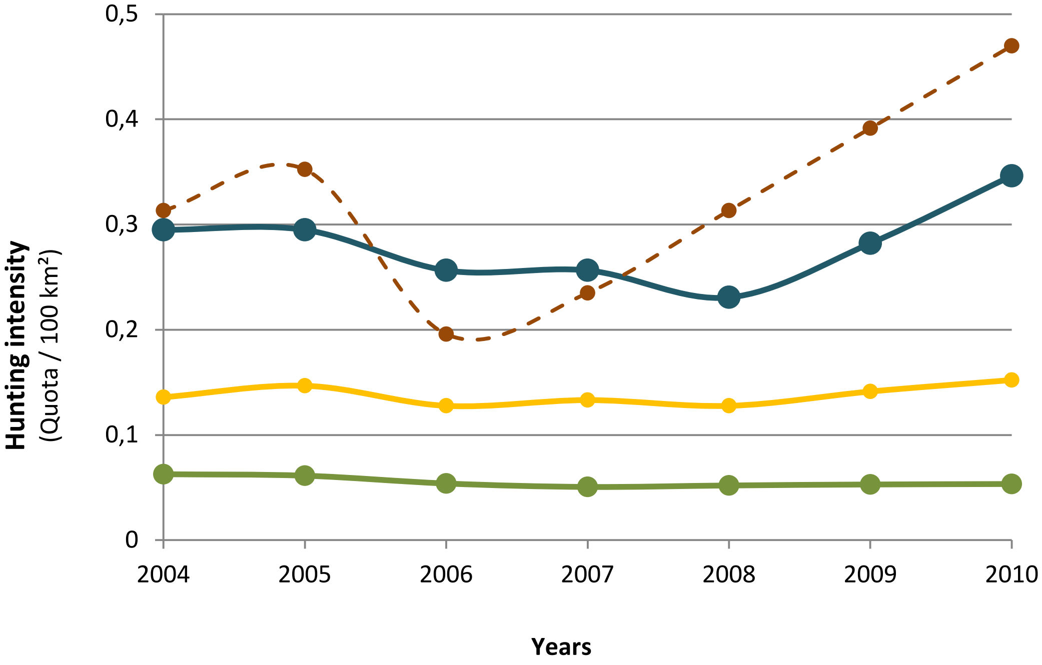


Figure 5.5: Comparison between leopard hunting intensity (quota/ 100 km²) country wide (green), of hunting blocks (HBs) within the Luangwa Valley (yellow), of hunting blocks surrounding the LNP (blue), and of only the GMA-A that was compared with LNP (brown).

The hunting intensity in Figure 5.5 indicates an increase from 2004 to 2005, a decrease in 2006 and from 2007 a continuous increase with a maximum in 2010.

The highest average hunting intensity (0.32 quota/100 km²) showed GMA-A. In 2008 GMA-A showed a hunting intensity of 0.31 (quota/100 km²) that would comprise 6.5% of the leopard density of 4.79/100 km² determined for the selected part of the GMA-A (see Chapter 2.3.1) for an unknown sex-ratio (see Figure 5.6).

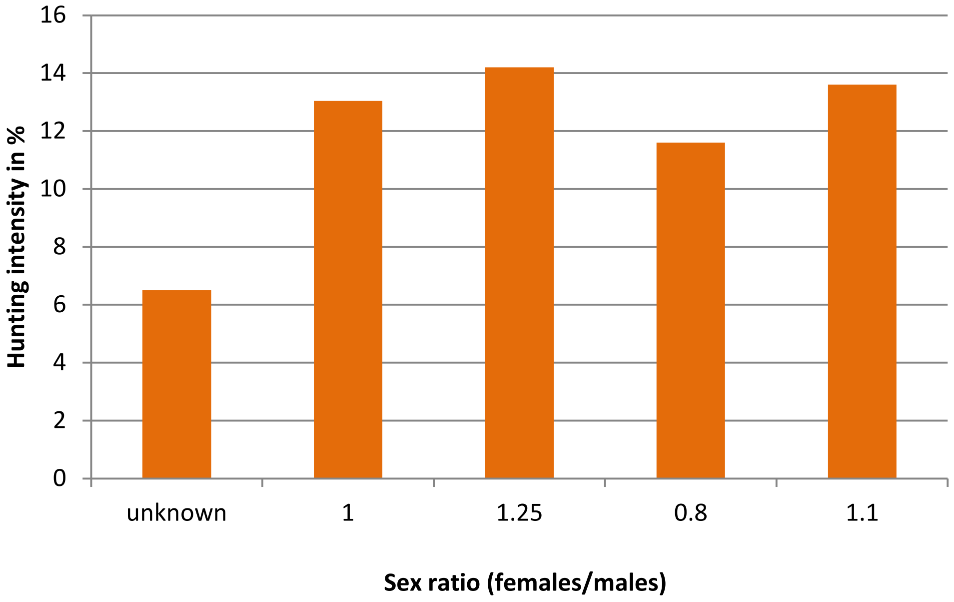


Figure 5.6: Hunting intensity in GMA-A-2008 (%) on density of all leopards/100km² (unknown sex ratio), and on density of male leopards/100 km², calculated for 3 possible sex ratios, and for a sex ratio (1.1) mentioned in Bailey 2005.

Considering the calculated sex ratios and densities of males (Table 5.3) the hunting intensity in GMA-A-2008 (0.31 quota/100 km²) comprises 11.6-14.2% of the densities of males/100 km². The sex ratio of 1.1 (females/males) is between the range of the sex ratios 0.8–1.25 (females/males), and is therefore the most reliable sex ratio with the minimum error.

5.3.2 Quotas of the main leopard prey species from 2004 to 2008

From six species which have been analyzed to be the preferred prey species of leopard (see Chapter 4) in the LNPand GMA-A, four were ungulate species, namely impala, bushbuck, puku and grysbok. Further species were baboon and warthog. Quotas of these species, summarized over all GMA's around the LNP, are provided in Table 5.4. According to these the small sized antelopes like grysbok was on quota with 13/19/19/17/16, summarizing to 84 individuals in total. Middle sized antelopes such as bushbuck, impala and puku show 31/36/41/36/35, 70/78/84/76/85 and 53/61/52/61/52 with 179, 393 and 279 individuals in total.

For baboons 38/40/39/41/24 and for warthogs 38/40/34/36/29 quotas were allocated within the years from 2004 to 2008 which makes a total of 182 and 186 individuals.

Table 5.4: Hunting quotas from 2004–2008 for the main prey species of leopard found in GMA-A and LNP, summarized from the four GMA's surrounding LNP

	Quotas allocated /Year					
Species	**2004**	**2005**	**2006**	**2007**	**2008**	**Total**
Grysbok (*Raphicerus sharpei*)	13	19	19	17	16	*84*
Bushbuck (*Tragelaphus scriptus*)	31	36	41	36	35	*179*
Impala (*Aepyceros melampus*)	70	78	84	76	85	*393*
Puku (*Kobus vardoni*)	53	61	52	61	52	*279*
Baboon (*Papio cynocephalus*)	38	40	39	41	24	*182*
Warthog (*Phacochoerus africanus*)	38	40	34	35	39	*186*

5.3.3 Leopards prey choice and the choice of trophy hunters

Species such as baboon and warthog, were significantly (p=0.04; p=0.001) more frequently eaten by leopards in GMA-A (Figure 5.7) than in LNP. Impala, bushbuck and puku were consumed in a larger amount inside the LNP than inside the GMA-A, while the highest amount of grysbok's were in the GMA-A. The comparison between prey consumed by leopards in the LNP and in the GMA-A and species hunted within the time of data collection (see Chapter 4) showed that species that were hunted in high numbers inside the GMA-A were less consumed by leopards than in the LNP. This can be also confirmed by the differences in the preferred body mass of prey species (Figure 4.10) between the LNP (>15-30 kg) and GMA-A (>1-15 kg).

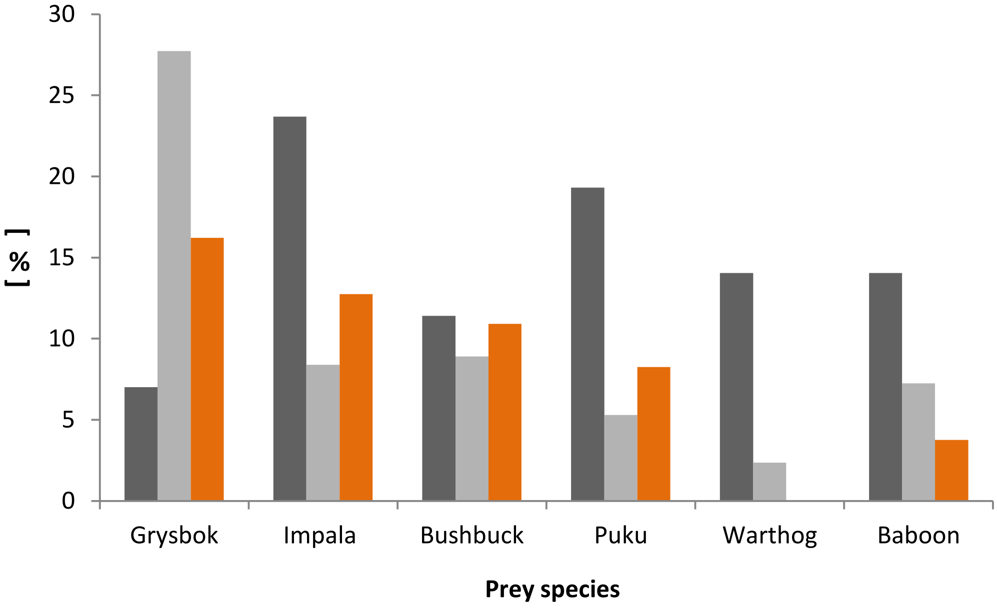


Figure 5.7: Comparison of individuals shot in GMA-A (dark grey) versus consumed in GMA-A (light grey) by leopards versus consumed individuals by leopards in LNP (orange) (%).

Figure 5.8 ($r^2 = 0.820$; p=0.013, SPSS) indicates that the heavier the species the more relevant it is for trophy hunting. Grysbok, which is the smallest antelope of the questioned species is of less significance, while puku which represents the largest antelope (within this research) of high significance.

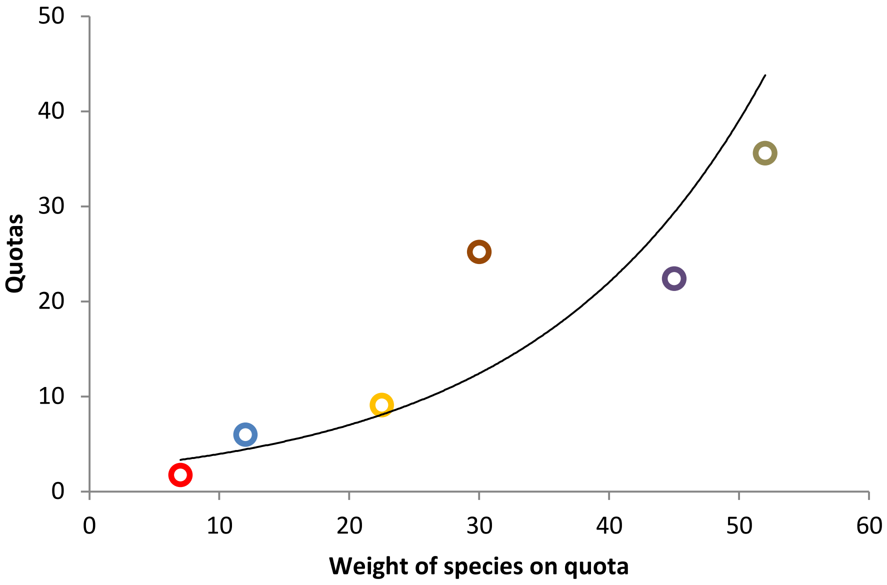


Figure 5.8: **R**elationship between hunting quotas and the weight of the trophy hunted species: The larger the species the more it is relevant for hunting safaris ($r^2=0.820$).
Red: grysbok,
blue: baboon;
yellow: bushbuck;
brown: impala;
violet: warthog;
grey: puku

From 2004 to 2008 impala was the most frequently hunted antelope within the four GMA's and showed annual quota ranging from 68 to 85 individuals with the highest quota in 2008. Puku was with 52 to 61 individuals annual on quota with the highest quota in 2007 and 2005. Bushbuck, with 31 to 41 individuals per year, was the highest quota in 2006. Grysbok was the least hunted species, ranging from 13 to 19 individuals per year with the highest quota in 2005 and 2006 (Figure 5.9).

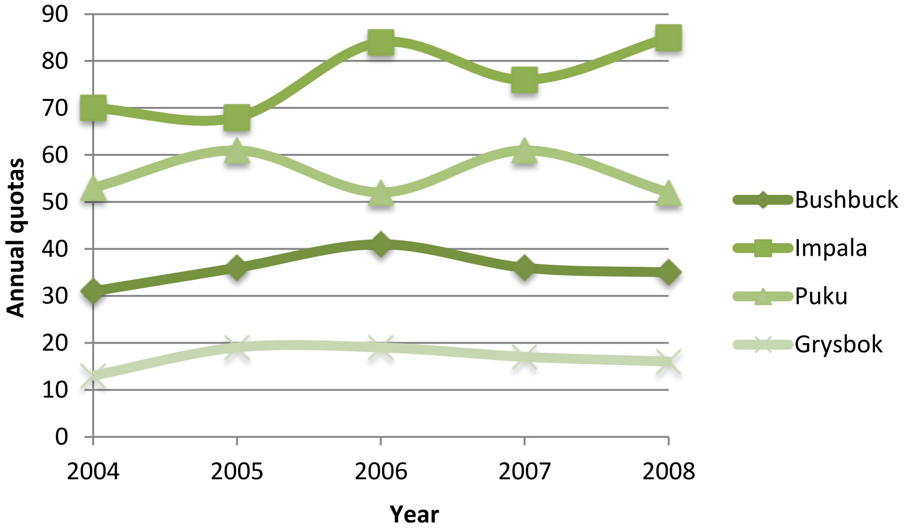


Figure 5.9: Summarized quotas of the important antelope species for the leopard in the four GMA's surrounding the LNP from the years 2004 to 2008

5.3.4 Relative abundance indices and the quotas of leopard in comparison with its competitors

The findings of relative abundance indices (RAI) for large carnivores and possible competitors to the leopard in the LNP from 2008 showed a RAI value of 4.59 for the leopard, 3.2 for the lion and 2.68 for hyena. In contrast the RAI for the GMA of 2008 was 5.33 for leopard, 2.13 for lion and 1.00 for hyena (see Table 5.5 and Chapter 4)

	GMA-A	**LNP**
Species	**2008**	**2008**
Leopard (*Panthera pardus*)	5.33	4.59
Lion (*Panthera leo*)	2.13	3.20
Hyaena (*Crocuta crocuta*)	1.00	2.68
Total (without leopard)	***3.13***	***5.88***
Total	***8.46***	***10.38***

Table 5.5: Relative abundance indices of leopard and its competitors in GMA-A and LNP (2008).

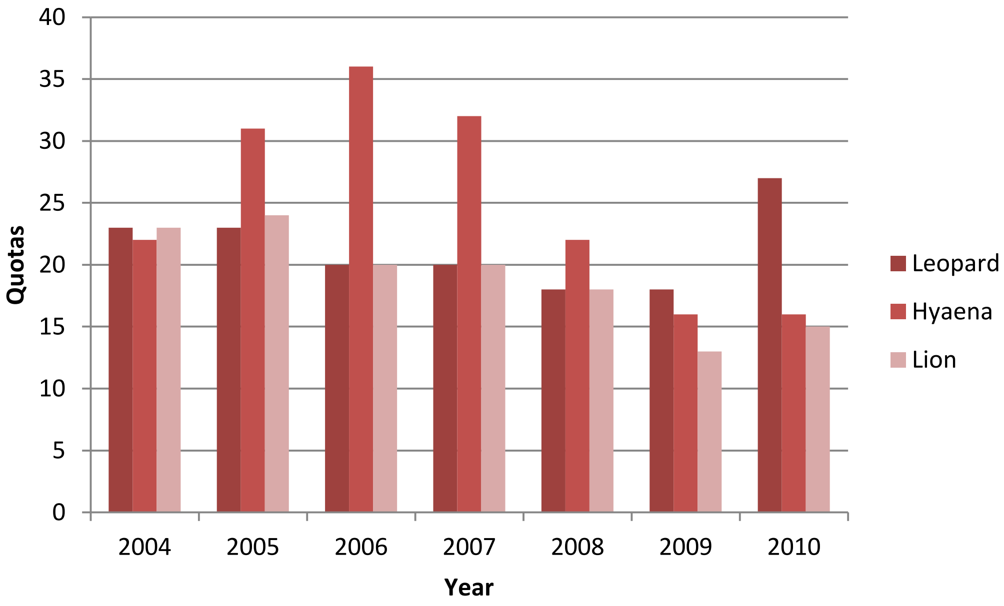


Figure 5.10: Comparison between the quotas (harvest (utilization)) of leopard, hyena and lion from 2004 to 2010 brought out from the four GMA's surrounding LNP.

The lion quotas summarized from all GMA's (GMA-A,B,C, and D) surrounding the LNP almost always coincide with the quotas of the leopard until the year 2008. The quotas for hyena exceeds both the quotas of the large cats until 2008 (see Figure 5.10). The quotas for leopard and lion decreased after 2005 and reached their lowest quotas in 2008. After 2008 the leopard quota increased and exceeds the quota (harvest) of lion and hyena. It reached the highest quota (harvest) in 2010. Although the quota (harvest) of hyena increased between the years (2005, 2006, 2007) they also decreased in 2008, but was still higher than the quota (harvest) of leopard and lion. In 2009 and 2010 the quota (harvest) of hyena reached its minimum and was far below that of the leopard quota (harvest). Nevertheless, the real utilization of the lion quotas until 2008 is unclear. Possibly not as many lions had been shot in 2008 especially in the GMA-A.

5.3.5 Measurements of leopard skeletons

Measurements and analyses of the three skeletons of leopards that were trophy hunted showed that two of the individuals were juveniles.

Table 5.6: Measurements, taken from skeletons of wild leopards (trophy hunted) and leopards that have been died in zoos.

Zambia	Skeletons, from wild leopards, hunted in the Luangwa Valley (LV), in the GMA's around LNP			
Juv. / adult	Femur (left) Length/width (cm)	Femur (right) Length/width (cm)	Tibia (left) Length/width (cm)	Tibia (right) Length/width (cm)
LVa (Juv.)	25.2 / 1.8	25.8 / 2.1	22.4 / 2	22.7 / 1.9
LVb (Juv.)	25.8 / 1.9	25.5 / 2	22.6 / 1.9	22 / 1.8
LVc (adult)	26.3 / 2.1	26.1 / 2.2	21.2 / 2.6	21.1 / 2.6
ZFMK	Skeletons, from leopards, died in the zoo Löhnebach (LB) and zoo Wuppertal (WT)			
Juv. / adult	Femur (left) length/width (cm)	Femur (right) length/width (cm)	Tibia (left) length/width (cm)	Tibia (right) length/width (cm)
LB (adult-41kg)	23.4 / 1.9	25.5 / 1.8	23.4 / 1.8	23 / 1.9
WTa (Juv.)	18 / 1.6	18.4 / 1.6	17.6 / 1.6	17.7 / 1.6
WTb (adult-35.5kg)	23.5 / 2	24.6 / 2.1	21.8 / 2.7	21.7 / 2.5

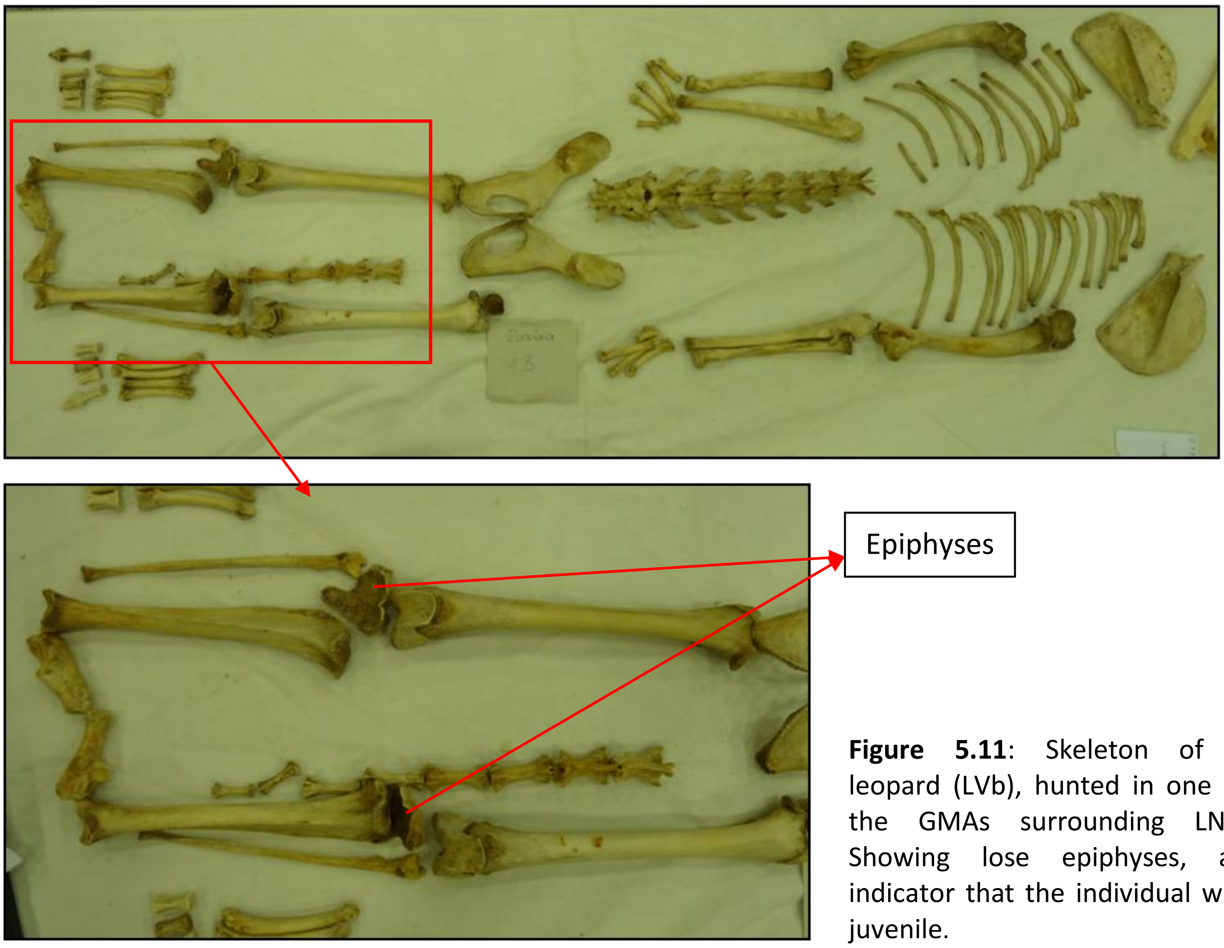


Figure 5.11: Skeleton of a leopard (LVb), hunted in one of the GMAs surrounding LNP. Showing lose epiphyses, an indicator that the individual was juvenile.

While the epiphyses of LVc were seamless fusioned with e.g. the femur or the tibia, the epiphyses of LBa and LBb were lose (Figure 5.11) (Kowalski 1976, Wagenknecht 1979).

The juveniles also differed in their size of femur and tibia from the adult specimen. The skeletons were incomplete and lacking in the skull, and paws, as those parts constitute the trophies together with the skin.

The measurements of femur and tibia of the reference skeletons from the leopards that died in zoos were smaller than the skeletons of the wild leopards (see Table 5.6).

5.4 Discussion

5.4.1 The signs of an impact of trophy hunting

The findings indicate that the Luangwa Valley is the area most exclusively affected by trophy hunting for leopard in Zambia. Although the area of hunting blocks inside the Luangwa Valley covers only 17% of Zambia's area which is provided for trophy hunting, nearly 43% (averaged) of the annual country wide quota of leopards come from hunting blocks located inside the Luangwa Valley. Further, 43% (average) of the ”Valley-wide” annual harvest is generated by the four GMA's surrounding the LNP, which represent only 3.6% of the country wide hunting area. Thus, this implies an extreme hunting pressure on the leopard. This can be confirmed by the highest hunting intensity for males country wide (0.28 individuals/100 km²) inside these four GMA's. GMA-A provided with 0.32 individuals per 100 km² the highest intensity among the four GMA's. It encompasses the highest harvest (considering the annual quota) among the four GMA's at 38%.

The real sex ratio in this study in the GMA-A is unclear since one individual could not be identified to sex level. BAILEY (2005) documented an average sex ratio of collared leopards of 1.1 females/males but 1.8 females/males for adults only (in Kruger National Park 1972-1974). If I exclude the “unknown” leopard in my study the tendency of this sex ratio would be 1 females/males. If I include it and assign it either to males or females the sex ratio ranges from 0.8 to 1.3 females/males. The average approximated sex ratio would be 1.1 females/ males, which is like the average sex ratio in the study of BAILEY (2005). Since in Bailey's study the sample size was higher this sex ratio appears reliable and is therefore used for further considerations in the present study.

By using the assumed sex ratio of 1.1 (52% females and 48% males) the density of males and females (based on the determined 4.79 leopards/100 km² (Chapter 2)) resulted in 2.5 females and 2.3 males per 100 km². Thus, the hunting intensity by GMA-A (2008) of 0.31 would comprise 13.6% of 2.3 male leopards per 100 km². This would obviously increase in the event of a higher sex ratio females/ males.

A natural mortality rate of leopards documented by BAILEY (2005) averaged 18.5%, with twice as many adult males that died as adult females and caused mainly by starvation and violent causes. Therefore it has to be considered, that the mortality rate in the study region must be much higher, because it consists of the natural mortality rate and anthropogenic caused mortality rate.

The comparison between the results of the diet analyses of the leopard (see Chapter 4) and the hunting quotas for the relevant prey species shows that most of the preferred prey species in LNP are hunted in high quantities in the GMA's. It indicates that the larger the species the more relevant it is for trophy hunting (Figure 5.8).

The leopard consumed middle sized antelopes such as impalas, pukus and bushbucks more in the undisturbed LNP than in the GMA-A and its consumption of Sharpe's grysbok as well as baboon is higher in the GMA-A than in the LNP (see Chapter 4). Consequently, I assume that the difference of prey choice and preferences between the "undisturbed" LNP and the "disturbed" GMA-A is dependent on trophy hunting activities. The species preferred by leopard are also important for hunting safaris and indicate that the leopard is in competition with human hunters (Chapter 4).

Additionally, the prey species are possibly more timid in the GMA's than inside the LNP according to the relative undisturbed situation there. Due to the larger size of the GMA-A (2,555 km²) the abundance of impala and puku is probably higher there than in the LNP (338 km²) (Chapter 4). The history of the LNP which is stamped by poaching contributes however, to a current lesser abundance in the LNP area.

I suggest that the choice habitat type and consistency (dense or open) for hunting prey plays an important role, especially in this case of the two adjacent areas. The region of the LNP is more undisturbed, and being aware of that, leopards also hunt middle sized prey species in open habitat, whereas in the GMA-A leopards choose more often species that occur in dense habitat. This supports the theory (Bodendorfer et al. 2006; Weckel 2006) that the leopard switches to smaller prey if its preferred prey is not adequate available to requirements (Chapter 4).

The offtake quotas signify a reduction of five individuals from 2004 to 2008. Nevertheless, the results show a stable number of leopards harvested across the years. Possibly responsible for that could be the harvests of competitors such as lion and hyena (Figure 5.10). This could have probably released leopards from high inter-specific competition (Crooks & Soule' 1999). Packer et al. (2009, 2010) reported previously that

hunting blocks in Tanzania with highest average lion harvests showed the largest increases in leopard harvest.

The harvests of lions and leopards are comparable in this study, but harvest of hyena is higher than that of large cats until 2008. After 2008 the leopard harvest reaches the highest harvest among the three predators.

Due to the deficit of long term abundance data for the three predator species within the investigation area the assumption cannot be proven as fact yet.

The only data representing estimates of leopard population have been determined within this research project, but not for a long term period over several years.

The increase in leopard harvest in 2009 and 2010 might imply unsuccessful lion and hyena harvests in these years which were tried to be compensated by a higher number of leopards on quota. The relative abundance indices (RAI) for the three predators for the year 2008 inside GMA-A indicate higher values for leopards than for lions and hyenas, with latter showing the lowest RAI. In comparison between the study sites LNP and GMA-A the RAI for all the species apart from the leopard was higher in the LNP than in the selected part of the GMA-A. It needs to be highlighted that the RAI just shows tendencies and this only for 2008, but it implies a higher abundance of leopards than lions and hyenas in the GMA-A. Anecdotal reports signify a decrease of lion abundance in the area.

Nevertheless, the latter could be one of the reasons for the higher leopard density per 100 km² in the selected part of the GMA-A (4.79 ± 1.16) in contrast to the LNP (3.35 ± 0.64). Further it was assumed that this relatively high abundance is perhaps just temporary (due to higher capture rates than recaptures rates in camera traps, see Chapter 2) and based in left "empty spaces" of killed leopards which are now tried to be occupied by new individuals (Loveridge et al. 2007). This could result in a high intra-specific competition associated with an unnatural rate of infanticide (Loveridge et al. 2007, Hunter & Balme 2004, Balme et al. 2010, Packer et al. 2010). Leopards live in a land tenure system (Bailey 1993) that appears to be dependent on the stability of long term relationships and they seem to tolerate familiar neighbors rather than strangers ("dear enemy effect": e.g. Ydenberg et al. 1988, Falls 1982 and Fisher 1954). Usually the home ranges of male leopards encompass the home ranges of several females, and the resident male's presence constitutes a protection of the cubs towards intruders who are inclined to infanticide. This was also assumed by Balme & Hunter

(2004) and Balme et al. (2010) in their leopard study in the Phinda-Mkhuze complex (protected game reserves) in South Africa. One of the collared male leopards in my study tried to overtake a probably left "empty space" by killing the cub of a resident female (see Chapter 3). During this observation I could not find any sign of another male's presence which led to the assumption that the father of the cubs was perhaps hunted when it crossed the boundary to a GMA that was only a few hundred meters apart. Infanticide is one of the reasons against excessive harvests of lions (Packer & Pusey 1984, Whitmann et al. 2004, Loveridge et al. 2007). According to the lions' life style infanticide within a pride is easier to observe than within solitary cats like leopards, but I suppose that it also plays an important role in leopard populations (as also suggested by Balme & Hunter 2004, Balme et al. 2010 and Packer et al. 2010).

The analyses of the three skeletons of hunted leopards showed that two individuals were juvenile. Sizes of leopards vary geographically; therefore it is not surprising that the measurements of the reference skeletons of the ZFMK were smaller than the ones of the wild leopards. Although these specimens were from African leopards died in zoos, it was not documented were they originated. Nevertheless, the "ZFMK" skeleton of the juvenile was from a leopard much younger than the hunted juveniles and explains the size differences. Although the sample size of three skeletons is too small to make profound conclusions, it indicates however that the risk of hunting juveniles exists.

5.4.2 Final conclusions

Population densities of large felids are positively correlated to the biomass of their prey (Van Orsdol et al. 1985, Stander et al. 1997, Karanth et al. 2004b). Putting into consideration how many individuals of the leopard's main prey were hunted within the years from 2004 to 2008 (see Table 5.4) I could confirm a possible competition between humans and the carnivore. The results of the prey choice analyses show in fact that the leopard shifted to smaller prey in the GMA-A than in LNP. The results and conclusions represented here definitely indicate an impact of hunting. The prey choice is possibly not a critical issue as long as enough adequate prey species are abundant and not limited by excessive trophy hunting harvest. Nevertheless, although it was not the topic here, the harvest of poaching has to be considered as well because it comes on top of the "legal hunting harvest". The sum of both could be critical in its consequences.

The population status of the leopard, concerning the cat's abundance and density, needs to get further explored. The fact that 18-27 male leopards can be hunted within one hunting season that lasts approximately six months supports the suggested possibility of a strong intra-specific competition and an increase of infanticide when more new individuals move up. The natural sex ratio of leopards would be disrupted. All of these would lead to an unstable population status.

Hunting subadult males would not be an alternative and a sign of overexploitation (e.g. Allendorf & Hard 2009, Packer et. al 2010).

The quotas signify a reduction of five individuals from 2004 to 2008 and any decline in harvest could probably reflect a decline of a healthy population (Packer et. al 2010). The relative strong increase of leopard harvest in 2009 and 2010 is probably correlated with the decrease in lion harvest. This implies an increasing hunting pressure on the leopard.

The fact that leopards can move freely across the borders, even for only temporary and short excursions as the radio-collared males showed (see Chapter 3) points at an impact on the leopard population living in an apparently undisturbed area such as the LNP. The situation of the leopard in this region does not appear as critical as it might be for the lion. But if lion quotas have to be reduced or abolished due to less lion abundance it is to be expected that the leopard will experience a higher hunting pressure in the future.

5.5. Summary

This study gives an insight into the hunting harvest of the leopard, its prey species and its competitors in Zambia and possible consequences based on scientific data determined in the Luambe National Park (LNP) and a bordering Game Management Area (GMA).

Country wide hunting quotas were compared with quotas of all hunting blocks located inside the Luangwa Valley of Zambia and additionally within only the four hunting blocks surrounding the LNP.

The comparison showed that 17% of Zambia's area covered by hunting blocks consists of hunting blocks situated in the Luangwa Valley. 3.6% are covered by the four GMA's surrounding the LNP. Despite the small size of the area, 43% of the country wide hunting quotas for leopards are covered by hunting blocks located in the Luangwa Valley, and 43% of the "Valley-wide" quota is brought out from the four GMA's surrounding the LNP. This implies a high hunting pressure to the leopard population living in the area of focus.

6 General Discussion

This study is the first to estimate the leopard population status in Zambia systematically including the estimate of population size and density, home range sizes, activity patterns and habitat preferences with telemetry data as well as the prey spectrum of this predator.

6.1 Critic of the methods

Methods like camera traps for population estimate (Karanth & Nichols 1998, Karanth et.al 2004a, Silver et al. 2004, Jackson et al. 2005, Balme et al. 2009, Henschel 2008), and radio-telemetry to determine the home ranges were used in previous studies and have been proven successfully. Therefore, they were considered as appropriate for this kind of study.

6.1.1 Camera traps

Due to the low financial budget the research project started with only six camera traps in the first year. Because of a parallel ongoing serval project also with six camera traps, certain important parts of the area could be covered with twelve cameras which were of benefit for both the projects. In 2007 and 2008 it was possible to acquire more camera traps, so that in the last year of the data acquisition a number of 40 (20/20) camera traps were available for both projects. Different types of camera traps were used within the course of this research project corresponding with a better developed technical standard and handling of the camera traps. Camera traps from the company BUSHNELL showed more frequent malfunctions and outages than the units from STEALTH CAM. This fact sometimes caused a temporary loss of data. Units (STEALTH CAM) used in 2008 provided a high compression of pictures that allowed the storage of up to 2,500 pictures on a 1GB memory card (SD). This facilitated the data acquisition because by this means the traps could be checked every week or every two weeks, instead of every two days. It would have been also practical to use subsets of cameras to capture individual leopards from the right and the left side, but this was not realizable due to the still insufficient number of camera traps.

However all captured leopards could be identified. Nevertheless, we have to consider that some animals developed a certain trap shyness which is reported in tigers (*Panthera tigris)* (Wegge et al. 2004). It is possible that individuals avoided camera traps having a negative reaction to the flash light and upon decreased the likelihood of recaptures. Most of the traps used in 2008 did not flash but captured pictures using infra red. However, a few units got seriously damaged by animals such as elephants, leopards, lions and hyenas which implied that the traps might have caused some further irritation. These were for example the cameras smell or very silent mechanical sounds made by the cameras or the red and green light (indicated that the cameras were switched on or off) that a few species probably were able to recognize.

6.1.2 Determination of telemetrical data

The leopards were equipped with simple VHF radio collars. This made it necessary to locate the animals always (usually 1 to 3 times a day) by triangulation with the antenna and a compass to get one record of coordinates. If it was not possible to locate an animal, coordinates for the certain hour could not be determined and had to be taken again the next day for this same hour.

An alternative would have been the more costly GPS collars that probably could have provided more data because those collars contain a kind of memory card that record more than one coordinate per day. Those could be downloaded as soon as the collared individual is close enough. This would have facilitated the data acquisition, but was not feasible due to financial limitations. Apart from these benefits it might have happened that the dense vegetation of the study area caused difficulties in recording sufficient coordinates on the GPS collar and then aggravating the download of those data.

Although the radio data were taken from a vehicle it could not be excluded that the observed leopards did not get disturbed in their natural activity behavior.

Still, it seems that wild animals are less disturbed by detection using a car than by humans moving on foot (Pohlmeyer 1991) and apart from that the animals in this region are used to vehicles because of photographic safaris.

Furthermore, for the activity pattern a stationary activity was noted when the fluctuation of signals and frequency (according to Pahl 2004) was strong. But we cannot rule

out the possibility that atmospherically fluctuations or strong moving branches caused similar fluctuations of signals. The mobility which was used as an indicator of location change was not subjected to this error and can be considered as the most reliable data in this case.

The numbers of locatings for analyzing the activity pattern was very heterogenic within the studied individuals. Since M1 destroyed his collar and M3 was captured much later than the other leopards the observation period for M1 and M3 was shorter which resulted in observation lacks in the activity data of the males. Despite these restraints the collected data represent clear tendencies of the observed leopards, as for example, the higher activity of males during night hours.

6.1.3 Baiting and trapping of leopards

The preparation for baiting and the following trapping of the cats needed detailed planning and were highly time consuming. The baits that worked best were pieces from impala, puku or hippo (30-60 kg), which were 2-7 days old. These baits were provided from professional hunters and could be collected by me when a predator safari had ended. As already mentioned before, keeping of live stock due to the presence of the tsetse fly, was not possible in the investigation area. Therefore, when those preferred baits were not available I used goats that had to be bought a 4-5 hours (150 km) drive away from the study areas. This took 1-2 days to organize appropriate baits. Although the baits were always set either in trees or later inside the live-trap that was placed 2m above ground to avoid other large predators, lions appeared regularly. This exacerbated the trapping of leopards because they disappeared as soon as they became aware of the presence of lions.

Further, young lions were capable of climbing inside the live-trap and finished the baits a couple of times. Another point is that according to the financial budget associated with all the requirements the construction of only 1 live-trap of 250 kg was possible. Therefore, a simultaneous trapping of leopards that could have been of great benefit for the data acquisition, was not realizable. The combination of all these facts is at last one reason of the late collaring of M3 during data acquisition that resulted in a shorter observation period in comparison to the other leopards.

Further observations are that leopards sometimes develop trap shyness and although they move around the trap they do not enter it for unknown reasons (similar observations were made in Botswana and Namibia, Schiess-Meier, verbal information). Bailey 2005 reported that females were more elusive and more difficult to capture than males. This cannot be confirmed in the present study because females here responded more quickly to baits than males.

Moreover, I noticed that closer to the rainy season leopards hardly fed from baits, in the LNP and the GMA's. Bailey 2005 also noticed that leopards were easier to capture during dry seasons, probably due to hunting difficulties in capturing prey at this time.

From September onward it was difficult to bait leopards, which was confirmed by experiences of professional hunters. Possible explanations were that at this time of year prey becomes more abundant because young warthog and impala would be born close to the rainy season. But according to my observations and interviews with local people the usual time for impalas giving birth in this area started from the end of October or November, which is also mentioned by Ansell (1960). Warthog was also not detected during the diet analyses for the LNP. Thus, the explanation above is not really convincing and the question remains open.

6.2 Estimate of leopard population size and density

Estimates of population size for the years 2006, 2007 and 2008 in the LNP (Table 2.4) did not show a significant difference between each other. The population size of seven leopards in 2006 is equal to the total number of leopards captured by camera traps and identified with reasonable certainty. Interesting is that the estimate of the population size for the LNP 2008 was twelve and for the GMA-A ten, which is comparably high considering the smaller size of the study area inside the GMA-A. The population density inside the GMA-A also resulted in a higher estimate (4.79 ± 1.16) per 100 km² than inside the LNP (3.36 ± 0.64). In contrast to studies conducted in the Phinda and Mkhuze Game reserve in South Africa (Balme et al. 2010) with densities of 7.17 ± 1.12 and 11.11 ± 1.31 per 100 km² my findings show a comparatively low leopard density.

In the study in South Africa only the density/100km² for a non protected area with 2.49 ± 0.87 was lower than in the present study. Henschel 2008 documented for rain forest areas

in Gabon densities of 2.69 ± 0.94 and 4.58 ± 2.58 and 12.08 ± 5.11. Comparing these densities with the densities in my study sites it is even more surprising since it is assumed (e.g. Bailey 1993, Jenny 1996) that leopard densities in rainforests are comparatively lower than in savannah habitats. Leopard densities are correlated with the abundance of mammalian prey which is lower in rainforests than in savannah environments.

Despite the fact I was informed that no leopard was hunted in the selected part of the GMA-A during the time of this study, it is possible that a leopard was shot which might have extended its excursions and overstepped the buffer of the effective sampled study area.

It is of significance that the “left empty space” of a hunted male leopard was (according to personal observations and interviews with professional hunters) taken soon by another male leopard inside the GMA-A study area. The enhancement of mating opportunities will perhaps attract more than one new individual that was trying to occupy the “empty space” and that would lead to an unnatural high intra-specific competition (Loveridge et al. 2007). The one who succeeded chased the competitors away which could be a reason for the high captures but less recaptures in this study area in comparison to the LNP. Thus, this might result in a temporary higher density of leopards in a relative small space. Leopards live in a land tenure system (Bailey 1993), where well established male residents and usually older leopards possess the older breeding rights that are associated with permanent stable land occupancy and territorial behavior. This implies that they need to be related with females long enough to breed. Both sexes defend territories against same–sex invaders (Bailey 1993), but they seem to tolerate familiar neighbors rather than strangers that e.g. Ydenberg et al. (1988), Falls (1982) and Fisher (1954) described as “dear enemy effect” where territory residents discriminate between neighbours and non-neighbors. Consequently, this land tenure system appears to be dependent on the stability of long term relationships (Bailey 2005).

Nevertheless, the most widely documented intra-specific mortality for felids is infanticide, recorded for most pantherines (Davies & boersma 1984, Bailey 1993, Smith 1993). Usually the home ranges of male leopards encompass the home ranges of several females, and although male leopards do not seem to show high parental care, the resident male’s presence constitutes a protection of the cubs towards intruders that are inclined to infanticide. This was also assumed by Balme & Hunter (2004) and Balme et al. 2010 in their

study about leopards in Phinda-Mkhuze complex in South Africa. The killing of a male leopard will thus have impact on the females surrounding him. One reason e.g. against excessive trophy hunting of lions was that it could be critical to kill male lions below the age of 6 years. After that they have more likely successfully reproduced and protected their cubs up to a subadult age from which they are not really threatened by new males (Whitmann et al. 2004, Packer et al. 2006). Although there are not many detailed studies (comparable to lion studies) concerning infanticide in leopards, it is already assumed that these factors also influence leopard populations (e.g. Balme & Hunter 2004, Ilani 1986, 1990). In this study I witnessed a case of infanticide by following M2 who left the study area and tried to settle in a new area (see Chapter 2). A safe age for leopards could be 7 years (Packer et al. 2009), but no age assessment criteria for leopards are available so far (Packer et. al 2010) in contrast to lion ages that can reliably estimated under field conditions (Whitman & Packer 2007).

An additional reason which could explain the higher density in the selected part of the GMA-study site is that it is a kind of congested area due to certain circumstances: the largest part of the selected area within the GMA-A cover grassland and Combretum-Terminalia woodland which could be an important leopard hunting habitat since these vegetation types comprise the largest part of the home ranges of the collared leopards as the habitat analyses showed (see Chapter 3). In the east, the area gets dry (as also in LNP) with less game and hardly water places which imply this to be an unattractive habitat for leopards. This can be also supported from the results of home range and habitat analyses of the radio tracked animals that did not encompass this kind of area. Therefore, no leopards were captured by camera traps and only 2 scat samples were found here. In the north-west villages exist which could be a disturbance for leopards as also Henschel 2008 documented in his study about rain forest leopards in Gabon.

It also needs to be emphasized that it makes no sense to project the determined density per 100 km² to the whole size of GMA-A (2,555 km²). The vegetation and habitat types deeper inside the GMA-A are not ascertained yet and I cannot simply emanate that the habitat is as appropriate to leopards as in the study areas. On top of it the second hunting block within the eastern part of GMA-A is classified as “secondary” by ZAWA. Although these two areas merge into each other, they are most reliable different in habitat quality. This implies that the leopard density is probably not as high as in the hunting block bordering

against LNP and which is categorized as “prime”. In addition to all these facts the villages within GMA-A offer no suitable leopard habitat. Therefore, a projected density of leopards for the whole size of this area would not be reliable.

Relative Abundance Indices (RAI) and inter-specific competition

According to my observation (without scientific base) and independently from the camera traps results, the abundance of certain animal species (such as impala, puku, buffalo, wildebeest, elephant) increased annually and the game was less timid than in the prior years. An explanation for this could be based in the historical fact that the Luangwa Valley in the north, which includes the whole of the LNP, was plagued by indiscriminate poaching. In the absence of adequate control in the area poaching was rife and very often carried out by the game scouts who were lowly paid and frequently went for months without receiving their meager salaries (interviews with local people). The situation inside the hunting areas was slightly different although villages occurred there. According to interviews and my personal impression the permanent presence of the professional hunters during the dry season minimized the poaching in that area. Patrols by scouts were also more regularly performed inside the GMA’s than inside the LNP. With the permanent presence of people (e.g. our research team 2006-2008) who did not provide a certain disturbance (e.g. poaching, especially with fire arms) game species seemed to become habituated to humans and less shy and aggressive. This, I noticed especially with elephants. We (members of the research camp) moved around everywhere inside the LNP also at night accompanied by local scouts, who were employed by us and exchanged every two weeks.

Regularly patrols by scouts inside the LNP also increased within the years from 2006 through 2008.

An annual growth of game abundance inside the LNP could be a reason for the increase of the RAI index for ungulates, primates and large carnivores from 2006 to 2008. It is also definitely partly substantiated in the different available number of camera traps with different technical quality standards covering the area (see Chapter 6.1). The latter is also applicable for the low RAI values in the selected part of the GMA, but also the smaller size of this study site. The RAI of leopards inside the LNP and also in the GMA 2008, showed every year higher values than those of lions. According to interviews with local people (villagers &

scouts), professional hunters and ZAWA, lion abundance had decreased over the years. Although the lion situation seemed to be critical (but without scientific proof) hunting activities were going on with apparently successful lion harvest (see Chapter 5). Mature male lions were rarely seen inside the LNP and camera traps only captured groups of two or single immature male lions, or lionesses with cubs or single lionesses, also at bait stations for leopards. Due to the very close proximity of the hunting area it was always possible that a male lion was killed as soon as it overstepped the boundary.

Although the competition by lions definitely existed in this area the leopard RAI increased or remained higher than the lion RAI probably due to the extensive lion harvest by trophy hunting. This was documented previously in Tanzania, where hunting blocks with highest average lion harvests showed the largest increases in leopard harvest (Packer et al. 2009, Packer et al. 2010). This could be also appropriate for hyenas, which RAI was also lower than the RAI of leopards. Competition by hyenas was also obvious especially according to their scavenging life style and they appeared on bait stations more often than lions did.

The hunting quotas of lions and leopards are comparable until 2008 whereas the harvest of hyenas remained the highest among the three predators until 2008. The quotas for lion and hyena decreased in 2009 and 2010 whereas the leopard quota increased (Chapter 5).

6.3 Home ranges inside and outside the National Park

It has been shown that the home range sizes of leopards vary according to the area and habitat availability. Therefore a wide range of home range sizes have been determined from 5.2 km^2 (Odden & Wegge 2005) to 1,164 km^2 (Stander et al. 1997).

In arid areas of low prey abundance home ranges can be much larger (Jenny 1996). In the Israeli desert the home ranges of males measured 137 km^2 and of females 84 km^2 (Ilany 1981). Stander et al. (1997) recorded in northern Namibia male ranges from 210 to 1,164 and female ranges from 183 to 194 km^2. The home range sizes of males in Nepal (Royal Bardia NP), Thailand (Huai Kha Khaeng NP), South Africa (Kruger NP, Phinda), Kenya (Tsavo NP, farmland) vary from 16.4 km^2 to 96. 1 km^2, whereas females' ranges varied between 5.2 and 18 km^2 (Odden & Wegge 2005, Rabinowitz 1989, Grassmann1999, Bailey 2005, Hamilton 1976, Mizutani & Jewell 1998).

The home range sizes of the leopards studied here are included in the described range sizes (♂ 28-56 km^2; ♀ 14-42 km^2), apart from F1's home range which shrunk to 3 km^2 while she had a young cub (approx. ≤ six months age). This is in accordance with the study by Odden and Wegge (2005) in Nepal where the home range of the female leopard was smallest when her cubs were under six months of age. Also studies of leopards in Kruger NP (Bailey 1993) and cougars *Felis concolor* (Hemker et al. 1984) showed that small cubs restrict the movement of the mother. In the present study, however, F1 home range did not grow larger during the months (04-11.2008) in which she inhabited the small range although her cub became older than 6 months. Therefore, the restriction of mothers by cubs, likely last until an age of ≤ 1 year of the cubs.

From the five collared leopards in this study M1 showed the largest home range and encompassed mostly the home range of F1.

It is assumed that M1 is the father of F1's cub due to the fact that her home range was included in M1's home range and both leopards were seen together several times.

The male M2, overlapped both these home ranges but because he left the area a couple of months later, this could be a sign that he was chased away by the older and larger male M1. The female F2, whose home range overlapped with none of the other collared leopards, also had at least one cub (evidence from a photo trap picture) which was already ≥ 12 months of age. M3's home range was the smallest of the three home ranges of the males which assumedly is substantiated in the short tracking period which can be also noticed in his activity pattern. Due to the fact that M3 was older and larger than M1, his home range was assumedly much larger as it used to be during the tracking period.

Thus, his home range would have probably overlapped with the home range of M1 to a larger extent. Although, already, Corbett (1947) documented that "male leopards are very resentful of intrusion of others of their kind in the area they consider to be their own", the overlapping of males home ranges is not unusual and has also been experienced in prior studies (Bailey 2005, Odden & Wegge 2005). The fact that they seem to tolerate each other under certain circumstances has been already described in Chapter 6.2.

Apart from F2, none of the collared leopards occurred primarily in the GMA's and their 50% home ranges were within LNP. I assume that leopards are aware of the disturbed situation in GMAs and the undisturbed situation in the LNP, due to my observation at bait

stations. Thus, their dominating distribution within the LNP could probably reflect a certain bias towards the disturbed situation in the GMA’s.

There were, with certainty, also leopards around that had their home ranges completely included inside the GMA-A, but those where possibly settled at a certain distance to the LNP, so that they were not aware of the differences between a disturbed and an undisturbed area like leopards living within the boundary area.

All the home ranges were settled close to the Luangwa River and none of those leopards moved deep into the eastern part of the LNP. In the western part existed not only the Luangwa River that dried out only partly with the proceeding dry season but also lagoons existed which contained water permanently. So this was a center of attraction for many species and also for prey species. Water is one of the most significant factors in the distribution as for example of impala (Whyte 1976), which is an important component of leopards’ prey spectrum.

I noticed no lagoons and waterholes carrying permanent water in the east over the entire dry period but a gradient of dryness from west to east. Antelope species were hardly recognized there. According to these circumstances I assume that this area did not attract leopards, which could support the theory of a congested area in the selected part of the GMA-A.

6.3.1 Activity pattern

The activity pattern for all leopards showed a higher average mobility during the night (41%) than during the day (24%). Bailey (2005) also observed in Kruger National Park a higher mobility of leopards during night (65%) than during day time (42%). The differences between these and Bailey‘s (2005) observations could be based in smaller sample sizes and shorter observation period within this study. Nevertheless, the tendency of these findings is in accordance of the observation in the Kruger National Park.

Especially during 11:01-13:01h, all animals showed a minimum of activity and mobility that implies that the cats avoid being active during the hottest hours of the day (Hamilton 1976, Bailey 2005, Bothma & Le Riche 1984). In the Luangwa Valley temperatures reaches degrees above 30°C between June and July and often above 40°C during the summer months between August and November.

The mobility of males in the course of a 24 hour day was significantly higher than those of the females. Males, especially at night were more mobile (24%) than females (11%). This could be confirmed by the low numbers of prior studies about leopard activity pattern (Bailey 1993, Odden & Wegge 2005) and other felids (Schmidt 1999, Wassmer et al. 1988) like lynxs (*Lynx lynx*) and mountain lions (*Puma concolor*).

Apart from the already discussed reasons, a further reason could be the distinctive territorial behavior of males who have to patrol a larger home range for that they tend to cover longer distances (Bailey 2005) than females within a 24 hours day. Therefore, they probably use the night hours for longer wanderings to avoid the heat of the day. The higher mobility of males at night could be another reason for females with cubs to be less mobile at the same time to avoid, apart from other predators such as lions, the infanticide by unrelated male leopards, which was also assumed by Odden & Wegge (2005).

This can be verified in this study with the example of F1 who possessed a smaller home range and covered shorter foraging distances (Bailey 1993, Sunquist & Sunquist 2002) and also showed a higher mobility during day times than the others. An additional reason for the higher mobility of F1 during day time could be that the motherhood made her feeding on a kill more often as usual.

All the leopards indicate an increase of activity and mobility before or during sunrise and sunset, which probably is related to the activity of prey species (Sunquist & Sunquist 2002, Jenny & Zuberbühler 2005). Important prey species for leopards in this area (see Chapter 4) such as Sharpe's grysbok (*Raphicerus sharpei*) and bushbuck (*Tragelaphus scriptus*), show their greatest activity during sunset and night time (Wronski et al. 2006; Kingdon 2007) as well as puku (*Kobus vardoni*) and impala (*Aepyceros melampus*) that are most active during early morning (6:00h) and evening (16:00-16:30h) hours (Rduch 2008, Simon 2008).

6.3.2 Habitat availability versus habitat use, and preferences

The home ranges of all leopards comprised the same habitat types although the percentages varied individually. Grassland encompassed the largest part of most of the home ranges (F1, M1, M2 and M3) followed by Combretum-Terminalia woodland whereas the home range of F2 included Mopane woodland to the greatest amount. The comparison between habitat availability and habitat use showed that the leopard’s use of grassland (apart from M3, see Chapter 3) is much less than its availability. This can be confirmed by the values of the Jacob Index of all leopards (apart from M3) that indicate tendencies for a preference of denser vegetation types rather than grassland (F1 (2007-2008)), M1, M2, M3). Nevertheless, it is obvious that males used grassland more often than females.

The high occurrence of grassland in the home ranges could be explained by the distribution of grazing antelopes such as pukus (*Kobus vardoni*) as one of the most consumed prey species by leopards in the LNP, but not in the GMA (see Chapter 3). Antelopes, like impala (*Aepyceros melampus*) were found also in grassland, but mostly presented in dense habitat (Simon 2008).

Grassland could offer a superior hunting opportunity although the difference between use and availability was higher in grassland than in dense vegetation types such as Mopane woodland, riverine woodland or Combretum-Terminalia woodland. This can especially hold true for males which are more mobile than females according to the activity pattern and also more defensive towards competitors such as lions (Bailey 2005).

These assumptions are particularly appropriate for females with cubs and are supported by the shrinkage of F1’s home range in 2008 in which the percentage of the habitat composition changed. Instead of grassland and Combretum-Terminalia woodland the highest amount of her range comprised riverine woodland, thicket and semi permanent water/aquatic association grass. Her use of these habitat types was very high in comparison to the availability and can again be explained by her motherhood. Avoiding competitors and foreign male leopards that otherwise probably result in infanticide, is a reason to use denser habitat, but also a higher hunting success by getting difficultly discovered by prey species. The fact that her reduced home range was now fully included within M1’s range, especially in his core area, could further imply the importance of the “father’s” presence that prevents infanticide as it was already described in Chapter 6.2. The prevention of inter-specific competition might play an important role, grassland lacks adequate trees for caching kills, which is important for leopards to avoid scavengers (Bailey 1993, Sunquist & Sunquits 2002) like lions, hyenas and wild dogs.

F2 also used riverine woodland, semi permanent water/aquatic association grass, acacia woodland and Combretum-Terminalia woodland more frequently or according to their

availability. I assumed a young male ≥ 12 months to be her cub because they were captured together by camera traps several times. This perhaps indicates that the size of a female's home range is depending on the age of the cub and implies that with progressing age of the cub the home range of the mother increases. Also Odden & Wegge (2005) and Bailey 2005 in his study from 1972-1974 recognized that the home ranges of female leopards changed with their age and the mobility of their cubs. Studies so far showed that home ranges of females included mostly important resources like habitat of prey richness and watering places (Bailey 2005, Bothma 1997, Mizutani & Jewell 1998, Kruuk 1986) which can be confirmed in this study. Vegetations types like riverine woodland, thicket and Mopane woodland are preferred by the chief prey of leopards in this study area (Chapter 4), that will be amplified in Chapter 6.4, and might explain the preferences by all leopards for these habitat types.

It is significant that although leopards use different hunting strategies varying with the prey species, they almost always rely on the habitat type (Hunter et al. in press). In order to approach the prey closely enough for a successful hunt, leopards need cover to conceal which grassland does not sufficiently provide. Nevertheless, the fact that males used grassland to a much higher extent than females implies a preference for this habitat in males and therefore a sex-specific choice of prey (Bailey 2005).

6.4. Leopard prey spectrum at the study sites

By scat analyses 18 natural prey species for leopards could be ascertained in the study area. Comparable studies as for example Mitchell et al. (1965) determined 22 prey taxa in Kafue National Park in southern Zambia. In South Africa Bailey (1993) proved 25 prey taxa in the Kruger National Park and Schwarz & Fischer (2006) 13 prey taxa for the area Soutpansberg. The number of prey species in my study areas does not differ much from those studies, but in this respect it is shown that the prey spectrum of leopards varies according to the region. This becomes obvious especially in comparison to leopards prey spectrum in tropical rain forest regions, where the number of prey species averaged higher at 33 (Hart et al. 1996), 25 (Ososky 1998) and 37 species (Henschel 2001) than in arid areas.

In all the study sites of this research, ungulates are the most preferred prey species. In terms of frequency of occurrence in the LNP the leopard preferred middle sized antelopes

in the following order impala, puku and bushbuck, whereas in the GMA-A the preference order was Sharpe's grysbok, impala, bushbuck and puku.

This can be supported by the preferences in body mass of prey species of >15-30 kg which includes impala and bushbuck in LNP and in the GMA >1-15 kg which comprises in most quantities grysbok, baboon, vervet monkey, oribi and young warthogs, this is followed directly by the weight class >15- 30 kg.

The difference in consumption between prey weight class >15-30 kg (45%) and >1-15 kg (23%) in the LNP is significantly higher than the difference in consumption of these two weight classes in the GMA-A with 34% of >15-30 kg and 41% of >1-15 kg. Nonetheless, impalas can be also found in grassland but they mainly occur in denser habitat like forest (Averbeck 2002, Oboussier 1965, Simon 2008) in contrast to pukus which as grazers prefer the open savannah grassland (de Vos & Downsett 1964, de Vos 1965, Rduch 2008). Grysbok and bushbuck are distributed in dense woodland and rarely seen in open habitat (Kingdon 1997, Ferrar & Walker 1974).

Habitat preferences of prey could explain the leopards' higher consumption of e.g. impalas as opposed to pukus because as it already emerged in this study, denser habitat like forest is preferred by leopards. Because leopards use trees or dense vegetation to hide their kills (Sunquist & Sunquist 2002) in order to minimize "kleptoparasitism", a further reason is perhaps the larger body mass of puku that lies in the class of 45-60 kg. An adult puku with 52 kg (not a young puku) is more difficult to carry into a tree than an impala of 30 kg. If in grassland a tree as caching possibility gets lost, the kill needs to be hidden somewhere at the ground. Here, depending on vegetation cover, the risk of discovery by scavengers such as lion and hyena is high.

In this study prey species above 60 kg were infrequently detected and do obviously not belong to leopards preferred body masses in this region. The fact that waterbuck (188kg) remains for example, were found in a small amount (3.32%) in the scat samples does not necessarily mean that a leopard was hunting a waterbuck but rather scavenging on a carcass. Nevertheless, leopards are capable of killing larger size animals (Kruuk & Turner 1967). Schaller (1972), for example, reported leopards killing an adult hartebeest (126 kg) and a yearling wildebeest (130 kg) in the Serengeti. Mitchell et al. (1965) documented for the Kafue National Park in Western Zambia that leopards also took "five full grown

hartebeest and a past prime time kudu", while duiker, reedbuck and puku were the primary prey of leopards.

This body masses confirms the results for leopards' body mass preferences in this study (eg. the body mass of duiker is comparable with the body mass of grysbok).

The preference for prey species below 60 kg is probably also an avoidance of competition with larger predators such as lions (Seidensticker 1976, Schaller 1972). A comparison between the consumption of impala, puku and bushbuck in both of the main study areas shows a high demand for bushbuck although its population abundance is the lowest among the three antelope species. This possibly underlines the importance of prey weight and habitat preferences.

The relative high proportion of impala and bushbuck (live weight: 30 kg; 22.5 kg) within biomass of consumed prey emphasizes the preference for prey of an average live weight of 25 kg, as determined by Hayward et al. (2006). By this the puku (52 kg) exceeds the average live weight according to Hayward et al. (2006) but is nevertheless an important prey species for the leopard in the study region. It probably preys on young pukus. In contrast to the findings of this study Hayward et al. (2006) reported that Sharpe's grysbok was significantly avoided by leopards.

However, it is conspicuous that antelopes such as puku were less and grysbok more consumed in the GMA-A than in the LNP. The abundance of impala and puku is likely higher in the GMA-A than in the LNP because of the larger size of the hunting area. In this context arises again the question what is more important: either the abundance of prey or its catchability (Balme et al. 2007)? Therefore, one reason for the prey choice in the GMA-A could be that middle sized antelopes are trophy hunted in a higher quantity than small sized antelopes in the GMA-A as the hunting quota showed (Chapter 5). In this case the leopard has to face competition with human hunters in GMA-A. This competition might be the reason why the leopard shifts to smaller sized antelopes which are either more available than middle sized antelopes due to hunting, or the leopard is more careful in hunting middle sized antelopes because it combines it with disturbances in open habitats.

During the study period I noticed that it took longer to get a leopard feeding at a bait in GMA-A than in LNP (average 2 days in LNP/average 4.6 days in GMA-A, see Table 3.1). Therefore I assume that leopards of the GMA's are more timid than leopards in the LNP due

to the hunting pressure. Additionally, I suggest that leopards prefer to hunt in GMA-A in the denser woodland were grysbok is more available than middle sized antelopes like impala and especially puku. In the undisturbed LNP they also hunt the middle sized prey species which provide meat for a longer time period, in open habitat. Baboons are also more often consumed in the GMA-A than in LNP, which supports the theory that leopards switch to smaller prey when their favorite prey is hunted (Bodendorfer et al. 2006, Weckel 2006). Seidensticker 1983 also considered that the leopard's predation on primates is correlated with the availability and abundance of alternative prey.

Baboons are also on hunting quota but not in these quantities like middle and large sized antelopes as it is shown in Chapter 5 (ZAWA-Off-take quota 2004-2008). I could observe that baboons at day time are able in displacing leopards but as perfect climbers the leopards hunt the primates at night when baboons are sleeping in trees. This is in accordance to the studies of Busse (1980), Brain (1981), Cavallo & Blumenschine (1989), Cavallo (1990a, 1990b and 1991) and Cowlishaw (1994), where baboons became the victims of nocturnal predation. Pienaar (1969) reported for the Kruger National Park that 77% of killed baboons were taken by leopard.

Hunting in trees is an alternative to grassland and perhaps more preferred in "disturbed" areas than open habitat in our study area. A similar explanation may also hold true for the higher consumption of warthogs in the GMA-A. Warthog was not detected as prey in the LNP. One reason could be a lower density of warthogs in the LNP than in the GMA-A. In the LNP probably sufficient numbers of preferred prey species are available for the leopard without getting in competition with human hunters. In so doing it does not need to risk a fight with a defensive warthog which would be a powerful opponent. Catching young warthogs the leopard would also risk a fight with the mother. In contrast in the GMA-A, the leopard is in competition with human hunters for its favorite antelope species such as impala and thus it switches to warthogs. In the LNP, the energy requirements might not meet the minimum energy expenditure combined with least risk (Elliott et al. 1977, Hayward & Kerley 2005, Krebs & Davies 1993) for the predator.

Following this, the idea shows that leopards, if they have the choice, that excludes disturbance and competition by human hunters would choose the middle sized antelope species in higher quantities.

It is difficult to make a reliable statement about GMA-C and GMA-D because the sample sizes there were much smaller than the sample sizes of the LNP and GMA-A. I can recognize that weight class >1-15 kg tends to be more frequently preferred in GMA-C than in GMA-D, which could also be due to the smaller sample size of GMA-D. Interviews with local people and professional trophy hunters implied that grysbok and puku do not occur in a high amount in the region of GMA-D in comparison with GMA-C and the other study sites across the river, but this is also without scientific base.

6.5 The role of trophy hunting and its impact on the leopard population in the study area

The described subjects in this study indicate finally an impact of hunting on the leopard population living in the study areas. The results document the differences between the study areas although they were bordering against each other.

The assumed effect of a higher intra-specific competition inside the GMA-A than inside the LNP caused by the offtake quotas of leopards should not be underestimated (8-12 individuals in every year in GMA-A, see Chapter 5). Especially, if we consider a natural survivorship of young cubs as an average of 50% (Bailey 2005), an unnatural increased infanticide could counteract a sustainable population growth (Loveridge et al. 2007, Balme & Hunter 2004).

The suggestions about prey choice associated with habitat preferences can be supported by the fact that population densities of large felids are positively correlated to the biomass of their prey (Van Orsdol et al. 1985, Stander et al. 1997, Karanth et al. 2004b). Prior studies documented that leopards and jaguars will change their prey choice caused by disturbance such as poaching and hunting of their prey species (Bodendorfer et al. 2006, Weckel et al. 2006). The study of Hayward et al. (2007) indicates that the leopard is heavily dependent on prey species of its preferred weight range and a depletion of species within this weight range could invariably lead to a decrease of leopard population density. The results of prey choice analyses indicate that the leopard is possibly in competition with human hunters.

Summarizing all the conclusions above, the different impacts of trophy hunting become more obvious if I consider that 43% of the country wide hunting quotas are provided by the

hunting blocks located in the Luangwa Valley. From these, 43% (average) of the harvests are generated by the four GMA's surround the LNP. In this context GMA-A showed the highest hunting intensity among the four GMA's. This (0.31 (quota/100 km²)) would comprise 13.6% of 2.3 male leopards per 100 km² in 2008.

The natural annual mortality rate for adult leopards in Kruger National Park in the 1970s (Bailey 2005) averaged 18.5%, with twice as many adult males dying as adult females. The dominating reasons for death cases were starvation and violent causes, especially in males.

The annual mortality rate for subadult individuals averaged 32% with more subadult females dying than subadult males; for young cubs the annual mortality rate averaged 50%.

If I assume the natural mortality rate in Kruger NP as similar as in my study areas, the anthropogenic caused mortality rate (13.6%) would not be much lower than the natural mortality. This becomes more obvious in up-lighting the fact that only the anthropogenic caused mortality for males is regarded here. Usually females are not hunted since this is not allowed on the hunting licenses. However, it happens that females are killed because of reported mistaken identities with males. Spong et al. (2000) found in Tanzania that from 77 hunted leopards 28% were females although all the examined skins were tagged as males. In addition to that would the hunting of subadult males also not be desirable and a sign overexploitation (e.g. Allendorf & Hard 2009). The high hunting pressure on males for trophies (e.g. in ungulates) can result in harvested populations with lower average ages of males and fewer old males than in unhunted populations (Langvatn & Loison 1999, Laurian et al. 2000, Apollonio et al. 2003).

The natural and anthropogenic caused mortality would therefore comprise 32.1% in total in here which is in fact high, especially in consideration of only 50% survivorship of young cubs.

This implies a high hunting pressure on the leopard which increased until 2010 by a higher number of leopards on quota corresponding with a decrease of lion harvest. The hunting quota in GMA-A with an offtake of 8-12 male leopards per year (in contrast to the other GMA's with 5-8) from the population appears to be too high in view of the possible wide ranging consequences that could result in a disturbance of a healthy reproduction rate and weaken the stability (Tuyttens & Macdonald 2000) of a leopard population.

Despite the fact that the LNP is an apparently undisturbed area, it appears consequentially that the leopard population living there is also influenced by the hunting activities outside of the Park. The fact that leopards can move freely across the borders, even for temporarily short excursions, makes it obvious that also males of the LNP population are part of the hunting harvests. In this context the small size of the LNP could be problematic. The smaller the reserve the more species are at risk of extinction, especially large species that become more rapidly extinct than small species (Frankel & Soulé 1981). Woodroffe & Ginsberg (1998) showed that in relative small reserves, wide-ranging carnivores are more likely to become extinct than those with smaller home ranges. Bailey 2005 noted that it could be difficult to conserve viable leopard populations in parks less than 500 km² in terms of genetic sustainability. For these issues larger undisturbed areas are required.

Leopards reared in LNP need space to disperse and have to leave the LNP one time due to its small size (338 km²). A successful dispersion of leopards and exchange among the leopard population living in LNP and GMA-A would be disturbed due to the barrier of the high hunting harvests in the region. Therefore serious conservation strategies are needed to maintain a viable leopard population.

7 Synthesis and Recommendations

This study was a first step towards providing a clearer understanding about leopards in Zambia and the impact of trophy hunting on this large predator. The findings are glaringly obvious that certain steps must be taken in order to maintain a sustainable leopard population.

There is a risk that conservation measures regarding leopards could disappear from the field of view. As this research has clearly shown, the population of leopards in the study regions is not as large as has always been assumed and is much smaller than in other regions of Africa (Chapter 6.2). Due to the fact that the Luangwa Valley is assumed as a core area for leopards this should give cause for much concern. Hunting operators in this region continue (every year) to advertise “leopard safaris” which will inevitably lead to the demise of the leopard in the near future unless better conservation measures are adopted. It would be ineffective if action to preserve leopard numbers is only taken when a decline in harvest signals a decline of leopard population.

In contrast to other regions, as for example in Namibia and South Africa or Kenya, human and predator conflicts due to predation on livestock do not exist in our research area. The biggest risk for the population that currently exists is the high mortality rate of leopards caused by trophy hunting in addition to the natural mortality rate.

In view of the fact that only a proportion of a population will be capable of breeding, it is estimated that 80 to 100 leopards are required for an effective population size with a minimum of 50 adult breeding individuals. Besides, it is important that a viable population exists in the adjacent regions (Bailey 2005) to allow a “healthy” migration of individuals and also replacement of leopards that have expired.

To achieve these numbers the hunting quota of leopards for this region needs to be reduced. The knowledge that a hunted leopard provides an “empty territory” which can be taken very quickly by a new male should be a good reason to hunt the next leopard in perhaps three home ranges distance to the previous locality.

The home range of an adult male leopard within this region can be taken from this study as a guide line. Further, in order to enable a new male to replace a hunted male and settle in this area successfully, leopard hunts should not proceed at the same place in consecutive years. An interval of 2-3 years for leopard hunts on one locality could perhaps

reduce the effect of infanticide. This is also in accordance to the assumptions by Bailey's (2005).

It is not always easy to discriminate between males and females despite leopards show sexual dimorphism. Large females can be sometimes mistaken as males. Nevertheless, those mistakes should not happen very often to an experienced hunter.

The results of this study shows that females more often occur in denser habitat than males. Thus, as a further strategy to reduce the risk of unintentional killing of females, baits could be primarily placed in more open habitats.

In order to avoid overexploitation and to control the degree of harvest long term population estimates of leopards should be extended to the whole area of all the GMA's (A-D) as they generate the highest leopard harvest within the Luangwa Valley. Successful conservation strategies require that hunting harvest should not exceed sustainable levels. Therefore, it is prudent to reduce the annual quota to let the population recover.

A limit of 2 leopards per 1000 km² (instead of e.g. 12 within 2,555 km²) in the region of focus would be wise at this time.

Game counts and long term population estimates in the hunting blocks of focus that include the prey species of the leopard are also expedient all the more if they could encompass prey species also relevant for lions and hyenas.

It would be certainly ideal to conduct population estimates for the whole valley including the South Luangwa, North Luangwa and Lukusuzi National Park to know if viable populations exist around the area of the high leopard harvest. This is probably difficult to perform regarding the required budget but not impossible if the hunting operators become party to this action.

Camera traps and capture-recapture models for the determination of population estimates would be an appropriate method and with a good management also economically priced. Further, a combined method of baiting and use of camera traps could prove if a successful replacement of a once hunted leopard has taken place within the 2-3 year interval. ZAWA and village scouts could be trained and included in such surveys as they undertake patrols in these regions in any case.

It has to be stressed that this study only have provided a ray of light on the impact of trophy hunting that mostly concerns safaris for non-resident clients. The harvest of the prey

species by resident hunters is not revealed in this study and should by all means be regarded in further studies. The impact of poaching on the leopard is also unclear as well as the impact of poaching on its prey species' that would affect the leopard population.

All this is definitely of significance for the hunting community as it would be affected if it becomes very difficult to hunt any leopards due to their population decline.

The financial loss by limiting the number of individuals on quota could perhaps be compensated in increasing the prices for hunting leopards. Because the abolishment of lion hunts is in discussion, the leopard will remain as the only huntable large cat. If the possibilities of successful leopard safaris become rare, clients will get habituated to the fact that hunting a leopard in the wild is unique and therefore willing to pay a certain price. But to make people aware of those details it is the task of the hunting operators to include important ecological and biological facts and the conservation strategies within their advertisement for predator safaris.

A careful management of hunting quotas and wide ranging conservation objectives should be worked out in cooperation with the hunting community. Considering the fact that hunting blocks encompass more of Zambia's area than National Parks, the hunting industry and its interest in a healthy wildlife could be of great benefit for conservation.

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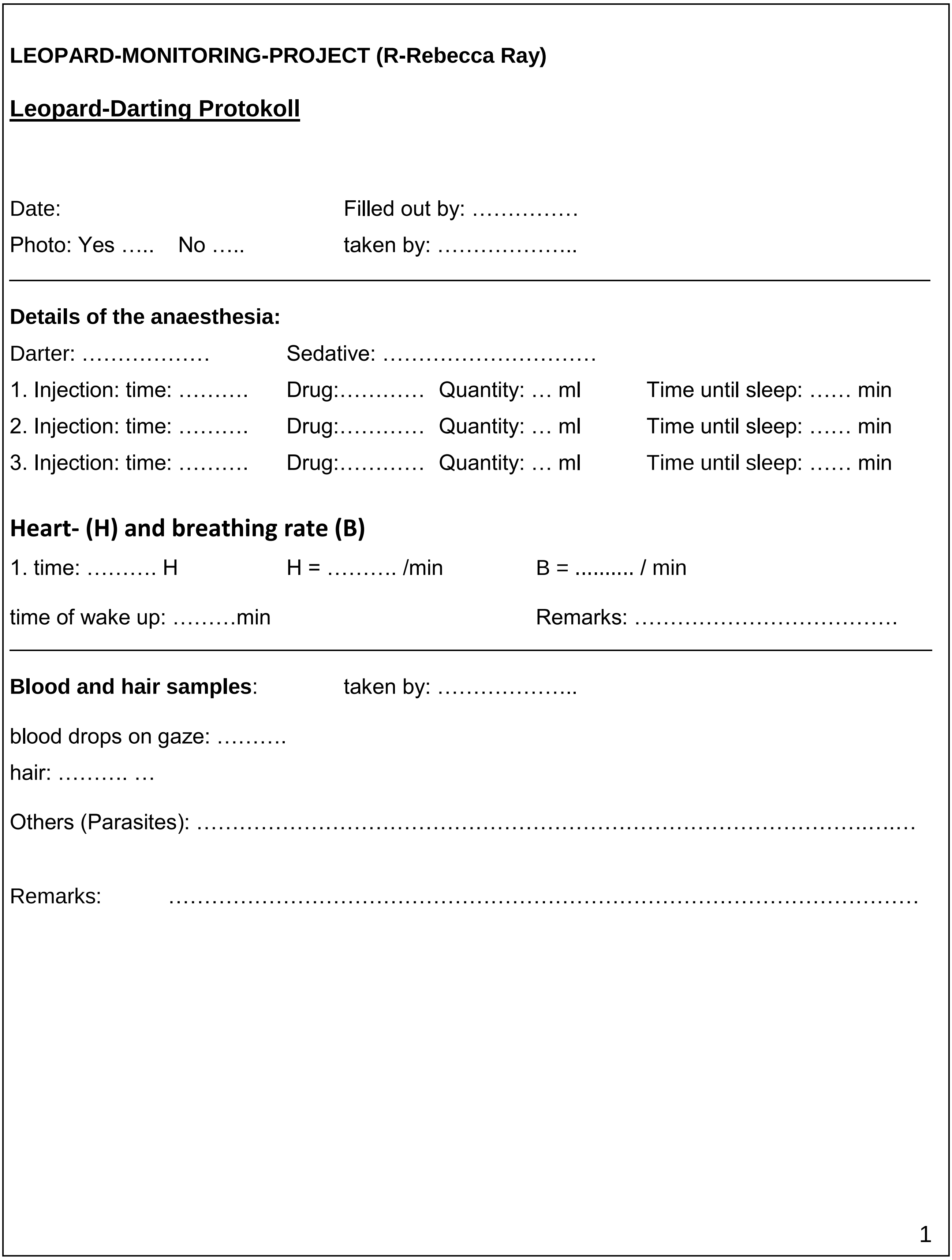
Appendix

Chapter 3: (Home range, habitat use and preferences)



LEOPARD-MONITORING-PROJECT (R-Rebecca Ray)

Leopard-Darting Protokoll

Date: Filled out by: ……………
Photo: Yes ….. No ….. taken by: ………………..

Details of the anaesthesia:

Darter: ……………… Sedative: …………………………
1. Injection: time: ………. Drug:………… Quantity: … ml Time until sleep: …… min
2. Injection: time: ………. Drug:………… Quantity: … ml Time until sleep: …… min
3. Injection: time: ………. Drug:………… Quantity: … ml Time until sleep: …… min

Heart- (H) and breathing rate (B)

1. time: ………. H H = ………. /min B = ... / min

time of wake up: ………min Remarks: ………………………………

Blood and hair samples: taken by: ………………..

blood drops on gaze: ……….
hair: ………. …

Others (Parasites): ……………………………………………………………………………….……

Remarks: ………………………………………………………………………………………

1

Leopard Data

Age: ……JUV:: …..   sex: …….

Condition: ……………………………………

Collar No. ….. ………………………………

Radio: Frequency: ………………….. MHz

Measurements:	taken by: ………………………….
Body length: ……………………….. cm (neck to rump)	Head length: : …………………….cm (nose to neck)
Tail length: …………………….….. cm	Neck circumference: : ……… cm
Shoulder height right: : ………….. cm	Shoulder height left: : ………….. cm
Leg length hind right: …………….. cm	Leg length hind left: ……………..cm

Paws:	front left:	length: …………cm	width: …………cm
	front right:	length: …………cm	width: …………cm
	hind left:	length: …………cm	width: …………cm
	hind right:	length: …………cm	width: …………cm
Pads:	front left:	length: …………cm	width: …………cm
	front right:	length: …………cm	width: …………cm
	hind left:	length: …………cm	width: …………cm
	hind right:	length: …………cm	width: …………cm

Ear right: …………………………... cm   Ear left: ……….cm

Canines: Upper Left: …………..mm   Right: …… …..mm

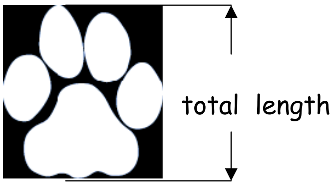
Lower Left: …………..mm   Right: …… …..mm

Canine distance Upper: ……….. mm   Lower: ………..mm

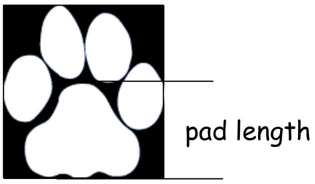
Body weight: ……..kg

Photos :   body: left and right side / head : left and right side and front
any special marks

Comments: ………………………………………………………………………………



Paw



Main Pad

Table. App.3.1: Habitat composition and use within the home ranges (females)

F1 (2007-2008)			
Habitat type	***area (%)***	***use (%)***	***locatings (use)***
Mopane woodland	6,85	18,18	14
Mopane Scrubland	2,54	6,49	5
Combretum Terminalia woodland	17,57	22,08	17
Acacia woodland	3,09	2,60	2
Grassland	51,34	12,99	10
Thicket	3,95	7,79	6
Riverine woodland and thicket	6,36	11,69	9
Semi permanent water/acquatic association grass	7,27	15,58	12
Water	1,04	2,60	2
Total	**100**	**100**	**77**
F1 (2008)			
Habitat type	***area (%)***	***use (%)***	***locatings (use)***
Mopane woodland	7,44	11,01	12
Mopane Scrubland	7,90	8,26	9
Combretum Terminalia woodland	28,71	38,53	42
Acacia woodland	5,67	2,75	3
Grassland	11,04	8,26	9
Thicket	5,83	7,34	8
Riverine woodland and thicket	16,99	14,68	16
Semi permanent water/acquatic association grass	13,89	8,26	9
Water	2,52	0,92	1
Total	**100,00**	**100,00**	**109**
F2			
Habitat type	***area (%)***	***use (%)***	***locatings (use)***
Mopane woodland	32,4	38,0	65
Mopane Scrubland	3,9	2,3	4
Combretum Terminalia woodland	38,4	33,3	57
Acacia woodland	1,4	1,2	2
Grassland	3,4	1,2	2
Thicket	12,5	14,6	25
Riverine woodland and thicket	3,5	5,3	9
Semi permanent water / acquatic association grass	2,5	4,1	7
Water	2,0	0,0	0
Total	**100,0**	**100,0**	**171**

Table. App.3.2: Habitat composition and use within the home ranges (males)

M1			
Habitat type	***area (%)***	***use (%)***	***locatings (use)***
Mopane woodland	6,63	10,66	13
Mopane Scrubland	3,03	3,28	4
Thicket	4,67	9,84	12
Combretum Terminalia woodland	18,95	22,95	28
Grassland	47,82	32,79	40
Acacia woodland	3,25	2,46	3
Riverine woodland and thicket	6,22	8,20	10
Semi permanent water / acquatic association grass	6,70	6,56	8
Water	2,72	3,28	4
Total	**100**	**100**	**122**
M2			
Habitat type	***area (%)***	***use (%)***	***locatings (use)***
Mopane woodland	8,6	14,5	8
Mopane Scrubland	3,4	5,5	3
Thicket	0,9	0,0	0
Combretum Terminalia woodland	22,3	23,6	13
Grassland	50,5	41,8	23
Acacia woodland	1,6	1,8	1
Riverine woodland and thicket	3,2	5,5	3
Semi permanent water / acquatic association grass	8,7	5,5	3
Water	0,8	1,8	1
Total	**100**	**100**	**55**
M3			
Habitat type	***area (%)***	***use (%)***	***locatings (use)***
Mopane woodland	10,21	5,45	3
Mopane Scrubland	4,60	3,64	2
Thicket	1,43	1,82	1
Combretum Terminalia woodland	23,35	16,36	9
Grassland	49,92	50,91	28
Acacia woodland	0,96	0,00	0
Riverine woodland and thicket	7,47	18,18	10
Semi permanent water / acquatic association grass	2,05	3,64	2
Water	0,00	0,00	0
Total	**100**	**100**	**55**

Table.App.3.3: Jacob Index (females)

F1 **(2007-2008)**

Habitat type	*Jacob Index*
Mopane woodland	0,56
Semi permanent water/acquatic association grass	0,45
Riverine woodland and thicket	0,35
Combretum Terminalia woodland	0,05
Grassland	-0,87
Mopane Scrubland	-
Thicket	-
Acacia woodland	-
Water	-

F1 **(2007-2008)**

Habitat type	*Jacob Index*
Mopane woodland	0,50
Semi permanent water/acquatic association grass	0,40
Riverine woodland and thicket	0,32
Combretum Terminalia woodland	0,14
Grassland	-0,75
Mopane Scrubland	-
Thicket	-
Acacia woodland	-
Water	-

F2

Habitat types	*Jacob Index*
Mopane woodland	0,12
Thicket	0,09
Combretum Terminalia woodland	-0,11
Mopane Scrubland	-
Riverine woodland and thicket	-
Grassland	-
Semi permanent water/acquatic association grass	-
Acacia woodland	-
Water	-

Table.App.3.4: Jacob Index (males)

M1

Habitat types	*Jacob Index*
Thicket	0,38
Mopane woodland	0,25
Riverine woodland and thicket	0,15
Combretum Terminalia woodland	0,12
Semi permanent water/acquatic association grass	-0,01
Grassland	-0,31
Mopane Scrubland	-
Acacia woodland	-
Water	-

M2

Habitat types	*Jacob-Index*
Mopane woodland	0,29
Combretum Terminalia woodland	0,04
Grassland	-0,17
Semi permanent water/acquatic association grass	-0,25
Mopane Scrubland	-
Thicket	-
Riverine woodland and thicket	-
Water	-
Acacia woodland	-

M3

Habitat types	*Jacob-Index*
Riverine woodland and thicket	0,47
Grassland	0,02
Mopane Scrubland	-0,12
Combretum Terminalia woodland	-0,22
Mopane woodland	-0,33
Thicket	-
Semi permanent water/acquatic association grass	-
Acacia woodland	-
Water	-

Table.App.3.5: Jacob Index-averaged data

Averages (Females)	
Habita types	***Jacob Index***
Mopane woodland	0,28
Riverine woodland and thicket	0,08
Combretum Terminalia woodland	0,08
Thicket	0,07
Semi permanent water/acquatic association grass	0,04
Mopane Scrubland	0,01
Acacia woodland	-0,12
Grassland	-0,30
Water	-
Averages (Males)	
Habita types	***Jacob Index***
Riverine woodland and thicket	0,20
Thicket	0,13
Mopane woodland	0,07
Combretum Terminalia woodland	-0,02
Mopane Scrubland	-0,04
Semi permanent water/acquatic association grass	-0,09
Grassland	-0,15
Acacia woodland	-
Water	-

Chapter 4 Prey Spectrum

Table. App.4.1: Prey composition of leopard in LNP & GMA-A

A: Live weight according to HAWARD et al. 2006
B: Correction factor following ACKERMANN et al. 1984
C: Number of times the species was found in scats
D=BxC; F=D/A
No correction factor, prey species < 2kg were not included in the calculation with the formula (see text)

LNP (n=187)	**A**	**B**	**C**	**D**	**E**	**F**	**G**
Prey species	Live weight (kg)	Biomass/faeces	Species quantity in scats	Biomass consumed (kg)	Biomass consumed (%)	Individuals consumed	Individuals consumed (%)
Sharpe's Grysbok *(Raphicerus sharpei)*	7	2,23	19	42,28	7,34	6,04	16,22
Impala (*Aepyceros melampus*)	30	3,03	47	142,41	24,73	4,75	12,75
Bushbuck (*Tragelaphus scriptus*)	22,5	2,77	33	91,33	15,86	4,06	10,90
Puku (*Kobus vardoni*)	52	3,80	42	159,60	27,72	3,07	8,24
Waterbuck (*Kobus ellipsiprymnus*)	188	8,56	5	42,80	7,43	0,23	0,61
Oribi (*Ourebia ourebi*)	14	2,47	5	12,35	2,14	0,88	2,37
Reedbuck (Redunca arundinum)	32	3,21	11	35,26	6,12	1,01	2,71
Warthog (*Phacochoerus africanus*)	45	3,56	0	0,00	0,00	0,00	0,00
Baboon (*Papio cynocephalus*)	12	2,40	7	16,80	2,92	1,40	3,76
Vervet Monkey (*Cercopithecus aethiops*)	3,5	2,10	4	8,41	1,46	2,40	6,45
Porcupine (*Hystrix africaeaustralis*)	10	2,33	6	13,98	2,43	1,40	3,75
Muridae species	0,2 - 0,13	0,2-0,13	8	1,04	0,18	8,00	21,49
Small carnivores		1 - 2,23	4	26		4,00	10,74
Birds	1,3 - 3,6	1,3 - 2,11	4			2,17	5,83

GMA-A (n=188)	**A**	**B**	**C**	**D**	**E**	**F**	**G**
Prey species	Live weight (kg)	Biomass/faeces	Species quantity in scats	Biomass consumed (kg)	Biomass consumed (%)	Individuals consumed	Individuals consumed (%)
Sharpe's Grysbok *(Raphicerus sharpei)*	7	2,225	41	91,23	13,85	13,03	27,73
Impala (*Aepyceros melampus*)	30	3,03	39	118,17	17,94	3,94	8,38
Bushbuck (*Tragelaphus scriptus*)	22,5	2,7675	34	94,10	14,28	4,18	8,90
Puku (*Kobus vardoni*)	52	3,8	34	129,20	19,61	2,48	5,29
Waterbuck (*Kobus ellipsiprymnus*)	188	8,56	7	59,92	9,10	0,32	0,68
Oribi (*Ourebia ourebi*)	14	2,47	13	32,11	4,87	2,29	4,88
Reedbuck	35	3,205	1	3,21	0,49	0,09	0,19
Warthog (*Phacochoerus africanus*)	45	3,555	14	49,77	7,56	1,11	2,35
Baboon (*Papio cynocephalus*)	12	2,4	17	40,80	6,19	3,40	7,24
Vervet Monkey (*Cercopithecus aethiops*)	3,5	2,1025	13	27,33	4,15	7,81	16,62
Porcupine (*Hystrix africaeaustralis*)	10	2,33	3	6,99	1,06	0,70	1,49
Muridae species	0,2 - 0,13	0,2-0,13	6	0,50	0,08	6,00	12,77
Small carnivores	1,0 - 7,0	1 - 2,23	3	5,45	0,83	1,64	3,48
Birds	1,3 - 3,6	1,3 - 2,11	0	0	0	0	0

Sieh, so ist Natur ein Buch lebendig, unverstanden, doch nicht unverständlich

(Johann Wolfgang von Goethe)