Ecology and Population Status of the Puku Antelope (*Kobus vardonii* LIVINGSTONE, 1857) in Zambia

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Vera Rduch
Bonn, im September 2013

Declaration

I declare that the research described within this thesis is my own work and that this thesis is my own composition. I certify that this thesis has never been submitted for any other degree or professional qualification.

Vera Rduch
Bonn, September 2013

Diese Dissertation wurde innerhalb des ZamBio-Projektes des Zoologischen Forschungsmuseum Alexander Koenig in Bonn in Zusammenarbeit mit der Zambian Wildlife Authority durchgeführt.

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Abstract: “Ecology and population status of the puku antelope (*Kobus vardonii* LIVINGSTONE, 1857) in Zambia”

by Vera Rduch
Dissertation for the degree of Doctor of Science (Dr. rer. nat.) in biology at the Rheinische Friedrich-Wilhelms-Universität Bonn.

Explaining patterns of animal distribution and abundance is one major challenge of ecology. The availability of habitats and food as well as predation determines the coexistence of animal species. Thus, knowledge about abundance, distribution and resource partitioning is of direct relevance to conservation and management of animal populations.

The puku antelope (*Kobus vardonii* LIVINGSTONE, 1857) was investigated in Zambia with a focus on Kasanka National Park and on the Kafue Region, i.e. Kafue National Park and surrounding Game Management Areas. Data about autecological and synecological aspects of the puku’s ecology and population status were collected between 2009 and 2011 during different seasons.

Road surveys along line transects were conducted at different times during the dry season. Puku occurred in small to large groups. They preferred grassland where estimated population densities were 36.15 puku/km² in Kasanka National Park and 14.66 puku/km² in the Kafue Region, respectively. Puku were observed in lower numbers in intermediate habitats and in miombo woodlands. Local population densities of the puku reached up to almost 150 animals/km². Puku assembled especially on floodplains, grasslands or next to rivers or lakes. For the survey period 2009/2010 in Kasanka National Park, a population size of 5,038 (3,268-7,238) puku was calculated. This is an eightfold increase since the survey in July 1994 and a result of the ongoing conservation work of Kasanka Trust Ltd. Assumed higher juvenile survival might positively affect the numbers of puku in Kasanka National Park, but may lead to differences in social organisation.

A reference collection of the epidermis of grasses was compiled for microhistological analyses of plant fragments in bovid dung samples in order to assess their diet and dietary overlap. Throughout all seasons and study regions, puku consumed almost exclusively grasses. Particularly, they fed on *Panicum* spp., *Brachiaria* sp., *Sporobolus* spp., *Hyparrhenia*/*Andropogon* grasses and *Eragrostris* spp. in different amounts depending on season, study region and sex. The puku’s dietary niche was broadest in the cool dry season and narrowest in the late rainy season. In Kasanka National Park, the analysis of puku dung from different sites revealed a high spatial variation in the puku’s diet which suggests an opportunistic choice of grass species.

In Kasanka National Park, there was a slight spatial overlap with sitatunga (*Tragelaphus spekii*). Between the puku and other bovids in Kasanka National Park, there was a slight dietary overlap during the cool dry season, but virtually no dietary overlap during the hot dry season. In the Kafue Region, puku and impala (*Aepyceros melampus*) occurred syntopicly. They had similar distribution patterns over the transect lines, but however, impala were encountered to a higher extent in woodlands and intermediate habitats. In the late rainy season, due to an increasing amount of grasses in the impala’s diet, the dietary overlap between the impala and the puku increased, while it was rather low in the cool dry season. Thus, one reason for high population densities of the puku in the study regions might be a generally low dietary competition, especially in the dry season.

To assess the impact of predation on puku populations, scats of predators were collected. In Kasanka National Park, hair of the puku and the sitatunga was found to almost equal amounts in the scats of Nile crocodile (*Crocodylus niloticus*), which probably is the most important predator of the puku, while large terrestrial predators were generally rare. White-tailed mongooses (*Ichneumia albicauda*) and African civets (*Civettictis civetta*) consumed puku presumably by scavenging only. In the Kafue Region, the puku occurred in the scats of lion (*Panthera leo*) and of spotted hyena (*Crocuta crocuta*) to considerable amounts, but for none of them, the puku was the preferred prey. Instead, puku were consumed in accordance to its availability. Predation pressure of large terrestrial predators appeared rather low in Kasanka National Park and in consequence does not limit the population of puku. In the Kafue region, predation was suggested to be higher and possibly regulates the puku's population to a greater extent.

However, considering the higher numbers of juveniles, male-groups and individuals in poor body condition, bottom-up regulation via rainfall and food is very likely to act particularly on the puku's population in Kasanka National Park.

The activity patterns of the puku showed that it is not predominantly diurnal. While puku grazed mainly at dawn, they rested during the day.

During this study, a lot of insight into the Zambian ecosystem could be gained, reaching from grasses over antelopes to carnivores. New information is presented about population densities and social organisation of the puku. For the first time in Zambia, the food plants of the puku were investigated by microhistological analyses of dung and the circadian activity patterns of the puku were assessed. Thus, besides confirming the few existing knowledge, this study revealed new facts about the puku's ecology and population status in Zambia.

keywords: puku, *Kobus vardonii*, Bovidae, Zambia, Africa, distance sampling, population status, habitat choice, microhistological analyses, diet, predation, activity patterns

Zusammenfassung: “Ökologie und Populationsstatus der Puku Antilope (*Kobus vardonii* LIVINGSTONE, 1857) in Sambia“

von Vera Rduch
Dissertation zur Erlangung des Doktorgrades (Dr. rer. nat.) der Mathematisch-Naturwissenschaftlichen Fakultät der Rheinischen Friedrich-Wilhelms-Universität Bonn

Eine der größten Herausforderungen der Ökologie ist es, Verbreitungsmuster und Abundanz von Tieren zu erklären. Die Verfügbarkeit von Habitaten und Nahrung sowie der Feinddruck bestimmen die Koexistenz von Tierarten. Kenntnis von Häufigkeit, Verbreitung und Aufteilung der Ressourcen ist unabdingbar für den Schutz und das Management von Populationen.

Die Puku Antilope (*Kobus vardonii* LIVINGSTONE, 1857) wurde in Sambia untersucht mit einem Schwerpunkt auf dem Kasanka Nationalpark und der Kafue Region, d.h. dem Kafue Nationalpark und angrenzenden sog. Game Management Areas. Daten über autökologische und synökologische Aspekte der Ökologie sowie zum Populationsstatus des Pukus wurden zwischen 2009 und 2011 zu verschiedenen Jahreszeiten gesammelt.

Datenerhebungen entlang von Linientransekten wurden zu verschieden Zeitpunkten in der Trockenzeit durchgeführt. Pukus kamen in kleinen bis großen Gruppen vor. Sie bevorzugten Grasland, wo die geschätzten Populationsdichten im Kasanka Nationalpark 36,15 Puku/km² und in der Kafue Region 14,66 Puku/km² betrag. In geringeren Populationsdichten kamen Pukus in intermediären Habitaten und auch im Miombo vor. Lokale Populationsdichten der Pukus erreichten fast bis zu 150 Tiere/km². Im Allgemeinen kamen Pukus vor allem auf Flussebenen, Grasland und in der Nähe von Flüssen und Seen vor. Für den Untersuchungszeitraum 2009/2010 wurde eine Populationsgröße von 5038 (3268-7238) Pukus für den Kasanka Nationalpark berechnet. Das ist ein achtfacher Anstieg seit einer Untersuchung im Jahr 1994 und ein Ergebnis der kontinuierlichen Arbeit des Kasanka Trust Ltd. Eine vermutlich geringe Sterblichkeit der Jungtiere beeinflusst positiv die Anzahl der Pukus im Kasanka Nationalpark aber könnte auch der Grund für Unterschiede in deren sozialen Organisation sein.

Eine Referenzsammlung zu Epidermisstrukturen von Gräsern wurde angelegt, um mikrohistologische Analysen von Pflanzenfragmenten im Dung von Boviden durchzuführen und so deren Nahrung und Nahrungsüberlappung zu ermitteln. Über alle Jahreszeiten und in allen Untersuchungsgebieten konsumierten Pukus nahezu ausschließlich Gräser. Sie fraßen vor allem *Panicum* spp., *Brachiaria* sp., *Sporobolus* spp., *Hyparrhenia*/*Andropogon*-Gräser und *Eragrostris* spp. in unterschiedlichen Anteilen je nach Jahreszeit, Untersuchungsgebiet und Geschlecht. Die Breite des Nahrungsspektrums war in der kühlen Trockenzeit am weitesten und in der späten Regenzeit am engsten. Die Ergebnisse der Analyse von an verschiedenen Stellen innerhalb des Kasanka Nationalparks gesammelten Dungproben ließ eine opportunistische Wahl der Grasarten vermuten.

Im Kasanka Nationalpark gab es eine geringe räumliche Überlappung mit der Sitatunga (*Tragelaphus spekii*). In Bezug auf die Nahrungspflanzen gab es zwischen Pukus und anderen Boviden eine geringe Überlappung in der kühlen Trockenzeit und gar keine Überlappung in der heißen Trockenzeit im Kasanka Nationalpark. In der Kafue Region kamen Pukus und Impalas (*Aepyceros melampus*) syntop vor. Sie verteilten sich sehr ähnlich über die Transektlinien, allerding wurden die Impalas eher in Waldgebieten und intermediären Habitaten angetroffen. Impala verändern ihren Nahrung mit den Jahreszeiten. In der späten Regenzeit konsumierten Impalas mehr Gräser und die Überlappung der Nahrungsspektren von Puku und Impala nahm zu dieser Zeit des Jahres zu. In der kühlen Trockenzeit gab es eine geringe Überlappung. Somit erfährt das Puku vor allem in der Trockenzeit in beiden Untersuchungsgebieten lediglich eine geringe Nahrungskonkurrenz, die mit ein Grund für die hohen Populationsdichten der Pukus sein könnte.

Um den Einfluss von Fressfeinden auf die Populationen der Pukus zu ermitteln, wurden Kotproben von Raubtieren gesammelt. Haare von Puku und Sitatunga wurden zu etwa gleichen Anteilen in Kot von Nilkrokodilen (*Crocodylus niloticus*) gefunden. Das Krokodil ist möglicherweise der wichtigste Feind der Pukus im Kasanka Nationalpark, wo größeren Landraubtiere selten sind. Weißschwanzmanguste (*Ichneumia albicauda*) und Afrikanische Zibetkatze (*Civettictis civetta*) fraßen Pukus, aber wahrscheinlich in Form von Aas. In der Kafue Region konnte das Puku in beachtlichem Maß im Kot von Löwe (*Panthera leo*) und Tüpfelhyäne (*Crocuta crocuta*) nachgewiesen werden. Allerdings bevorzugt keiner von diesen Räubern das Puku; der Anteil in der Nahrung geht mit der Verfügbarkeit einher. Im Kasanka Nationalpark schien der Prädationsdruck von großen Landraubtieren auf das Puku eher gering und limitiert nicht die Population des Puku. In der Kafue Region hingegen wurde eine größere Prädation auf das Puku angenommen, so dass die dortige Population hierdurch in größerem Maß reguliert wird.

In Anbetracht der großen Anzahl von Jungtieren, Männchengruppen und Individuen mit schlechter Körperverfassung im Kasanka Nationalpark scheint es wahrscheinlich, dass bottom-up Regulation in Form von Regenfällen und Nahrung die Populationen der Pukus vor allem dort beeinflusst.

Beobachtungen zu den Aktivitätsmustern der Pukus ergaben, dass es vorwiegend nicht tagaktiv ist. Pukus grasten vor allem in der Dämmerung. Am Tag ruhten sie.

Während dieser Studie konnten viele Einsichten in das Ökosystem in Sambia gewonnen werden, die von Gräsern über die Antilopen bis hin zu den Raubtieren reichen. Neue Informationen zu Populationsdichten und sozialen Organisation der Puku werden vorgestellt. Zum ersten Mal wurden für Sambia die Nahrungspflanzen der Pukus über mikrohistologische Untersuchungen von Kot ermittelt sowie die Aktivitätsmuster über Tag und Nacht. Somit, neben der Bestätigung des bereits Bekannten, konnte diese Studie dazu betragen, neue Erkenntnisse zu Ökologie und Populationsstatus der Puku in Sambia zu gewinnen.

Schlagwörter: Puku, *Kobus vardonii*, Bovidae, Afrika, distance sampling, Populationsstatus, Habitatwahl, mikrohistologische Analysen, Nahrung, Prädation, Aktivitätsmuster

Résumé: “L’écologie et l’état des populations de l’antilope puku (*Kobus vardonii* LIVINGSTONE, 1857) en Zambie“

rédigé par Vera Rduch
Thèse de Doctorat en biologie à la Rheinische Friedrich-Wilhelms-Universität Bonn

Expliquer la distribution et l’abondance des populations d’animaux est l’un des défis de l’écologie. La disponibilité des habitats, de la nourriture et la prédation influent sur la coexistence des espèces animales. Connaître l’abondance, la distribution et la répartition des ressources est essentiel pour la conservation et la gestion des populations.

Les populations de pukus (*Kobus vardonii* LIVINGSTONE, 1857) (ou Cob de Vardon) ont été étudiées en Zambie, principalement dans le Parc National de Kasanka et dans la « région Kafue » c’est à dire dans le Parc National du Kafue ainsi que dans ses environs (Game Management Areas). Le but de l’étude a été de rechercher des aspects autécologiques et synécologiques affectant le mode de vie et les populations des pukus. La collection des données a été faite de 2009 à 2011, à des saisons différentes.

Des transects en lignes ont été effectués le long des chemins pendant plusieurs périodes de la saison sèche. Les pukus se rassemblaient dans des groupes de petite à grande taille. Ils préféraient vivre en prairies où la densité de leur population avoisinait les 36,15 pukus/km² au Parc National de Kasanka ; elle était de 14,66 pukus/km² en Kafue région. Le nombre des pukus était plus réduit dans des habitats intermédiaires et dans le miombo. La population a pu atteindre localement jusqu’à 150 pukus/km², principalement dans les plaines inondables, en prairie et à proximité des rivières et des lacs. Pour la période couverte par l’étude de 2009 à 2010 la population totale des pukus a été évaluée à 5038 (3268-7238) animaux. C’est-à-dire huit fois plus qu’en Juillet 1994 ; ce qui fut certainement le résultat positif de la politique de conservation menée par Kasanka Trust Ltd. Le taux de survie des juvéniles semblait plus élevé au Parc National de Kasanka favorisant l’accroissement de la population ; il faut noter que cela semblait modifier aussi l’organisation sociale.

Une collection de référence de la structure des épidermes de graminées a été créé pour pouvoir faire des analyses microhistologiques des fragments de plantes contenus dans les excréments de Bovidés et mieux connaître leur alimentation et les interférences alimentaires. Partout et toujours, le régime alimentaire des pukus était constitué presque exclusivement de graminées : surtout *Panicum* spp., *Brachiaria* sp., *Sporobolus* spp., *Hyparrhenia*/*Andropogon* et *Eragrostris* spp. en quantité différente selon la période de l’année, la région et le sexe. La variété du régime alimentaire du puku était plus étendue pendant la saison sèche et froide et plus ciblée à la fin de la saison des pluies. L’analyse de la nourriture des pukus à des endroits différents dans la Parc National de Kasanka a révélé une variation importante dans la nourriture et suggéré un choix opportuniste de graminées par les pukus en fonction des circonstances.

Dans le Parc National de Kasanka les pukus et les sitatungas (*Tragelaphus spekii*) cohabitaient de temps en temps. La compétition entre les pukus et les autres Bovidés sur le plan alimentaire était minimale pendant la saison sèche et froide et n’existait pas en saison sèche et chaude. En région Kafue les pukus et les impalas (*Aepyceros melampus*) vivaient de façon syntopique : ils avaient une distribution comparable au long des transects, mais les impalas étaient plus fréquents dans des habitats intermédiaires et dans le miombo. A la fin de la saison des pluies l'impala changeait son régime alimentaire, la proportion de graminées était plus élevée, et la concurrence alimentaire avec les pukus était alors plus sensible. En saison sèche et froide cette concurrence était très atténuée ce qui pourrait expliquer le nombre des pukus dans ces régions.

Pour étudier l'impact de la prédation sur les populations des pukus, les excréments des carnivores ont été analysés. Les pukus et les sitatungas étaient consommés en quantité équivalente par le crocodile du Nile (*Crocodylus niloticus*) qui est probablement le prédateur le plus important de pukus dans le Parc National de Kasanka où les grands carnivores terrestres sont rares. La mangouste à queue blanche (*Ichneumia albicauda*) et la civette africaine (*Civettictis civetta*) avaient consommé du puku, probablement à l'état de cadavre, en charognard. En région Kafue, un nombre considérable de pukus a été la proie des lions (*Panthera leo*) et des hyènes tachetées (*Crocuta crocuta*). Cependant aucun des deux prédateurs ne recherchait particulièrement le puku mais ils le consommaient simplement parce qu'il est très commun. La pression de la prédation des grands carnivores terrestres était faible au Kasanka et elle n'influe pas sur la population des pukus. Au contraire en région Kafue, les prédateurs semblent être un vecteur de régulation de la population.

En particulier au Parc National de Kasanka, si l'on considère la proportion plus élevée de juvéniles, de groupes de mâles, ou d'individus physiquement affaiblis, les populations de pukus paraissent davantage tributaires des précipitations et donc de la nourriture disponible.

L'éthologie du puku a révélé que l'antilope n'était habituellement pas active pendant la journée mais qu'elle s'alimentait surtout au crépuscule. Les journées étaient consacrées au repos.

L'étude a permis de collecter un grand nombre de données sur l'écosystème en Zambie, à partir des graminées mangées par les antilopes jusqu'aux grands carnivores. De nouvelles informations ont été rassemblées sur la densité des populations et l'organisation sociale. Pour la première fois en Zambie, les plantes dont se nourrissent les pukus ont été identifiées grâce à une analyse microhistologique des excréments, et l'observation de comportements des pukus a été faite de jour comme de nuit. Cette étude a mis en évidence le peu de connaissance sur les pukus et elle a apporté des informations nouvelles sur l'écologie et l'état des populations de pukus en Zambie.

mots-clés: puku, *Kobus vardonii*, Bovidae, Afrique, distance sampling, état des populations, le choix de l'habitat, analyses microhistologiques, nourriture, predation, comportement

> “Here I lay, looking at the graceful forms and motions of beautiful pokus, leches and other antelopes, …”
>
> DAVID LIVINGSTONE

1 General Introduction

1.1 General conception

This PhD-thesis was conducted in the context of the Zambian Biodiversity Project (ZamBio Project) of the Zoologisches Forschungsmuseum Alexander Koenig, the Zoological Research Museum Alexander Koenig, (ZFMK) in Bonn, Germany. Independent from the sections within the ZFMK, but encompassing different research approaches and subjects, the ZamBio Project aims to investigate the biodiversity of Zambia. During previous research within the ZamBio Project, the diversity and the distribution of African reptiles with a focus on agamid lizards (Wagner 2010) as well as the ecology and the population status of cats namely the serval (*Leptailurus serval*) (Thiel 2011) and the leopard (*Panthera pardus*) (Ray 2011) were examined. The scientific results gained shall help to improve natural conservation measures in Zambia to protect its unique wildlife.

My diploma thesis about habitat preferences and distribution of the puku (*Kobus vardonii*) in Luambe National Park (Rduch 2008) already contributed to the ZamBio Project. During that research I concluded that there was need for further research on the puku. Thus, I decided to investigate the puku antelope with a focus on Zambia during this PhD-thesis in order to help improving to natural conservation measures.

In Zambia, the territoriality of male puku has attracted much attention and scrutiny of previous researchers. In Tanzania, where most of the research data comes from, the puku was investigated focussing on population assessment and habitat use. While the research in Tanzania was conducted mainly in Kilombero Valley, most of the information on Zambia's puku comes from South Luangwa NP. Only a few studies come from areas other than these two study regions or investigated beyond these two topics. Recent studies on the puku were not undertaken in Zambia. However, knowledge about numbers and abundance is very important for conservation (Shorrocks et al. 2008, Ogutu et al. 2006), but it is just as important to know how these numbers emerge. Following this the general question is: What affects the abundance and distribution of the puku in selected areas of Zambia?

Three factors determine distribution patterns: the dispersal capacities of the species, the spatial distribution of favourable environmental conditions and the biotic environment constituted by the species' competitors, predators and pathogens, together with the availability and dynamic of resources (Sobéron 2007). This indicates a relationship between distributional areas and niches (Sobéron 2007). One major challenge of ecology is to explain those patterns of animal (and plant) distribution and abundance (Hunter & Price 1992). To explain abundance and distribution of the puku in Zambia, the investigation of the puku's ecological niche, its role in the Zambian ecosystem is important and thus the common theme of this study.

The term "niche" used here conforms to Elton's definition of the ecological niche which means "the animal's place in its community, its relation to food and enemies, and to some extent to other factors" (Elton 1927). The ecological niche is one of the most important concepts in ecology (Godsoe 2010). The functional concept niche of Elton (Whittaker et al. 1973) is defined by biotic interactions and resource-consumer dynamics which both can be measured (Soberón 2007). In contrast to variables, applicable for the Grinnelian niche concept, resources can be consumed and populations may impact and compete for them (Soberón 2007). It is generally accepted that environmental variables and resources can interact and hence that the distinction is rather artificial (Soberón 2007). Competition affects realised niches (Whittaker et al. 1973) and it is the dominant process that affects ungulates (Sinclair 1979a). It is a result of shortage or, vice versa, without shortage there is no competition (White 1978). The question 'how many' survive is answered by the factor, e.g. food, the competition decides 'which ones' survive (White 1978). Interspecific competition results in selection pressures that can lead to resource partitioning (Walter 1991). Regardless of the origins of the differences, resource partitioning are differences in resource use between species (Walter 1991). Thus, among coexisting species, differences in resource use can be observed (Schoener 1974). On food as example for resource Schoener (1974) discussed that it can be consumed in different habitats, at a different time of the day or of the year, at different vertical scales (in trees) or that different sizes or parts of the food source are consumed.

Antelopes partitioned the African ecosystem into many small segments (Estes 1991). The African continent provides a lot of ecological opportunities for the bovids to exploit with regard to habitats and food (Estes 1991). Together with predation, habitat and food determine evolution, adaptation and thus coexistence of bovid species (Sinclair 1983). This speciation processes in African bovids were promoted by climatic changes during the

Pliocene-Pleistocene, where the major radiation of bovids took place (Sinclair 1983, Estes 1991). These climate changes caused expansion and contraction of the equatorial rain forest or the arid regions, respectively, in pluvial or interpluvial periods (Sinclair 1983, Estes 1991). Knowledge of competition or resource partitioning is fundamental to understanding not only evolution but also sympatric occurrence of bovid species nowadays. The knowledge of resource partitioning is of direct relevance to conservation and management of the (protected) area (Jarman & Sinclair 1979). The understanding of the ecological niche of the organisms is of interest for natural conservation issues, too. Specialists characterised by a narrow niche experience a higher risk of extinction relative to generalist species (Devictor et al. 2010).

Data sets of Eltonian niches have to be measured in field studies (Sobéron 2007) and this is what was done for this study. The basis of this study is data about the population status and the distribution of the puku. These data is complemented by data about autecological and synecological aspects of the puku's ecology. Thus, the study is structured into sections in order to deal with different questions:

- What are the population densities of the puku in the study regions? How are puku distributed within the study areas? Are there any other bovid species that have similar distribution patterns? It is suggested that in grassland areas, puku occur at higher densities than in woodlands. They might be more abundant in areas near water sources where they assemble especially with the ongoing dry season. If impala occur sympatrically with puku, impala should occur in woodlands at higher densities than in open grasslands.

- What are common group sizes and group compositions of the puku? General traits of the social organisation are suggested to be similar in the study regions: small to medium group sizes, groups of females with young and single males occur and the sex ratio is biased towards the females.

- Puku are suggested to feed to a high extent on monocotyl plants. But which plants are the main food sources? As the two study regions lie in the miombo ecoregion the actual food plants might be similar. Sympatric occurrence with other antelopes might be enabled by differences in the diets.

- Puku are supposed to be prey of different carnivore species. But which predators do actually occur in the study regions and what about it the amount of the puku in their diet?

- What activity patterns do puku show? They are suggested to have specific times of day and night where they show feeding and resting behaviours. The general patterns of activities are alike between study areas, but might differ between the puku and antelopes that occur the same habitats or areas.

The puku is classified as "near threatened" by the IUCN Red List (IUCN SSC Antelope Specialist Group 2008). This often raises the question why one should invest into research in that case. The answer: Even if the puku is not endangered, research can help to reveal what conditions are most suitable for them. Future changes in ecology can be detected. Awareness of the factors that might affect the abundance and distribution of animals can useful to point out potential threats and hence provide the background for purposeful conservation measures.

Data collection was carried out within three separate field trips to Zambia. I focussed on the puku population in Kasanka National Park in northern Central Zambia, where I visited on three different seasons of the year. These data were complemented by data collected from Kafue National Park and adjacent Game Management Areas (GMA).

Out of necessity, I virtually conducted this research project without an extensive funding. All methods applied during this study and presented here required a relatively low budget. Undeniably, they still require certain amount of equipment. This was partially offered by kind sponsors or provided by the facilities of the ZFMK. Nevertheless, the results gained provide detailed and reliable information on different aspects of the ecosystem as required for good conservation practice.

1.2 The puku – an outline

The puku (*Kobus vardonii* LIVINGSTONE, 1957) is a medium sized antelope (SKINNER & CHIMIMBA 2005). Its shoulder height is about 77 to 94 cm with the males being taller than females (HUFFMAN 2011, STUART & STUART 2006). The tail is not bushy and has a length of 28 to 32 cm (SKINNER & CHIMIMBA 2005, KINGDON 2007). Weight is about 77 kg for males and 66 kg for females (HUFFMAN 2011). Beside these differences in physical dimensions, puku are sexually dimorphic as only the males carry lyre-shaped, stout horns (Figure 1-1) (SKINNER & CHIMIMBA 2005, HUFFMAN 2011). These horns reach an average length of 45 cm and are strongly ridged for about two third of their length, smoothing towards the tips; the longest horns were recorded in Luangwa Valley, Zambia, measuring 56.2 cm (STUART & STUART 2006, SKINNER & CHIMIMBA 2005). The pelage is about 32 mm long and somewhat coarse (SKINNER & CHIMIMBA 2005, HUFFMAN 2011). The upperparts as well as the tail are golden-yellow, and underparts, throat, sides of the muzzle and hair around the eyes are off-white as are the insides of the limbs and the inside of the ears (Figure 1-1) (STUART & STUART 2006, SKINNER & CHIMIMBA 2005, HUFFMAN 2011). Active preorbital glands cause a small tuft of black hair and these glands with their greasy secretion are responsible for the dark neckpatch of territorial males (HUFFMAN 2011, ROSSER 1990).

Figure 1-1: Puku (*Kobus vardonii*) in Kasanka National Park, Zambia: a male (A) and a female with a calf (B).

The puku's distribution (Figure 1-2) is widely fragmented across Southern Central Africa along the margins of lakes, swamps, rivers and floodplains with Zambia being the centre of occurrence (STUART & STUART 2006, KINGDON 1982, MILLS & HES 1999). Otherwise, puku are common in Tanzania (BONNINGTON et al. 2010) but also occur in Angola, east Namibia, northeast Botswana, southeast DR of Congo, and north and west Malawi (HUFFMAN 2011). Total numbers of the puku are estimated to be 76,000 to 130,000 animals (HUFFMAN

2011). 75% of all puku live in the unprotected Kilombero Valley in Tanzania, the majority of the remaining puku lives in Zambia (Huffman 2011) (see also Chapter 2). Puku are threatened by anthropogenic factors: above all habitat fragmentation (IUCN SSC Antelope Specialist Group 2008), habitat loss, illegal hunting, and competition with cattle herds (Huffman 2011). The puku is classified as "Near Threatened" by the IUCN Red List (IUCN SSC Antelope Specialist Group 2008).

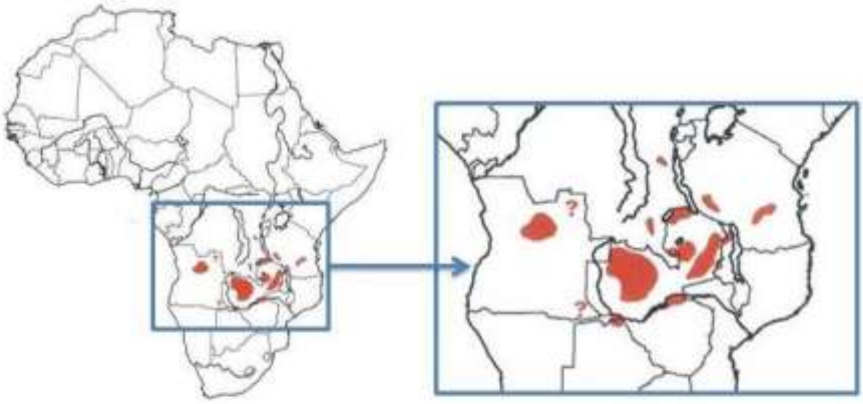


Figure 1-2: Geographic range of the puku (*Kobus vardonii*) (modified from Jenkins 2013).

The puku was first described by David Livingstone in his diaries "Missionary Travels and Researches in South Afrika", published 1857 in London. He writes: "I propose to name this new species 'Antelope Vardonii', after the African traveller, Major Vardon." (Livingstone 1857). Thus, Livingstone latinised the name of Major Vardon. I will use his spelling *vardonii* for the epithet of species in this thesis – although there is another spelling (*vardoni*) to be found in literature. The common name is derived from "phuku", the antelope's name in the Setswana language. In Zambia, the puku is called "Nsebula" by the Bemba people or "Nseula" by the Nyanja people (Ansell 1978). Concerning the plural ending of the puku, two spellings exist, which are "puku" (confer e.g. Wilson & Mittermeier 2011, IUCN SSC Antelope Specialist Group 2008, Dipotso & Skarpe 2006, Skinner & Chimimba 2005, Jenkins et al. 2003 Corti et al. 2002, Goldpink et al. 1998, Child & von Richter 1969) and "pukus" (confer e.g. Kindgon & Hoffmann 2013a). In this thesis I will use the plural form "puku". This is similar for other antelopes as impala or sitatunga.

The puku is a member of the order Artiodactyla if following the established systematic also used in Wilson & Mittermeier (2011); other authors include this order in the Cetartiodactyla (Price et al. 2005). However, the order is the puku further belongs to the family Bovidae, the hollow-horned ruminants (Huffman 2011). Within the tribe of the Reduncini, the puku is classified nowadays as a member of the genus *Kobus*. Two subspecies, *K.v.vardonii* and *K.v.senganus,* are mentioned by Ansell (1960a, 1978). They are considered invalid by Huffman (2011a), but recent findings suggest that puku in Tanzania differ from those in Zambia (Jenkins 2013). The kob antelope (*Kobus kob*), is the puku's next relative (Birungi & Arctander 2001). The relation between those two can be considered somewhere between the level of subspecies and full species, what Estes (1991) calls a superspecies. The puku has heavier proportions, a coarser coat and the horns are shorter, less lyrate shaped than the kob (Kingdon 2007). Living in allopatry, they replace each other ecologically: kobs occur in the northern savannahs and puku in the southern ones (Birungi & Arctander 2001, Shorrocks 2007, Estes 1991). Basing their research on mitochondrial cytochrome b data, Birungi & Arctander (2001) revealed that the puku is a highly differentiated population of the kob, separated around 150.000 years ago, which would justify the designation of the puku as a distinct species. Still, the puku is treated as an own species by recent literature or the IUCN (e.g. Skinner & Chimimba 2005, Stuart & Stuart 2006, IUCN SSC Antelope Specialist Group 2008, Huffman 2011). The genus *Kobus* comprises further the waterbuck *Kobus ellipsiprymnus*, the lechwe (*Kobus leche*) and the Nile lechwe (*Kobus megaceros*). According to mitochondrial cytochrome b data, the waterbuck (*Kobus ellipsiprymnus*) is considered to be the sister group of kob and puku (Birungi & Arctander 2001).

Puku are gregarious occurring mostly in small groups (Skinner & Chimimba 2005). Larger groups up to 100 individuals can be found, though (de Vos & Dowsett 1964). The groups are rather unstable as the individuals move freely among the groups (de Vos & Dowsett 1964). Puku are grazers (Gagnon & Chew 2000). They are said to be highly specialised in their habitat requirements (Dipotso & Skarpe 2006): They inhabit floodplains and adjacent well-watered grasslands, therefore they can be found along rivers, swamps or lakes and on dambos (Huffman 2011, Kingdon 2007, Skinner & Chimimba 2005).

Adult territorial males hold territories from a few days to several months (Skinner & Chimimba 2005). The territories are mostly in open habitats; overlap between territories is possible (de Vos 1965). Rosser (1992) differentiates between clumped grouped territories located in open floodplain areas that are small (0.05 km²) and the more dispersed single territories in woodland areas that are larger (0.14 km²). These territory types represent two alternative strategies of male mate access (Rosser 1992). Grouped territories attract more females, intermale competition is higher and chances of male mate access can be very high. Single territories are more likely to be kept by the owning male, but the opportunity for mating is generally reduced (Rosser 1992). Female puku move across one to four territories within 12 hours (Balmford et al. 1992). When in oestrus, females can mate with up to 3 different males (Balmford et al. 1992). Females base their choice of the male on characteristics of the territories (Balmford et al. 1992). These might be food quality or a reduced predation risk (Balmford et al. 1992). Nevertheless, the condition of males, which is advertised by the intensity of the territorial males' neckpatch, is to be considered as an important selection criterion as well (Rosser 1990, Rosser 1992). This patch underlines the neck muscles both visually and olfactorily and thus states the males' ability to fight. This again often helps to reduce agonistic interaction between territorial males to not more than face-offs and displays. Chases occur more often between territorial and bachelor males (Rosser 1990). To highlight their status, territorial males vocalise two to four whistles (Rosser 1990). In contrast to the territorial whistle, a single whistle is given by all puku when alarmed (Rosser 1990). Young puku can be found at any time of the year (Rosser 1989). In Luangwa Valley, Rosser (1989) describes a peak of births in the rainy season from January/February to April/May. Other sources speak about a lambing period in Zambia from May to September with a peak from June to August (Ansell 1960b). The main season for matings is in May/June for Luangwa Valley (Rosser 1989). Length of gestation is presumed to be eight month and new-born puku weigh about 5.8 kg (Huffman 2011). The single lamb hides for the first four weeks of its life (Ansell 1960b, Estes 1991). The relationship between females and their young does not seem very close (de Vos & Dowsett 1964). The lambs show only a poorly developed following response and were observed to flee in the opposite direction when being chased by a predator (de Vos & Dowsett 1964).

In this thesis I refer to two terms: '**bovid**' and '**antelope**'. The term 'bovid' is the only one that labels all members of the family Bovidae, the hollow-horned ruminants. On the other hand 'antelope' is often used for the species that are of more delicate built (Wilson & Mittermeier 2011). When I use the term 'antelope' it means members of the tribes Boselaphini, Tragelaphini, Neotragini, Aepycerotini, Antilopini, Reduncini, Hippotragini, Alcelaphini, Oreotragini and Cephalophini. Hence, by speaking of bovids that generally adds the tribes bovini and caprini to the aforementioned I encompass the African buffalo *Syncerus caffer*. The recently published 'Handbook of the mammals of the world' (Vol. 2 Hoofed Mammals) edited by Wilson & Mittermeier (2011) proposes a new systematic establishing new species from subspecies and by this presents a new nomenclature for a lot of bovids. However, I follow the established nomenclature, as it is also applied in Kingdon & Hoffmann's (2013a) 'Mammals of Africa'. By this I try to counteract possible confusion within this thesis and with results from other authors.

1.3 The study region

Zambia (The Republic of Zambia) is a landlocked country in southern central Africa (Drescher 1998) (Figure 1-3). It covers an area of 752,614 km² (Leonard 2005). Situated between 8° and 18° south and 22° and 34° east (Leonard 2005), it belongs to the outer tropics (Schulz 1983). The following countries border on Zambia: Angola, the Democratic Republic of Congo, Tanzania, Malawi, Mozambique, Zimbabwe, Botswana and Namibia (Leonard 2005).

Zambia is a well-watered and wooded country (Ansell 1960a). It consists in large parts of a flat or gently undulating plateau (Jeffery et al. 1989) that elevates to altitudes between 1000 and 1500 m (Schultz 1983). In the south-west, there is a general decline of the plateau toward the Kalahari basin (Leonard 2005). The Luangwa and the Zambezi Valley cut across the plateau (Jeffery et al. 1989). These valleys can be regarded as a south-western extension of the East African Rift system (Jeffery et al. 1989, Leonard 2005). The areas of the valleys are situated almost entirely under 600 m in elevation (Schultz 1983). These valley regions are bordered by steep escarpments (Jeffery et al. 1989). Other lowland areas are the regions around Lakes Mweru and Tanganyika in the north (Leonard 2005). Only in a small area in the north, altitudes reach more than 2000 m: these are the Nyika Plateau and the Mafinga and Makutu Mountains (Leonard 2005). The Zambezi system drains 70% of Zambia (Leonard 2005). Kafue and Luangwa River are the main tributaries to the Zambezi (Ansell 1978). The remaining area drains into the Congo: the main rivers are Kalungwishi, Chambeshi and Luapula (Leonard 2005). The climate in Zambia is closely related to its relief (Drescher 1998). The high altitudes in combination with the degree of latitude result in a temperate-tropical climate for Zambia. A hot-tropical climate may be found only in some valley regions (Schultz 1983). The rains fall within one annual rainy season (Schultz 1983). The duration and intensity of the rainy season depends on the latitude: In northern Zambia, the rainy season lasts from October to April and 1000 to 1500 mm precipitation come down. In the south, the rains last from November to March and result in 700 to 1000 mm precipitation (Schultz 1983). The combination of precipitation and temperatures results in 3 distinct seasons (Drescher 1998, Leonard 2005). The warm **rainy season** between November and April is followed by a **cool dry season** between May and August. During this period, minimum temperatures lie between 2 and 15°C. A **hot dry season** lasts from September to November, when daytime temperatures average 27-38°C (Leonard 2005).

Zambia holds “some of Africa’s most magnificent wildernesses and a spectacular diversity and abundance of antelopes and other wildlife” (East 1998). Its wildlife is plentiful: there are 233 species of mammals, 731 species of birds, 145 species of reptiles and 200 species of fish (CHM-CDB 2012). A number of 22 antelope species are present – 11 of them are threatened (CHM-CDB 2012). Additionally, there are at least 5,500 vascular plant species (CHM-CDB 2012). A general look at the (large) mammals shows that Zambia lies in the Ethiopian faunal region (Ansell 1978). In Zambia, the East and South African sub regions overlap (Ansell 1960a). Mammal species can be discontinuously distributed from east to south and southwest Africa with a more or less extended gap in or over Zambia (Ansell 1960a, 1978).

Zambia has got 19 national parks that cover 8% of its surface area that are 63,820 km² (Drescher 1998, Leonard 2005). A number of 36 Game Management Areas (GMA) cover a further 22% of Zambia’s surface surrounding most of the national parks like a buffer zone (Figure 1-3) (Leonard 2005, Drescher 1998). Thus, a total of 30% of Zambia’s land mass is protected land under wildlife management (Nyirenda et al. 2008). Kafue NP and the national parks in Luangwa Valley constitute some of the largest protected areas in Africa and their international importance for antelope conservation is outstanding (East 1996). Generally, Zambia’s population economically and in matters of livelihood depends on the use of natural resources (CHM-CDB 2012). While only non-consumptive use is allowed in national parks, both non-consumptive and consumptive uses are permitted in GMAs (Nyirenda et al. 2008). This includes unrestricted entrance and residence as well as controlled hunting (Leonard 2005). Beside national parks and GMAs, another 70,000 km² of Zambia are managed by the Forest Department as Protection and Production Forest Reserves. Additionally, privately controlled land provides protection of natural resources: Game Ranching is expanding in Zambia (Leonard 2005, Drescher 1998), offering hunting, game-bird shooting safaris or wildlife experiences to the paying public – others concentrate on breeding (Leonard 2005).

The Zambian Wildlife Authority (ZAWA) is semi-autonomous within the Ministery of Tourism, Environment and Natural Resources, established by the Act of Parliament, Zambia Wildlife Act No. 12 of 1998 (Leonard 2005, Nyirenda et al. 2008). ZAWA is charged with the control, management, conservation, protection and administration of NP and GMAs, Bird Sanctuaries and Wildlife Sanctuaries (Leonard 2005). Its aim is to “conserve Zambia’s wildlife resources for biodiversity and social-economic enhancement” (Nyirenda et al. 2008). ZAWA is further responsible for all licenses and permits in relation to capture, hunting, sale, import and export of animals and birds as well as those for tour operators and guides (Leonard 2005).

Data for this study were collected in Zambia in two different study regions: in Kasanka National Park (Kasanka NP) situated in the north of the Central Province of Zambia adjacent to the DR of Congo border and in Kafue National Park and surrounding GMA (called Kafue Kafue Region in the following) situated in the western area of Zambia (Figure 1-3).

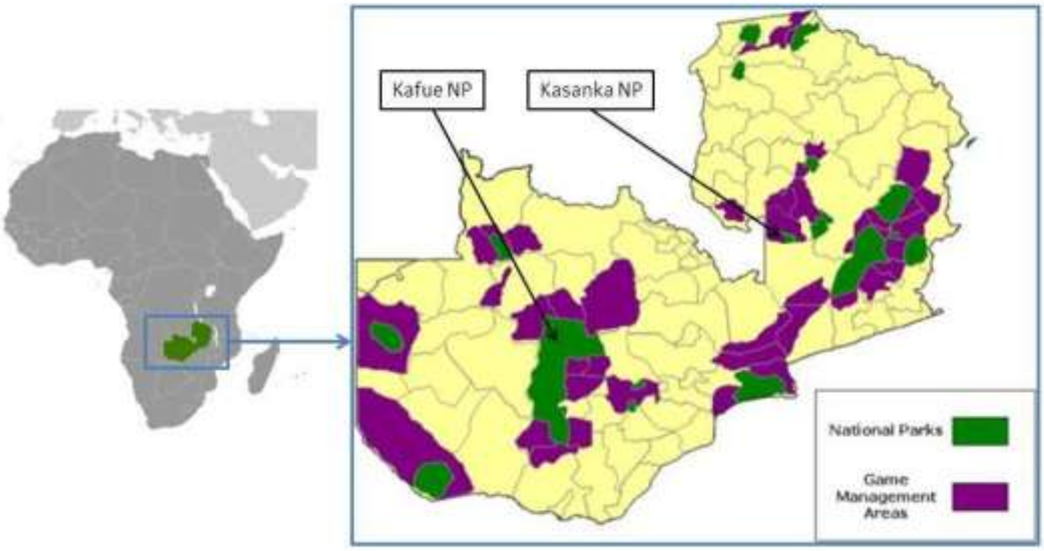


Figure 1-3: The situation of Zambia on the African continent (left) and the protected areas of Zambia (right). Kafue and Kasanka National Park, the study areas, are indicated. Sources: Map of Africa: https://www.cia.gov/library/publications/the-world-factbook/graphics/locator/afr/za_large_locator.gif - downloaded on 29th August 2013, map of the protected areas: modified from Richardson et al. 2012.

Kasanka NP, run by the Kasanka Trust, is the first Zambian NP that is privately managed and entirely dependent on tourism and charitable funding (Kasanka 2013). Covering 390 km², it is the smallest NP of Zambia's NP (Kasanka 2013) – stretching for a maximum of 35 km from east to west (Hupe & Vachal 2009). Kafinda GMA encloses Kasanka NP (Nyirenda et al. 2008). The park lies at the edge of the Bangweulu basin (Leonard 2005) within the catchment area of the Luapula River (Goldspink et al. 1998). Mulembo River, which forms the northern frontier of the park, as well as Kasanka and Luwombwa River, which traverse the park northwards, constitute the main rivers (Kennedy et al. 2008) (Figure 1-4). About 70% of the total area of Kasanka NP is covered by woodland (Kennedy et al. 2008). The largest part – about 80% – is miombo (Kennedy et al. 2008). Small patches of evergreen riverine gallery forests and wet evergreen swamp forest are also present (Kennedy et al. 2008). The area has an unusually high number of pans, papyrus swamps, dambos and floodplains (Leonard 2005). Kasanka NP has a rich birdlife (Kasanka 2013). Highlight of the

NP, however, is the millions of straw coloured fruit bats (*Eilodon helvum*) that occupy the NP from November to December. Ten species of antelopes occur in the park: the sitatunga (*Tragelaphus spekii*) population is the most visible and densest in Africa and the very abundant population of puku is striking (KASANKA 2013, KÜPPER & KÜPPER 2001). During the field trips Kabwe camp represented the research camp. Situated in the centre of Kasanka NP (Figure 1-4), a lot of areas could be easily accessed by the dirt roads.

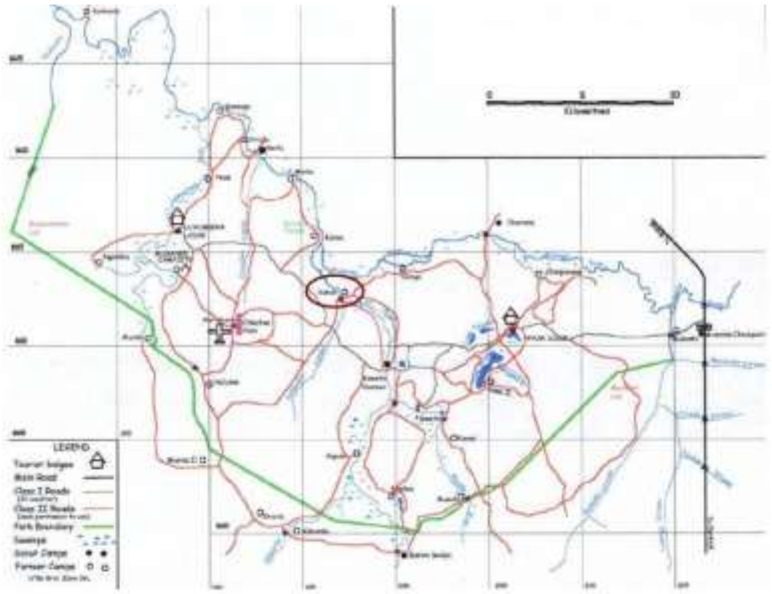


Figure 1-4: Road map of Kasanka NP, Kabwe camp is highlighted. Map downloaded and modified from KASANKA 2013, 30th July 2013.

Data collection in **Kafue Region** was carried out in two different sub regions: in the following those will be referred to as **'PukuPan & Kaingu-Region' (PPKR)** and **'Kafue NP'**. Data in Kafue NP were collected in the surroundings of McBrides Camp and thus do not speak for the situation in the entire NP. This camp is situated at the eastern bank of Kafue River in the northern part of Kafue NP (Figure 1-5). Puku Pan Lodge and Kaingu Lodge lie outside Kafue NP on the eastern bank of the Kafue River (Figure 1-5) and are located within two different GMAs: Puku Pan Lodge lies within Mumbwa GMA and Kaingu Lodge lies in Namwala GMA. Data in PPKR were collected in the GMA only; no data were collected in Kafue NP on the other border of Kafue River.

The Kafue NP is the oldest and largest NP in Zambia: founded in 1950 as a Game Reserve, it became national park in 1972 (MKANDA & CHANSA 2011), and covers 22,480 km² (ZAWA 2010). Thus, 36% of the total surface area of Zambia's national parks belongs to Kafue NP; nine GMAs surround it almost entirely (ZAWA 2010). The Kafue River passes through Kafue NP in the north and borders Kafue NP in the southern parts, forming floodplains (MKANDA & CHANSA 2011). Kafue NP is cut in half by the Mongu Road (MKANDA & CHANSA 2011). Generally, the park is characterised by extensive miombo woodlands (EAST 1996). The northern parts of Kafue NP get more rainfall which in consequence leads to richer vegetation and a taller miombo (LEONARD 2005). Due to the Kalahari sands, the southern parts, which are basically marked by Kalahari woodland joining the miombo, are drier (LEONARD 2005). The Busanga Plains in the north-west and the Nanzhila Plains in the south offer open grasslands (EAST 1996). Of all Zambian NP, Kafue NP has the greatest diversity of animal species (ZAWA 2010).

Figure 1-5: Location of the study regions in and outside Kafue NP. Map (modified) downloaded from http://www.africa-insites.com/maps/pencil_kafue.jpg on 25th September 2013.

Only two habitats closely interconnected and as well as typical for the Zambian environment and so also for the study regions shall be introduced here. The most characteristic vegetation of Zambia is a mosaic of miombo woodland and grassy dambos (LEONARD 2005).

The **miombo** is the dominant natural vegetation on the plateau (JEFFERY et al. 1989) and covers about 50% (LEONARD 2005) or up to 4/5 (ANSELL 1978, KÜPPER & KÜPPER 2001) of Zambia's surface– and generally about 3 million km² in southern central Africa (SHORROCKS 2007). This woodland is dominated by species of *Brachystegia*, *Isoberlinia* and *Julbernardia* (LEONARD 2005, ANSELL 1978, PHIRI 2005) – which are all leguminous plants (PHIRI 2005). The name “miombo” was inspired by the traditional name of *Brachystegia boehmii*, which is

‘Muuyombo’ (Shorrocks 2007). The miombo probably arose as a result of human activity (fires, clearing and agriculture) from an evergreen, dense, moist or dry forest (Drescher 1998). It is able to grow back again almost unchanged after impacts (Ansell 1978). Trees in miombo woodland are 15 to 20 m high (Leonard 2005, Shorrocks 2007). The canopy is light (Leonard 2005) and thus the grass layer is closed (Drescher 1998). Normally a shrub layer is present (Shorrocks 2007). The miombo ecoregion supports important populations of fauna, especially large mammals (CHM-CDB 2012), but due to poor soils which lead to a low nutritional value of its vegetation, it is not made for large mammals in high densities (Shorrocks 2007). Typical antelopes of miombo woodland are sable antelope (*Hippotragus niger*), Lichtenstein’s hartebeest (*Alcelaphus lichtensteinii*) and reedbuck species (*Redunca* spp.) (Shorrocks 2007).

Dambos are characteristic grasslands in miombo woodlands, where they form long drainage lines (Ansell 1978). The term ‘dambo’ is a Bantu word that means ‘meadow grazing’ (Boast 1990, Acres et al. 1985) – other words such as ‘mbuga’ (in Swahili), ‘fadama’ (in Hausa) or ‘vlei’ (in Afrikaans) are used for the same landform (Acres et al. 1985, Boast 1990). In literature, a lot of definitions and uses apply for this type of grassland (Acres et al. 1985): e.g. Mäckel (1974, verbally cited from Boast 1990) disregarding the formative process behind, defines dambo as ‘… shallow linear depressions in the headward zone of rivers without a marked stream channel. They are seasonally waterlogged and grass-covered bearing no true woodland vegetation.’ The term ‘dambo’ is used by Boast (1990) to describe ‘any flat, grass covered depression at the head of streams within the tropics, which lacks a definite channel, except, perhaps in the lower parts and which is seasonally saturated’. Acres et al. (1985) highlight that, ‘dambos should not be confused with similar features such as floodplains, alluvial plains and pans’. Generally dambos, a complex ecological system (Mäckel 1985), vary a lot in key characteristics i.e. distribution, morphology, geology, soil type and vegetation (von der Heyden 2004). In Zambia, dambos range from narrow and dry to broad and muddy or even wet and can even include perennial rivers or permanent swamp (Leonard 2005). According to Phiri (2005), two kinds of dambos – depending on soil characteristics – exist on the Zambian plateau: the acid dambos on sandy soils and the sweet dambos on clay soils which are characterised by higher pH values. According to the position in the landscape Acres et al. (1985) present four types of dambos occurring in Zambia: headwater dambos, slope dambos, hanging dambos and river dambos. The first mentioned are the most widespread form and are situated, as their name suggests, in the headwater zone of valleys. Slope dambos grow on steeper slopes whereas hanging dambos suspend above escarpments on plateau margins. River dambos correspond to the downward extension of headwater dambos and may be found on both sides of river channels or floodplains.

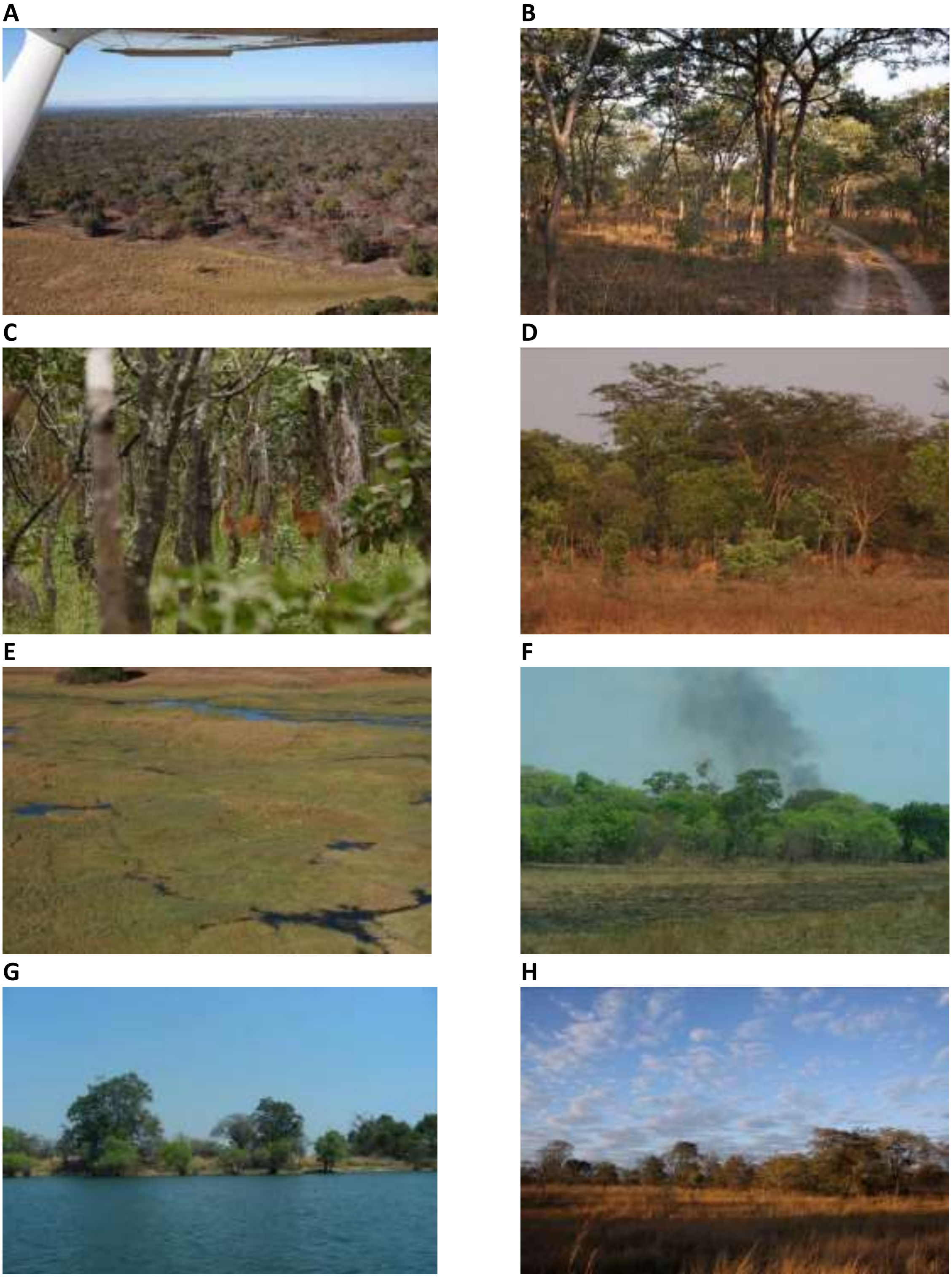


Figure 1-6: Different habitats within the study regions. Miombo woodland in Kasanka NP in the cool dry season (A, B) and in the late rainy season (C); The transition zone between miombo and open habitats in Kasanka NP (D) and the floodplain along Kasanka River (E) in the cool dry season and a dambo in the early rainy season (F). Riverine vegetation along Kafue River near McBrides's Camp (G) and near Puku Pan Lodge (H) in the cool dry season.

2 Population status, distribution patterns and habitat choice

Abstract

Knowledge about abundance and distribution of wildlife species are the most fundamental and extremely important information to improve conservation measures. This research aims to assess the population status, distribution patterns and habitat choice of puku (*Kobus vardonii*) in Kasanka NP and Kafue Region.

Road surveys along line transects were conducted in Kasanka NP and in Kafue Region in the dry season 2009 and 2010. Data of all antelope species encountered were collected and included information on group size, group composition, body condition and habitat used. Further, camera-trapping was carried out. Data were analysed with DISTANCE 6.0 (Thomas et al. 2009) others were analysed statistically; relative abundance indices were calculated from the pictures of the camera-traps. For Kasanka NP, an extrapolation of the results in order to get a population size of puku was possible.

Puku preferred to occupy grassland where estimated density was 36.15 puku/km^2 in Kasanka NP and 14.66 puku/km^2 in Kafue Region, respectively. Puku occurred in lower densities near and in woodlands. Puku were observed in lower numbers in miombo woodlands. Local population densities of puku reached up to almost 150 animals/km^2, they assembled especially on floodplains, grasslands or next to rivers or lakes. For the survey period 2009/2010 in Kasanka NP, a population size of 5,038 (3,268-7,238) puku was calculated. This is an eightfold increase, since the survey in July 1994 by Goldspink et al. (1998) and a result of the ongoing conservation work of Kasanka Trust Ltd.

In Kasanka NP, spatial overlap with other antelope species was low. Puku overlap slightly with sitatunga (*Tragelaphus spekii*). In Kafue Region, puku and impala (*Aepyceros melampus*) occurred syntopicly; they had similar distribution patterns over the transect lines and habitats. However, impala were encountered to a higher extent woodlands and intermediate habitats.

Puku occurred in small to large groups. Mean and range of group sizes were larger in Kasanka NP than in Kafue Region, probably a result of the high densities of puku especially along Kasanka River. The amounts of different group compositions were generally similar in the two study regions: breeding groups, with or without the presence of one male were very common, as well as single males. Assumed higher juvenile survival might positively affect the numbers of puku in Kasanka NP, but lead to differences in social organisation. More puku showed a medium or poor body condition in Kasanka NP than in Kafue Region.

Assessments of the populations of puku should be carried out regularly in the study regions but also in other protected areas of Zambia. It is recommended to collect not only data regarding the numbers of puku but also data of social structure and body condition. Only by this, the population status of the puku and the development of the populations can be evaluated in order to improve natural conservation measures.

2.1 Introduction

Knowledge of distribution and abundance, of the population density or the population size is virtually important and indispensable. On that basis only, the ecology of the animal and its relationship with its environment can be fully explored. Estimating populations is important for management and conservation of wildlife (Newson et al. 2008, Shorrocks et al. 2008, Ogutu et al. 2006, Buckland et al. 2006), especially in the light of the growing loss of biodiversity due to human influence (Buckland et al. 2006). Long-term monitoring of populations can reveal timing, direction and extent of changes in abundance of animals (Ogutu et al. 2006). This information again can be utilised for reintroduction programmes as they were carried out for the Arabian oryx (*Oryx leucotis*) (Seddon et al. 2003), but may also detect and hence prevent population decreases. Changes in social organisation and demography can indicate changes in population densities: the kob antelope (*Kobus kob kob*) in Comoé NP, Ivory Coast, changed its social organisation and demography after having been heavily poached which again had another negative impact on the population (Fischer & Linsenmair 2006, Fischer & Linsenmair 2002).

Populations of puku (*Kobus vardonii*) in Zambia were surveyed. Line transect sampling was carried out from roads in Kasanka NP (cool dry season 2009 and hot dry season 2010) and Kafue Region (cool dry season 2010) in order to investigate population densities, distribution patterns, habitat choice, population structure and condition of the populations. In supplement to line transect sampling, camera-trapping was carried out to discover rare, cryptic or nocturnal species as competitor or predator of the puku antelopes. The following questions will be dealt with in this chapter:

- How is the spatial distribution of the puku within these areas? In which habitat type do occur most of the observed puku occur? It is suggested that puku occur mostly in open habitat as such as grasslands or floodplains. However, local population densities of puku within the study areas are suggested to be in the same range.

- Is there a spatial competition with other antelope species in the study regions? A high spatial overlap is suggested between puku and impala (*Aepyceros melampus*) in Kafue Region, as the two species are reported for this region (Leonard 2005). Such kind of observations were made in Luambe NP in the course of the ZamBio Project (RDUCH 2008, SIMON 2008) and presumed alike for Kafue Region.

- Are there any differences in population structure or in the body condition of the puku between the study areas? As generally reported puku may occur in small to medium group sizes and have a sex ratio biased towards the females. Groups of females with one male are the most common group composition.

- The ongoing conservation measures of Kasanka Trust Ltd. are suggested to influence positively the development of the population of puku in Kasanka NP. How did the puku population develop since the study of GOLDSPINK ET AL. (1998) conducted in 1994?

- Does camera trapping reveal additional information about the abundance and distribution of mammal species in the study areas? Is it possible i) to detect other antelopes than revealed by line transect sampling and ii) to reveal spatial distribution of both antelopes and predators and iii) to detect possible predators of the puku antelopes? Further, one camera trap was mounted at an artificial waterhole and another one close to artificial saltlick set up by the Kaingu Lodge. With a focus on antelopes, the frequentation of these places can be displayed.

In the past, puku occurred widely in suitable grasslands in south-central Africa (EAST 1998). Nowadays, they disappeared from very large parts of their former range (SKINNER & CHIMIMBA 2005). This reduction is due to human activity: human settlements and cultivation result in habitat destruction and fragmentation, especially cattle herds are competing with puku for the same habitat and the puku is hunted (IUCN SSC ANTELOPE SPECIALIST GROUP 2008). The overall size of population is estimated to be 76,000 to 130,000 individuals (HUFFMAN 2011), and it is considered to decrease (IUCN SSC ANTELOPE SPECIALIST GROUP 2008). Their distribution is now discontinuous and scattered (SKINNER & CHIMIMBA 2005). Thus, populations are fragmented and isolated (IUCN SSC ANTELOPE SPECIALIST GROUP 2008) which represents a potential risk (EAST 1998). In protected areas, puku remain common (SKINNER & CHIMIMBA 2005).

Zambia, the centre of the puku’s distribution, is one of the major countries with a large number of puku (Figure 2-1). Latest population estimates for Zambia are provided by EAST (1998): he estimated this population to have over 21,040 animals; 17,840 animals occur in protected areas. The important regions for the puku in Zambia are the Luangwa Valley, Kafue NP and Nsumbu NP (EAST 1998). In 1998, GOLDSPINK et al. published an assessment about the puku in Kasanka NP giving a population size of 613.1 animals. Characterised by a high amount of grasslands, the western half of the Luambe NP was estimated to be home of 2,081 puku in 2007 (Rduch 2008). For the conservation status of the species, the puku's population in Kilombero Valley, a Game Controlled Area, is considered very important (East 1998, IUCN SSC Antelope Specialist Group 2008, Bonnington et al. 2010). There are 50,000 to 60,000 animals in Kilombero Valley (Jenkins et al. 2003, Bonnington et al. 2010) suggested to represent 75% of all puku (Huffman 2011). Beside Kilombero Valley, puku occur in Tanzania at Lake Rukwa in smaller numbers (East 1998). The population at the northern end of Lake Malawi disappeared before 1960 (Rodgers 1984). The southernmost population of puku is in Botswana, in Chobe National Park that contains 101 to 152 puku (Dipotso & Skarpe 2006). The population in Malawi covers an estimated number of 140 individuals; puku occur in Kasungu National Park, Vwaza Marsh Game Reserve and Nyika National Park (East 1989). In Angola and DR Congo, puku are diminished and only reported as vagrant in Namibia (East 1998).

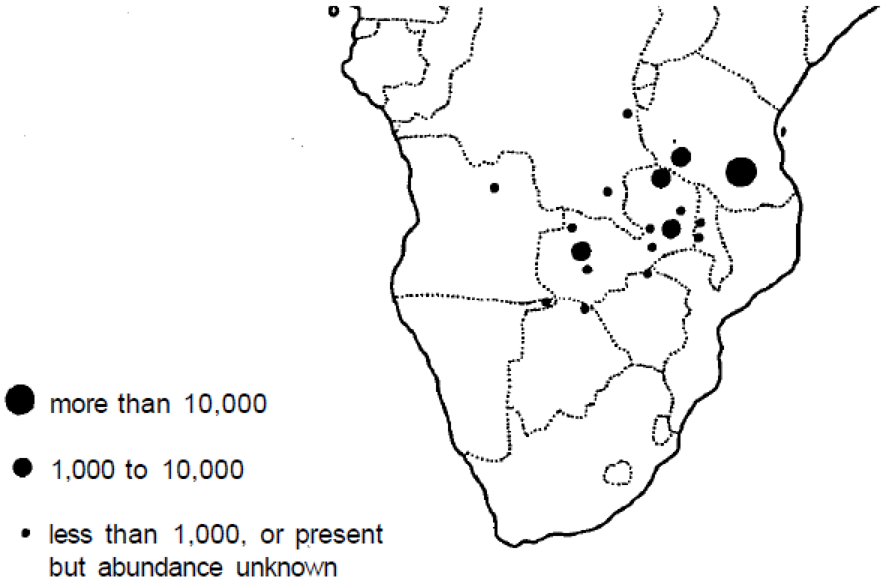


Figure 2-1: Abundance of the populations of puku (*Kobus vardonii*) in southern central Africa (modified after East 1998).

Several studies about the populations of puku in Tanzania have been published in recent years (e.g. Starkey et al. 2002, Corti et al. 2002, Jenkins et al. 2003, Bonnington et al. 2010). The last published study about population of puku in Zambia dates back to 1998 (Goldspink et al. 1998). Thus, new data about the populations of puku in Zambia is required.

Distance sampling is often used as an efficient approach to estimate the population density (*D*) or the population size (*N*) (Buckland et al. 2001) especially in challenging field conditions (Thomas et al. 2010). The main methods are line and point transects where distances from objects from a line or from a point are recorded (Thomas et al. 2002). These objects can be animals, groups of animals, plants, cues of animals (e.g. whale blows) or signs (e.g. dung or nests) (Thomas et al. 2010). With increasing distance from the observer, the objects get harder to detect, which results in less detection with increasing distance (Thomas et al. 2002). A detection function (*g (y)*) which represents the key to distance sampling (Thomas et al. 2002) is fitted to the observed distances. This function allows estimating the objects missed by the survey (Thomas et al. 2002). Thus, also undetected individuals are taken into account (Newson et al. 2008). Distance sampling is mainly suitable for animals that are difficult to catch (Greenwood & Robinson 2009).

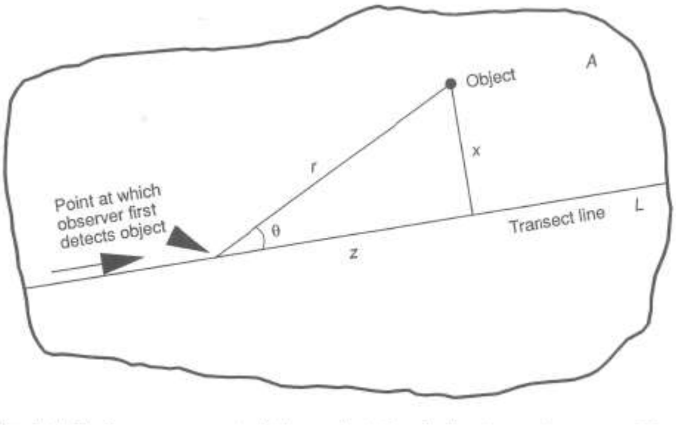


Figure 2-2: Basic measurements on line transects (Buckland et al. 2001). *A* is the area sampled, *L* is the length of a single line, *r* is the sighting distance, *0* is the sighting angle, *x* the perpendicular distance.

Line transect sampling, applied in this study, is the most widely used form of distance sampling (Thomas et al. 2010). Line transects are regarded as simple, economical and precise (Cassey & McArdle 1999). They are often used for surveys of big game (Greenwood & Robinson 2009). In line transect sampling, the observer moves along a line and records detected objects by noting the distance from the line to that object (Figure 2-2) (Buckland et al. 2001). As the observer is moving while sampling the line, transects are said to be very efficient (Barraclough 2000). Three assumptions are essential to get reliable estimates from both line or point transect sampling (Buckland et al. 2001): 1) Objects on the line are detected with certainty: All objects on or near the line should be detected. 2) Objects are detected at their initial location: The basic idea is that a 'snapshot' is taken: while the survey is carried out, the animals should 'freeze' (Thomas et al. 2010). It is not a problem if an animal is recorded several times on different occasions of sampling on the same transect – but it is problematic if the same animal is recorded more than once during the same ongoing data collection on the same transect. 3) Measurements are exact: Recorded distances (and angles when needed) are exact. Accuracy can be increased via training and technology like a laser rangefinder (Thomas et al. 2010). Sometimes a fourth assumption is given (Thomas et al. 2002): Whether an object is detected is independent of whether any other object is detected. Especially if objects are in clusters, as do puku, this assumption is menaced as there is a tendency of secondary-records in areas of high density (Buckland et al. 2001). It is thought that at the moment one animal is seen the entire cluster is detected (Thomas et al. 2002). Measurements of distance (and angle) are taken from the geometric centre of the cluster (Buckland et al. 2001). The density of individuals is then estimated by multiplying the estimated cluster density (D_S) with average cluster size (*E(s)*) (Buckland et al. 2001, Thomas et al. 2002). In general, attention needs to be drawn onto the fact that with increasing distance from the line, only large clusters tend to be detected (Buckland et al. 2001). Most of the data acquired by distance sampling are analysed using the DISTANCE software (Thomas et al. 2010).

Camera trapping is a non-intrusive method (Silverira et al. 2003) which is more and more applied for species inventories or abundance estimation (Treves et al. 2010, Stein et al. 2008) and applicable in a wide range of environments (Carbone et al. 2001, Stein et al. 2008). As an advantage to other sampling methods (e.g. line transects), this methods can be used for cryptic animals (Silveira et al. 2003, Carbone et al. 2001, Jenks et al. 2011), for rare animals (Carbone et al. 2001), for both diurnal and nocturnal species (Silveira et al. 2003), for large (>1kg), terrestrial mammals and birds (Treves et al. 2010). Camera-traps surveys are often carried out on individually identifiable species (e.g. Karanth et al. 2004). But they can also be used for non-identifiable species (Treves et al. 2010, Jenks et al. 2011) and result in an abundance index. The Relative Abundance Index (RAI) can be considered as a good tool to assess the occurrence and the spatial distribution of wildlife (Jenks et al. 2011).

Christine Haunhorst used some of the data collected on the transect lines in Kafue Region for her diploma thesis (Haunhorst, 2011). For this thesis, I re-analysed the raw data under different parameter settings.

2.2 Material and Methods

2.2.1 Data collection on the transect line

To assess the population of the puku and eventually other antelope species, line transects were conducted. The gained data should serve above all to estimate population density and population size of the antelopes. But the data also provided general information the population (sex ratio, age classes, group sizes and group composition), about habitat preferences and activity patterns (see Chapter 5). Therefore data collection was not limited to the information necessary for the DISTANCE program, but included additional data.

In theory, the transect lines are straight (Thomas et al. 2002). They are placed at random or systematically – parallel lines are recommended (Greenwood & Robinson 2009). Line length depends on the observer's ability to concentrate, that ceases after 3 to 5 hours (Barraclough 2000) or 2 to 3 hours (Wilson et al. 1996). The transect lines should be placed with a certain spacing in order to avoid overlap of sightings (Wilson et al. 1996). Wilson et al. (1996) recommend marking the lines via GPS so one is able to repeat them. The speed at which the observer moves along the line should be slow enough to detect all animals on and along the line, but fast enough to avoid double-counts or elopement of animals (Greenwood & Robinson 2009). The distance from observed animals can be determined in two different ways: distances to the line can be assigned to distance intervals. This is advantageous if data collection has to be fast as from aircrafts (Wilson et al. 1996, Buckland et al. 2001). The other way is to measure the distances either by measuring the perpendicular distance to the line or by measuring the radial distance and the sighting angle – the perpendicular distance will be calculated later (Greenwood & Robinson 2009).

In practice, the transect lines follow roads and thus they are not straight, but "this doesn't really matter" (Shorrocks 2007). This was the case for the transect lines driven in this study. In national parks it is not permitted to leave designated roads and tracks – invariably it is often not feasible e.g. due to dense vegetation. The aim was to cover the study regions evenly; aiming further on getting information about habitat use, the transect lines covered different habitat types. The lines were established on the second or third day of the stay without exact knowledge of the distribution of the antelopes. Preferable distance between line transect was at least 1 km. Transect line length was 2.3 to 6.3 km in Kasanka NP and 2.2 to 3.9 km in Kafue Region (see Chapter 2.3). To facilitate the performance of the data collection, the launch and the end of the line transects were situated at landmarks, especially crossings or trees. The lines were marked and also their situation was checked via GPS (Garmin eTrex Legend). The lines were named according to their characteristics or situations. A vehicle (Toyota Landcruiser BJ 40) was used to carry out the data collection on the line transects. The advantages of using a car concerned safety reasons and eliminated the need of a WPO (Wildlife Police Officer) escort. Additionally, the antelopes are less frightened by cars then by pedestrians (own obs.). Another important aspect was the time saved. More time was available for other research tasks in between the surveys on the lines and more transect lines could be done during a day than it would have been possible if no car had been used. The speed during data collection was 3.5 to 4.5 km/h which was first gear without or with little use of the accelerator. Two persons observed both sides of the transect line: driver and co-driver were able to look out for animals. If possible, driver and co-driver changed between transect lines to avoid bias. As I could not carry out data collection alone I was assisted by students of biology.

Generally, data collection on the transect lines covered different times of the day. Four start times were set: 7 am, 10 am, 1 pm and 4 pm (Zambian local time, UTC+2). It was aimed to sample each transect line once a day only. In Kasanka NP, data collection on the transect lines took place during four surveys: in July 2009 (from 8th to 29th July 2009, in the cold dry season), in August 2009 (from 23rd to 29th August 2009, in the progressing dry season), in October 2010 (from 7th to 12th October 2010, before the beginning of the first rains, in the hot dry season) in November 2010 (16th to 24th November, after the first rains but still in the hot dry season). Not all the transect lines were driven during each survey. Generally, each transect was driven 4 times during each survey – beginning data collection at the predefined start times. Only Puku-Loop was sampled twice, i.e. 8 times, in the two surveys 2009. Due to the fact that Kasanka River should not be crossed via the pontoon after sunset, the transect lines Fibwe, Mulembo and Wasa – all situated on the eastern side of Kasanka River – were not sampled at 4 pm in the two surveys 2009. Mulembo was not sampled at all in 2010. For the same reason the transect Nafulwe had to be shortened in 2010. Furthermore, a survey was planned in April 2011. Unfortunately, it could not be conducted due to ongoing inundation on nearly all transect lines. In Kafue Region, data collection on the transect lines in Kafue Region took place from 13th July to 22nd August 2010 in PukuPan & Kaingu-Region (PPKR) and from 29th August to 3rd September 2010 in Kafue NP. The transect lines River and Plains in PPKR were surveyed for a second time from 20th to

21st September 2010. Exceptionally, transect lines were driven twice a day. Unfortunately, the line River could not be sampled at the 10 am start time.

After BUCKLAND et al. (2001), all animals may be recorded regardless how far they are from the line. Following this, all animals observed, bovid species only, were noted during data collection on the transect lines. In the case of detection, the following information was noted: time of the day, species, number of animals in the group, sighting (radial) distance and sighting angle. These are the main information needed for the basic analysis in distance; thus, getting this information had the priority over the following. These were: angle to northwards direction, GPS coordinates of the vehicle, habitat characteristics, number of adult males, subadult males, adult females, juveniles and neonates in a group (according to the definitions in Table 2-1), actual activity of the individuals (according to the ethogram, see Table A. 13), body condition of adult males, subadult males and adult females (according to the definitions given by RINEY (1960), Figure 2-3). Whether animals belonged to a group, or to which group, was decided intuitively, as it is commonly done in practise (MARTIN & BATESON 2007): individuals standing relatively near to others were considered as a group.

Table 2-1: Definition of sex and age classes used for the observations along the transect lines.

sex and age class	characteristic of the puku	summarizing term used
adult male	full grown individual with lyre shaped horns	adult puku
bachelor male	full grown individual with growing horns that are not yet lyre shaped	
female	full grown individual without horns	
juvenile	shoulder height lower than shoulder height of full grown individuals	young puku
neonate	shoulder height lower than belly of full grown individuals	

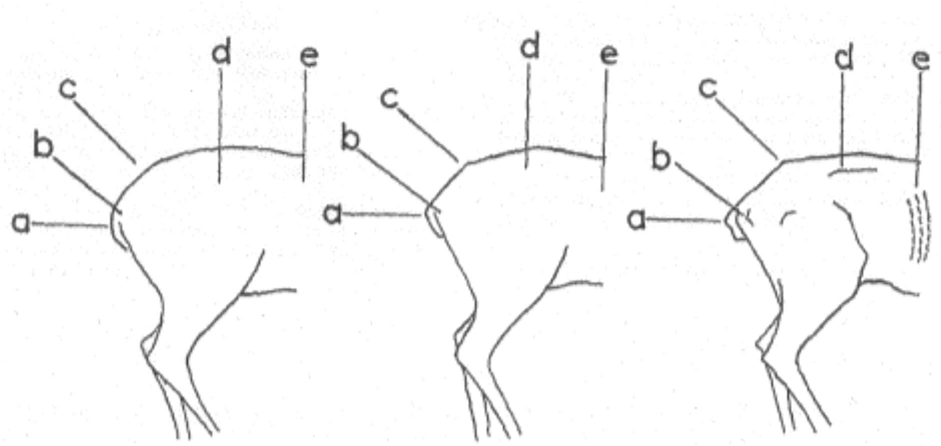


Figure 2-3: The general appearance of the hind quarters of ungulates in good, medium and poor condition (from RINEY 1960). Good condition: If no angles appear at the points corresponding to a) and c). Medium condition: If any angles appear at the points corresponding to a) and c). Poor condition: if any of the points indicated at b), d) or e) can be observed.

After a detection of animals, the car was stopped, so information could be gathered and noted. Binoculars were used (Steiner, SkyHawk 10x42). Distance from the observer to the animals was measured with a laser rangefinder (Carl Zeiss, Victory 8x26 T* PRF). The angles determined with the use of a compass were rounded to 10°. While determining the sighting angle, the car was presumed to be 0°. To avoid double-counts data collection at one point was restricted to 5 minutes. If disturbed by other human presence (other cars, bikers or pedestrians coming toward or overtaking) data collection was interrupted for 5 minutes.

2.2.2 Location and short description of the transect lines

Only a brief overview on the placement and general characteristic of the line transects are given here. The maps of their situation were created using ESRI ArcMap 10.0. More detailed information is presented in the Appendix (Table A. 1, Table A. 2 and Table A. 3). All transect lines are situated along established dirt roads.

Nine transect lines were located in Kasanka NP. Their length ranges between 2.3 and 6.3 km (Table 2-2). The transect lines sum up to 35.3 km. As line transects were driven to a different extent during the four surveys, each survey resulted in a different survey effort. For all surveys added together, the overall survey effort was 397.6 km. The transect lines covered a high amount of the area in Kasanka NP. The region west of Luwombwa River was not covered because of a lack of access. For logistical reasons, the eastern parts of Kasanka NP were generally low covered by transect lines. We were staying at Kabwe camp and crossing Kasanka River, only possible at the pontoon, was to be avoided in the dark. The transect lines cover different types of habitat, i.e. miombo and (wet and dry) grasslands.

In Kafue Region, 13 transect lines were established, subdivided into 9 transect lines for PPKR and 4 for Kafue NP (Table 2-3). The length of the lines ranges between 2.2 and 3.9 km (Table 2-3). Within Kafue NP, as well as for the surrounding GMAs, only a small fraction of the protected area was covered by the lines. The transect lines cover different habitat: miombo, riverine woodlands and grassland areas. Additionally, the transect lines are situated at different distances to and at different orientation towards Kafue River (Figure 2-5 and Figure 2-6): e.g. the transect line River has a maximum distance of about 0.4 km and is orientated parallel to Kafue River – Miombo East is more or less upright to Kafue River with a maximum distance of about 10.2 km. The survey effort (Table 2-3) was 104.0 km for PPKR and 45.6 for Kafue-NP. Thus, the total survey effort for Kafue Region was 149.6 km.

Table 2-2: Overview on the length and survey effort of the transect lines in Kasanka NP. * Nafulwe was not driven to full extent in November 2010.

transect line	line length [km]	number in Figure 2-4	survey effort			
			July 2009 [km]	August 2009 [km]	October 2010 [km]	November 2010 [km]
Luwombwa	3.2	1	12.8	0	12.8	12.8
Chikufwe	6.3	2	25.2	25.2	25.2	25.2
Nafulwe	4.0	3	16.0	0	0	12.8*
Katwa	2.8	4	11.2	11.2	11.2	11.2
Kafubashi	3.2	5	12.8	0	12.8	12.8
Puku-Loop	5.1	6	40.8	20.4	20.4	20.4
Mulembo	2.3	7	6.9	0	0	0
Fibwe	2.9	8	8.7	8.7	0	11.6
Wasa	5.5	9	16.5	0	0	22.0
total	35.3		150.9	65.5	82.4	128.8

Figure 2-4: Situation of the transect lines in Kasanka NP. The numbers along the transect lines refer to the information given in Table 2-2.

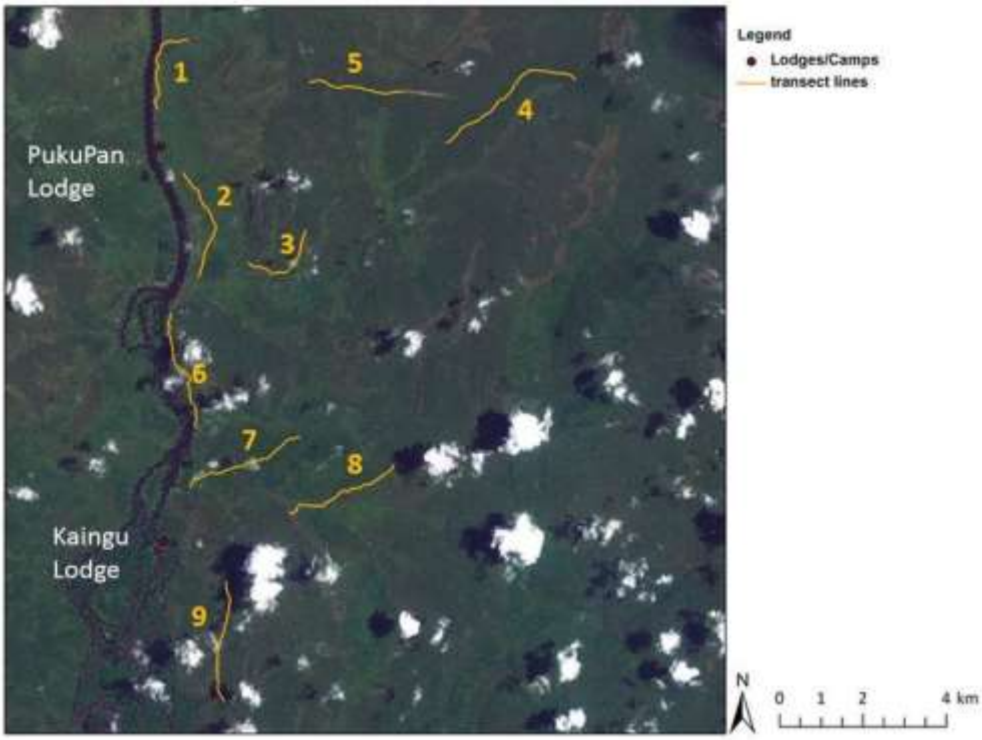


Figure 2-5: Situation of the transect lines in PukuPan & Kaingu-Region (PPKR). The numbers along the transect lines refer to the information given in Table 2-3. All transect lines lie in GMAs on the eastern bank of Kafue River whereas Kafue NP is on the western bank.

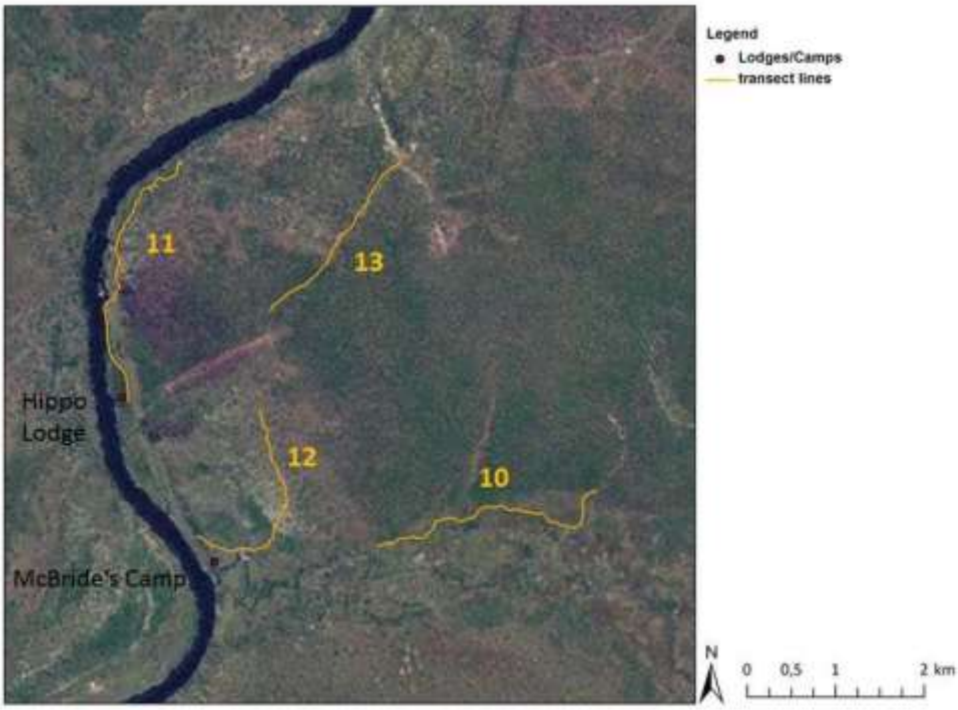


Figure 2-6 Situation of the transect lines in Kafue NP around McBride's Camp. The numbers along the transect lines refer to the information given in Table 2-3

Table 2-3: Overview on the length of the transect lines in Kafue Region. The survey effort is stated for July to August 2010.

subregion	transect line	line length [km]	number in Figure 2-5 and Figure 2-6	survey effort [km]
PPKR	Kafue North	2.4	1	9.6
	Kafue South	2.9	2	11.6
	Between	2.2	3	8.8
	Miombo East	3.9	4	15.6
	Miombo West	2.3	5	9.2
	River	3.1	6	12.4
	Main Road	3.1	7	12.4
	Plains	3.1	8	12.4
	Kopje	3.0	9	12.0
	total	26.0		104.0
Kafue-NP	Dambo	3.1	10	12.4
	Hippo	3.3	11	13.2
	Camp	2.6	12	10.4
	Airstrip	2.4	13	9.6
	total	11.4		45.6
total		37.4		149.6

2.2.3 Setting camera-traps

Camera traps (Prowler, Stealth Cam LLC., Grand Prairie, TX 75053, USA) with an infrared sensor were employed. This infrared sensor detects motions in front of the camera which trigger the camera. All camera-traps were turned on 24 hours per day. At night-time, they had infrared emitters. Each photograph recorded date and time. The cameras were set in such a way that once the infrared sensor was released sequences of 2 to 5 photographs were taken with a minimum gap of 1 minute between camera releases. In order to fit to the schedule with other research conducted, camera-traps were checked in periods between one and 16 days. Like in the studies of Trolle et al. (2008) or Jenks et al. (2011) cameras were placed on dirt roads or on animal trails as they represent routes of travel for many species (Carbone et al. 2001). They were fixed on trees at 1 m from the ground, straightforward oriented parallel to the ground. In contrast to other studies (e.g. Giman et al. 2007) no lure or bait was used to attract wildlife, except the saltlick or the waterhole. To reduce the risk of false releases, shaking vegetation was removed as well as possible from the camera’s field of view.

Camera trapping was conducted mainly in Kasanka NP but also in PPKR. For Kasanka NP, focal regions were chosen for sampling: the area at Chikufwe, Katwa, Kabwe, Puku-Loop, Fibwe-Area and Fibwe-Forest (Figure 2-7). These regions fit with the placement of some transect lines (see 2.2.2) or grids for the search of faeces and signs of predators (see Chapter 4) to allow comparison. While the camera stations at Fibwe-Area covered grassland and miombo, the cameras at Fibwe-Forest covered the evergreen forest. For Kasanka 2009 and Kasanka 2010, a replication of the same camera sample location was not intended. For both 2009 and 2010, camera-trap survey in Kasanka NP comprised 14 camera-trap stations. PPKR was sampled with 12 camera-trap stations (Figure 2-8). Two camera trap stations, one situated next to an artificial waterhole and another one on an artificial saltlick, 100 m away from each other, represent 'special' places. The positions were taken with a GPS device (Garmin eTrex Legend HCx); maps of their situation were created using ESRI ArcMap 10.0. Data collection on the camera-trap stations was carried out between 15th July and 1st September 2009 for Kasanka NP in 2009, between 5th October and 26th November 2010 for Kasanka NP in 2010 and between 13th July and 25th August 2010 for PPKR. Accordingly, it covered a duration of 52, 48 and 43 days, respectively.

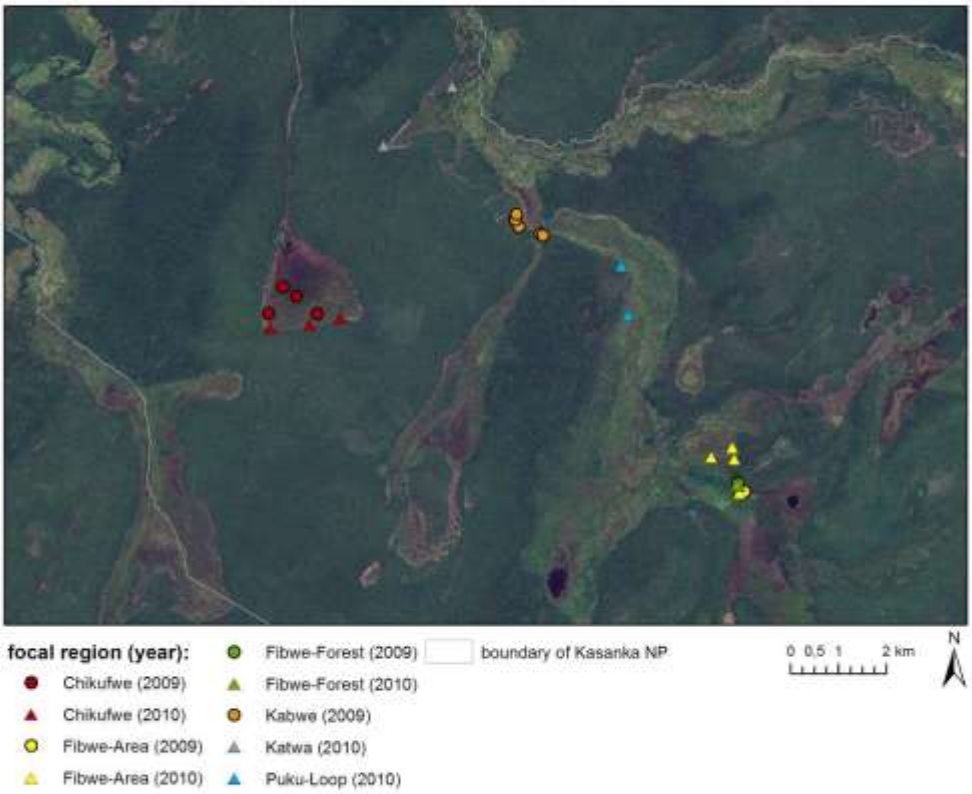


Figure 2-7: The camera-trap stations in Kasanka NP during the survey in July/August 2009 and October/November 2010.

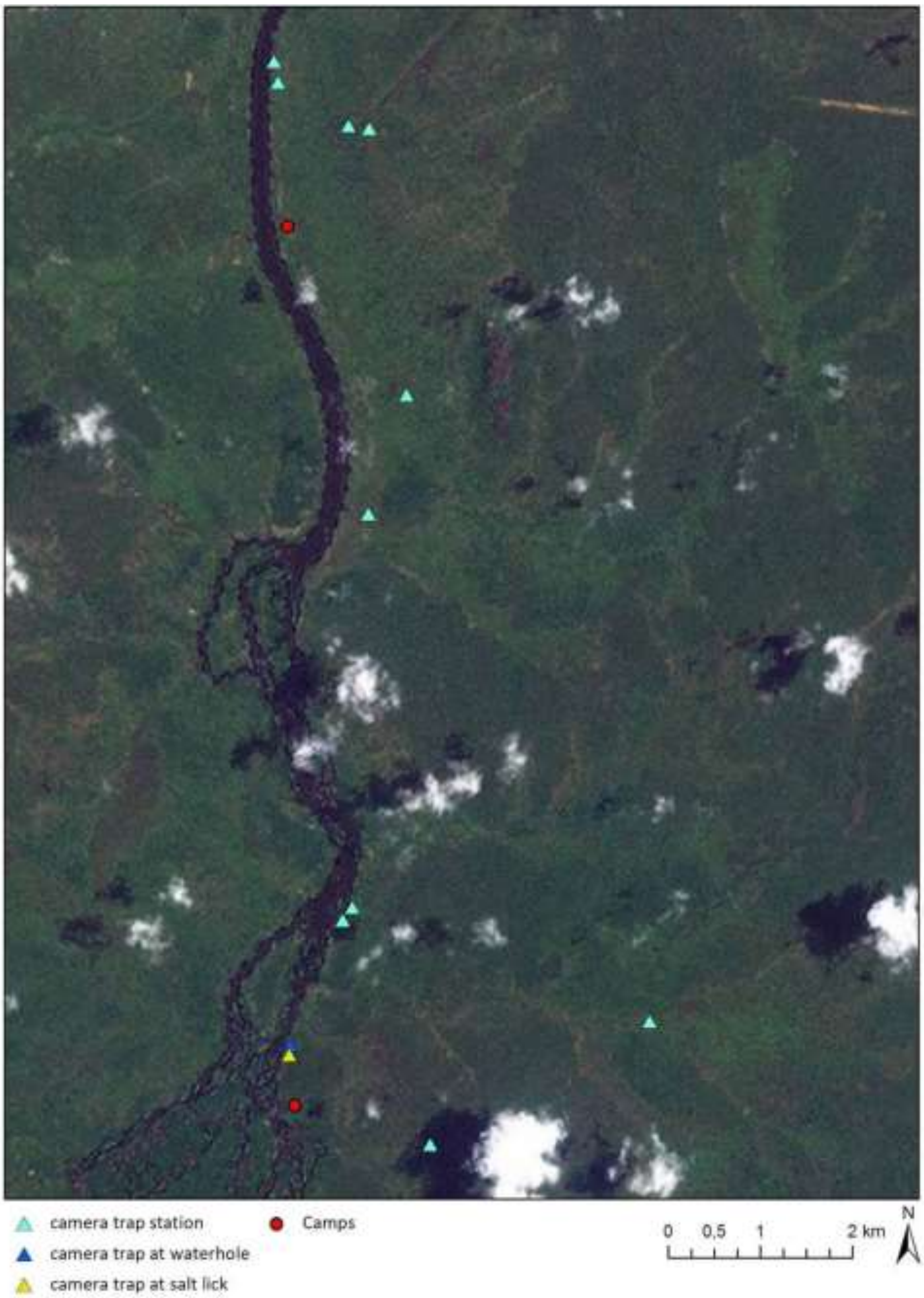


Figure 2-8: The camera-trap stations at PPKR in during the survey in July/August 2010.

2.2.4 Data analyses

In order to check seasonal differences in habitat use, group sizes, group compositions and body condition in Kasanka NP, only the data from the surveys in July 2009 and November 2010 were considered; as they comprise all transect lines, except Mulembo in November 2010. This way, comparability was ensured, as different habitat patterns along the transect lines might influence the data. The transect Puku-Loop was sampled twice at each time of the day during the survey in July 2009. To assess the habitat choice and social structure of puku in Kasanka NP and to ensure comparability between surveys, only one data collection of each time of the days was considered. Similar for Kafue Region, data collected on the transect lines resurveyed in September 2010 in PPKR, Plains and River, were not used to assess habitat choice, social structure and body condition.

Generally, although a single animal does not form a group in the proper sense, in this thesis I refer to the group size of one single individual and to group compositions of one single male, subadult, female or young puku.

Statistic tests were performed to evaluate differences between observations. Depending on the structure of the data, the Chi^2-test, the Mann-Whitney-U-test (U-test), the Kruskal-Wallis-test (KW-test) or the Wilcoxon-test were used to check the significance of the observed differences. Correlations between data were checked via Spearman analyses. All statistical analyses were performed with SPSS 13.0. Graphs were created with SPSS 13.0 or Microsoft Excel 2010.

Habitat choice

Analyses for habitat choice, i.e. comparison itself and statistics were based on the proportional amount of observed animals in the habitat categories. The same habitat categories as used for the analyses in the MCDS engine in DISTANCE (Table 2-5) were used here. In order to assess habitat preferences in Kasanka NP, the JACOBS Index (JACOBS 1974) was used: $D = (r-p) / (r+p-2pr)$. In this case, r is the estimated density of the antelope in a habitat, and p the ratio of this habitat in Kasanka NP. To get the proportions of the estimated densities, the sum of all estimated densities was set 1. As the habitat category 2 stands for intermediate habitats, it was excluded. The JACOBS index results in values from -1, meaning avoidance, to 1, indicating maximum preference. In order to compare habitat use during the different times of the day, the data from transect lines were split up according the starting time of the transect lines. Some transect lines took more than one hour to sample, especially the transect line Puku-Loop in Kasanka NP, all observation from that survey were considered without respect the actual time of observation.

Population estimates

All estimates for this PhD thesis are conducted using the software DISTANCE 6.0 release 2 (downloaded at http://www.ruwpa.st-and.ac.uk/distance, 10th June 2010). A graph was created by plotting the observed cluster size against the recorded distances. Thus, as recommended by Buckland et al. (2001), equal detection of all cluster sizes at any distance could be checked. The analysis in DISTANCE itself is composed of three elements (Thomas et al. 2010): the survey, the data filter and a model definition. The survey defines which data layers will be used for the estimation (Thomas et al. 2010); these were the observations of either all antelope species or observations of puku or impala only. The data filter selects only a subset of the data (Thomas et al. 2010). In this context, the Right-Truncation needs some attention: Here, outliers are cut out and the modelling of the data becomes easier – precision of the estimation can be improved (Buckland et al. 2001). If there is no truncation in the field, as it is with this study, Buckland et al. (2001) recommend truncating about 5 to 10% of the largest observations. During these analyses, truncation was different ranging from 0 to 10% of the largest observations. Several models of the detection function (*g(y)*) are proposed for the analysis (Buckland et al. 2001). The true detection function is unknown and a model has to be created based on the observations (Buckland et al. 2001). Therefore, it is very important that the model is robust and thus able to take a lot of possible shapes (Buckland et al. 2001). As the main assumption for line transect sampling is the certainty of detections on the line the models should have a 'shoulder' (Buckland et al. 2001). Thus, functions with a spike near zero distance are excluded (Buckland et al. 2001). Then, a good model should result in estimations with low variance which says that the model is very efficient (Buckland et al. 2001). All the models for the detection function included in DISTANCE have these three important characteristics (Buckland et al. 2001). They are composed of a 'key function' and a 'series expansion'. The key functions in the Conventional Distance Sampling Engine (CDS) are: uniform, half-normal, hazard rate and negative exponential; series expansions can be cosine, simple polynomial and hermite polynomial (Thomas et al. 2010). Not every combination should be used; the use of the negative exponential key function is generally not recommended (Thomas et al. 2009). Buckland et al. (2001) show useful models (Table 2-4). The Akaike's Information Criterion (AIC) should be used by the DISTANCE software to choose the best model for the data (Buckland et al. 2001). It gives a relative measure of fit (Thomas et al. 2010). The smallest AIC indicates the best model for the data (Thomas et al. 2010): this model fits the best, but also has the fewest parameters (Buckland et al. 2001). Comparison of models with AIC is only allowed if the models are applied to exactly the same data, meaning that the same data filter should have

been applied (THOMAS et al. 2010). Analyses with more than one model can be run (THOMAS et al. 2010); this was done in this study. Then DISTANCE chooses itself the best model via the AIC (THOMAS et al. 2010).

Table 2-4: General useful models of g(y) as proposed by BUCKLAND et al. (2001). Note that the uniform key-function is not available in MCDS (MARQUES et al. 2007).

Key function	Series expansion
Uniform, 1/u	Cosine, $\Sigma^{m}_{j=1}a_j\cos(j\pi y/w)$
	Simple polynominal, $\Sigma^{m}_{j=1}a_j(y/w)^{2j}$
Half-normal, $\exp(-y^2/2\sigma^2)$	Cosine, $\Sigma^{m}_{j=1}a_j\cos(j\pi y/w)$
	Hermite polynominal, $\Sigma^{m}_{j=2}a_jH_{2j}(y_s)$
Hazard-rate, $1-\exp(-(y/\sigma)^{-b})$	Cosine, $\Sigma^{m}_{j=1}a_j\cos(j\pi y/w)$
	Simple polynominal, $\Sigma^{m}_{j=1}a_j(y/w)^{2j}$

The CDS engine is the engine normally used and pre-set in DISTANCE. In this engine, the probability of detection depends only on the observed distances (THOMAS et al. 2009, THOMAS et al. 2010) and the detection on the line is certain (THOMAS et al. 2010). Multiple Covariates Distance Sampling, analysed with the MCDS Engine, does not assume that detection depends only on the observed distances (THOMAS et al. 2009, THOMAS et al. 2010); but detection is a function of supplementary covariates included in the estimation (MARQUES et al. 2007, THOMAS et al. 2010). Bias in stratum-specific estimates can be eliminated (MARQUES & BUCKLAND 2004). The covariates can be factor covariates like discrete classes such as habitat (MARQUES et al. 2007), as it was the case in this study, or nonfactor covariates e.g. group size (MARQUES et al. 2007). These covariates influence only the scale of the detection function, whereas the general shape remains (THOMAS et al. 2009). Thus, the covariates change the rate at which detectability decreases with distance, but the overall character of the detection functions stays the same (THOMAS et al. 2009). In contrast to CDS, the uniform key function is not included in MCDS (MARQUES et al. 2007). For the purpose of the use of MCDS engine, all observations were categorised into three classes of habitat, based on the notes made on habitat characteristics (Table 2-5). In a first step, the two engine types provided by DISTANCE were used for a general analysis of the data. The qualities of the analyses were evaluated according to AIC and precision of the estimation. The best engine was then used for further analyses of the data in question.

Table 2-5: Definition of classes of habitat used for MCDS-engine analyses and for analyses of habitat choice.

habitat category		**features of habitat characteristic**
1	grassland	open, short grassland
2	scrubland	scrubs, open woodland, light scrubland, edge of woodlands, long grass
3	woodland	dense woodland, miombo, thicket

I pooled data from different species into one analysis as well as data from different surveys, i.e. seasons. All cases assume that detection functions are similar across surveys as also done by Ogutu et al. (2006). This is probably true for all the surveys performed for this study: They were all accomplished at different states of the dry season, but it is important to consider that this might be different in a survey during in the rainy season, when green, freshly sprouting vegetation is abundant. In order to deal with possible differences in detection probability between the study regions, I did not merge data from Kasanka NP and Kafue Region. Other antelopes than puku or impala were encountered in much lower occasions during the data collection of the transect lines. In order to estimate their population density it was assumed that detection probability was similar for all antelope species, although they differ in body size and colour as well as in group sizes, behaviour patterns and habitat choices. The stratification carried out in this study was the post-stratification. As the transect lines were driven to different extent, either the multiplier option was used and/or the survey effort (by changing the line length) of the specific transect lines was adopted like it is suggested in Thomas et al. (2009).

The parameter setting for all estimations made is given in the Appendix (Table A. 4, Table A. 5). Results of estimations given by DISTANCE were rounded to 2 decimal places.

According to Kennedy et al. (2008) about 70% of Kasanka NP are covered by woodlands. This was the foundation of the analysis of habitat preference of puku which made it possible to estimate the population size for puku in Kasanka NP based on the estimation of population densities in the habitat categories. Habitat category 2 standing for intermediate habitats was not considered in any case. Since Kafue NP is much larger, and includes different habitats and animal communities not covered by the study, such an extrapolation was not intended for this study region.

The map to compare the findings of Goldspink et al. (1998) to the results of this study was created using ESRI ArcMap 10.0.

Camera-traps

This study uses the camera traps not to identify individuals but to compare photographic rates between areas. The animals on the photographs were determined to the lowest possible taxonomic resolution. Most could be identified up to species level; sometimes animals were pooled at the level of family or even order. To reduce the risk of overestimation, only photographs were counted showing the same species and separated by 30 min or more (Silveira et al. 2003, O'Brien et al. 2003). Only then, they were considered to be 'independent'. If several individuals were shown on one photograph, the photograph was counted as a single for that species (Jenks et al. 2011). For the calculation of the Relative Abundance Index (RAI), the total number of trap-nights is needed. A trap-night is defined as a 24h period where the camera was functional (Kawanishi et al. 1999). The total number of trap-nights (TN) is defined as follows: $TN = \Sigma_{i=1} tn_i$. *i* is a trap location, *tn* is a trap-night at the *i*th location (Kawanishi et al. 1999). Following this, TN is the summation all trap-nights of the trap locations (Kawanishi et al. 1999) taken into account. Following the explanations of Kawanishi et al. (1999), Jenks et al. (2011) or Treves et al. (2010) the RAI is the sum of all independent camera traps, hence the sum of the independent photographs *d*, multiplied by 100 and divided by the total number of camera nights *TN*: $RAI = \Sigma_{i=1} d_i * 100/ TN$.

The RAI was calculated per species as done by e.g. Kawanishi et al. (1999), Jenks et al. (2011), Treves et al. (2010) and for taxonomic groups, as proposed by Giman et al. (2007), for the different study regions and focal regions (only Kasanka NP). Further, the two camera trap stations, on an artificial waterhole and on an artificial saltlick, were analysed separately and not included in the general RAI figure for PPKR.

2.3 Results

2.3.1 Sightings on the transect lines

During all survey in Kasanka NP, a total of 1,194 sightings of antelope species were noted. Eight antelope species were observed (Table 2-6). Group sizes ranged from 1 to 169 individuals. The highest perpendicular distance to the line was 368.80 m. Even small group sizes of puku were detected up to far distances (Figure 2-9) e.g. one animal was recorded at 348.76 m perpendicular distance to the line. 627 sightings, more than half of the sightings, were made in a distance of up to 100 m from the line. Concerning group sizes, more than half of the sightings (603 sightings) accounted for group sizes of up to 5 individuals, 836 sightings (about 70%) resulted in a group size of up to 10 animals. About 8% of the recorded group sizes are groups of 30 and more individuals. The largest group of 169 was observed at about 79 m perpendicular distance from the line. The sightings yielded a result in 12,202 individuals of observed animals. The antelope species observed the most concerning both the sightings and the number of observed individuals was the puku (Table 2-6). A total of 1,082 sightings of puku were recorded which split up into 11,972 individuals. All other antelopes were recorded in much fewer sightings and individuals: sitatunga (*Tragelaphus spekii*), bushbuck (*Tragelaphus scriptus*), reedbuck (*Redunca arundinum*), Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*), orebi (*Ourebia ourebi*), bush duiker (*Sylvicapra grimmia*) and sable (*Hippotragus niger*). Differences between species with regard to sighting numbers (Chi^2-test: $p<0.001$, $N=1{,}194$) and observed animals (Chi^2-test: $p<0.001$, $N=12{,}202$) were significant.

In Kafue Region, a number of 284 sightings of antelopes were made on all transect lines, without taking into account the resurvey of the transect lines River and Plains in September. They subdivided into 133 sightings for the 9 transect lines in PPKR and 151 sightings for the 4 transect line in Kafue-NP. The highest observed distance was 590 m. The largest observed group size was 79. Generally observations decreased as the perpendicular distance to the line increased. But small cluster sizes were detected at high distances from the line (Figure 2-10): e.g. a single individual was observed at a distance of 496 m. About 83% of the sightings were made at a perpendicular distance less than 100 m. 61% of the sightings included group sizes of up to 5 individuals, 77% of the sightings included group sizes of up to 10 individuals. Only 3% of the sightings were groups with 30 and more individuals (Figure 2-10). Puku reached a total of 146 sightings, whereas 102 sightings of impala (*Aepyceros melampus*) were recorded. Beside puku and impala, the following antelopes were noted: bushbuck, greater kudu (*Tragelaphus strepsiceros*), waterbuck (*Kobus ellipsiprymnus*), Lichtenstein's hartebeest, reedbuck and Sharpe's grysbok (*Raphicerus sharpei*). Other antelope species only reached small numbers of sightings. The differences in the amount of sightings were generally significant (Chi²-test: $p<0.001$, N=284) as well as the differences between sightings of puku and impala (Chi²-test: $p=0.005$, N=248). Concerning the amount of recorded animals, impala had a number of 1129 which exceeded the 845 puku observed (Table 2-6). Recorded individuals of puku and impala were many more than of other antelope species. The general differences in observed individuals were significant (Chi²test: $p<0.001$, N=2,061), and so were the differences in observed individuals between puku and impala (Chi²-test: $p<0.001$, N=1,974).

Table 2-6: Total amount of sightings and recorded individuals per species in Kasanka NP and Kafue-Region.

study area	antelope species	sightings	observed individuals
Kasanka NP	puku (*Kobus vardonii*)	1,082	11,972
	sitatunga (*Tragelaphus spekii*)	46	83
	bushbuck (*Tragelaphus scriptus*)	28	33
	reedbuck (*Redunca arundinum*)	22	41
	Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*)	7	46
	orebi (*Ourebia ourebi*)	1	1
	bush duiker (*Sylvicapra grimmia*)	7	7
	sable (*Hippotragus niger*)	1	19
Kafue Region	puku (*Kobus vardonii*)	146	854
	impala (*Aepyceros melampus*)	102	1,129
	bushbuck (*Tragelaphus scriptus*)	13	16
	greater kudu (*Tragelaphus strepsiceros*)	8	33
	reedbuck (*Redunca arundinum*)	1	1
	waterbuck (*Kobus ellipsiprymnus*)	7	28
	Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*)	2	3
	Sharpe's grysbok (*Raphicerus sharpei*)	1	1
	bush duiker (*Sylvicapra grimmia*)	4	5

The different antelope species were recorded to different extent (in sightings and individuals) through the survey period and over the different transect lines in Kasanka NP (see Table A. 6, Table A. 7). Puku were not seen at Nafulwe. They were seen once at Luwombwa and Chikufwe. They were observed in low numbers at Katwa, Kafubashi and Mulembo. They were noted in high numbers along Wasa and Fibwe. Surveyed in double amount, the numbers from Puku-Loop had to be divided by two for July 2009 to get comparability and for statistics. Nevertheless, puku reached highest numbers in both sightings and individuals along this transect line. Reedbuck, hartebeest, sable and orebi were seen only at Chikufwe. Sitatunga were seen at Puku-Loop, Fibwe and Wasa. This was similar for the bushbuck, whose sightings are supplemented by a single animal seen along Luwombwa. Comparing the observations of puku in July and August 2009, it can be stated that for the transect lines resampled in August, puku sightings and observed individuals increased along Fibwe and Puku-Loop. Comparing puku in October and November 2010, the amount of sightings increased, but the number of individuals decreased at Puku-Loop and Kafubashi. For Katwa, puku sightings and individuals increased. Comparing puku in July 2009 and November 2010: in the two periods they occurred in very low numbers reaching even zero at Luwombwa, Chikufwe, Nafulwe and Kafubashi. At the line transects Katwa, Puku-Loop, Fibwe and Wasa, numbers for both sightings and individuals were much higher in November 2010.

Concerning the distribution of species on the transect lines in Kafue Region differences were evident (see also Table A. 8, Table A. 9). Puku reached a high amount in sightings along the transect lines Kafue North and Hippo, but also on Kafue South, Dambo and Camp. Except for Camp, these trends were the same in impala. The distribution of the observed animals on the transect lines showed similarities to the distribution of sightings. Compared to the sightings, the numbers of puku were much higher on River. The opposite applied for Kafue South transect line. Puku and impala showed an overlap in occurrence on the transect lines: the two species were frequently observed in numbers on the transect lines Kafue North and above all on Hippo. The transect line Camp resulted in more individuals for puku; Kafue South and Dambo showed more observed impala.

The transect lines River and Plains were resurveyed in September 2010. River was driven only thrice. Overall sightings on these two transect lines showed a slight increase from August to September (see also Table A. 10). There was no big increase in sightings, same goes for the observed animals. Also the amount of observed animals remained more or less the same in puku and impala. But remarkable differences could be found in the distribution of the animals on the two transect lines: Puku were noted to a much higher extent on River, whereas the number of impala increased on Plains. Sightings and numbers remained stable for kudu and hartebeest, but there was a small decrease in sightings and numbers of waterbuck. Bushbuck and reedbuck were generally not often noted, but it has to be mentioned that reedbuck could only be observed in September on transect line Plains.

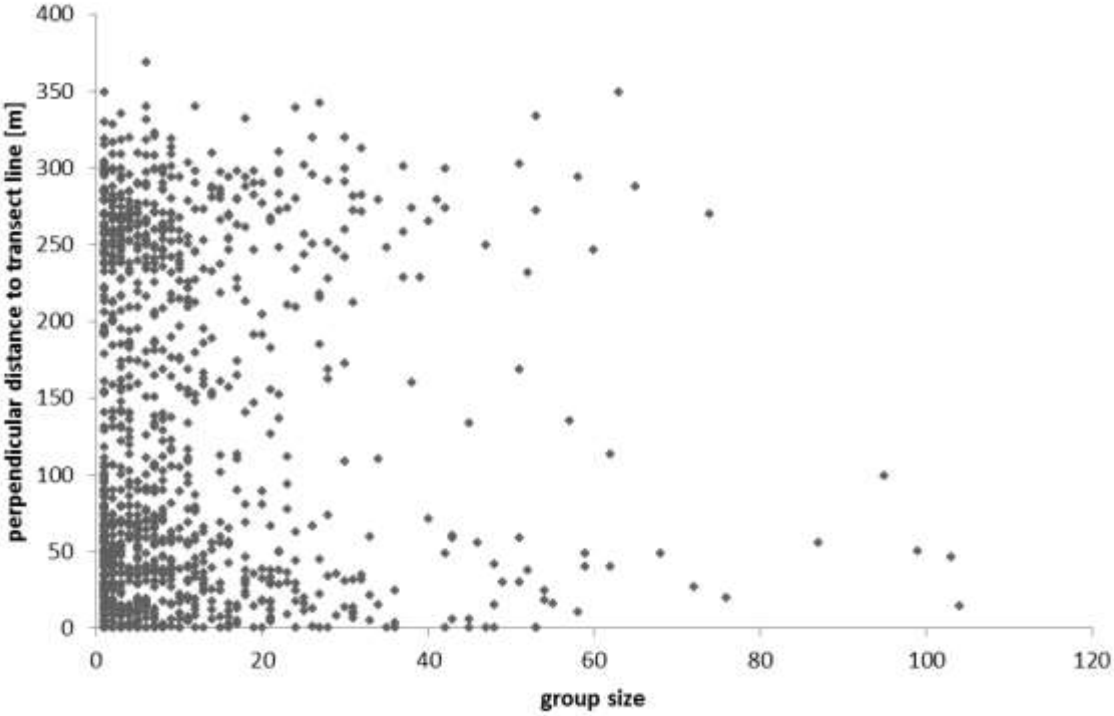


Figure 2-9: Scatter plot showing the group sizes in relation to the observed perpendicular distances in Kasanka NP: only sightings of puku (*Kobus vardonii*) are presented, the largest group size of 169 puku is excluded.

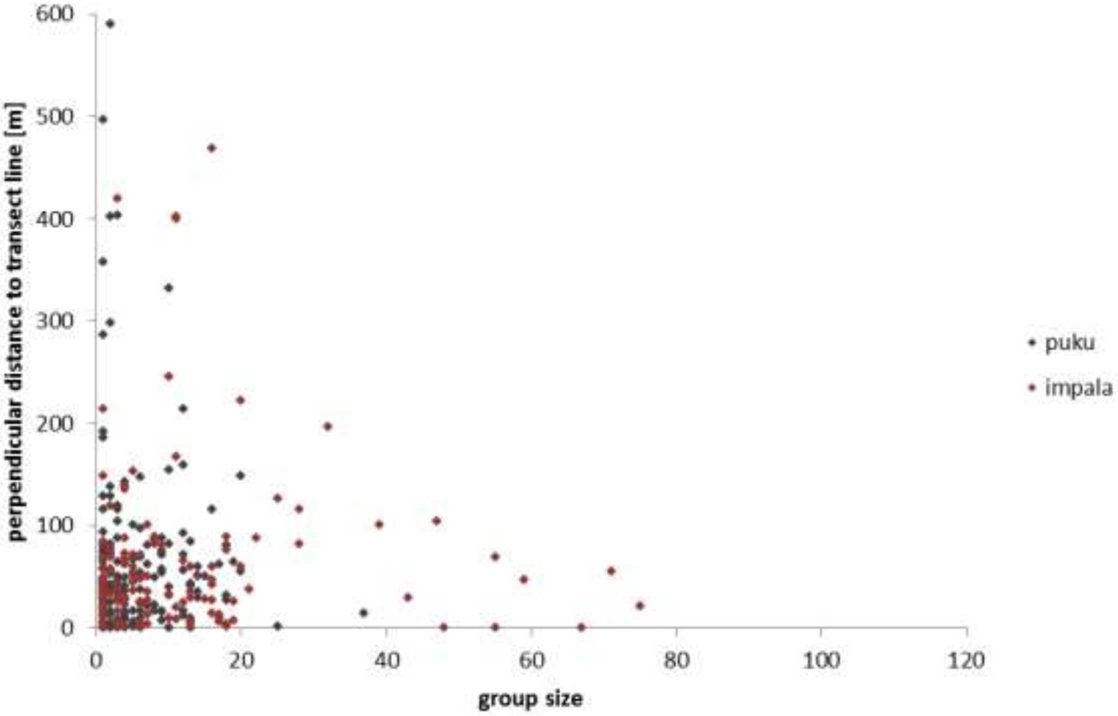


Figure 2-10: Scatter plot showing the group sizes in relation to the observed perpendicular distances in Kafue Region: observations of puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) are shown.

2.3.2 Habitat choice of antelopes

The same categories that were employed for the estimation via DISTANCE were used here. Along the transect lines different antelope species were observed in different habitat types.

In Kasanka NP (Figure 2-11), puku, sitatunga and reedbuck were observed mostly in grassland. Half of the bushbuck and hartebeest observed occurred in grassland, but intermediate habitats and woodland made up about 25% of the observed animals each. Only a total of 7 bush duiker were observed along the transect lines but occurring mostly in woodland. At one occasion a group of sable was observed in woodland. The differences in habitat choice were significant (Chi^2-test, $p<0.001$, N=9,943). The general amount of puku observed in the different habitat remained almost unchanged in July 2009 and November 2010 (Figure 2-15); puku were observed in grassland to over 80%. This was supported by the results of Chi^2-test ($p=0.613$, N=4843).

In Kafue Region (Figure 2-12), the amount of observed animals in woodland was about the same for puku and impala. More than 50% of the observed puku were encountered in grassland, for impala 30% were observed in grassland; inversely the pattern for intermediate habitat. Kudu were encountered to 2/3 in intermediate habitats. Waterbuck were observed to more than 80% in grassland. The numbers of observed bush duiker, grysbok, hartebeest and reedbuck were low. While bush duiker and grysbok were encountered in intermediate habitats and woodland, respectively, hartebeest and reedbuck were observed only in grassland. Bushbuck were seen in all habitat types. The differences in habitat choice were significant (Chi^2-test: $p<0.001$, N=2,062). Within Kafue Region, the observations of puku and impala can be split up for the two subregions (Figure 2-13). In PPKR, both puku and impala were observed mostly in intermediate habitats, followed by grassland and woodland. This similar pattern in distribution over the habitat types were supported by the Chi^2-test: the differences were not significant ($p=0.141$, N=1,004). In Kafue NP, puku were observed to 70% in grassland, whereas impala were observed to almost similar amounts in all habitat types. These differences between puku and impala in Kafue NP were significant (Chi^2-test: $p<0.001$, N=970). There were significant differences between puku and impala in the two subregions, respectively (Puku in PPKR vs. puku in Kafue NP: Chi^2-test: $p<0.001$, N=845, impala in PPKR vs. impala in Kafue NP: Chi^2-test: $p<0.001$, N=1,129).

Comparing the amount of puku observed in the cool dry season in the different habitat types between the study regions, i.e. Kasanka July, PPKR and Kafue NP, the differences turned out significant (Chi²-test: $p<0.001$, N=11,699). In Kasanka NP more puku were observed in grassland, contrary in PPKR where less puku were observed in this habitat. In PPKR, compared to Kasanka and Kafue NP, more puku were observed in intermediate habitats.

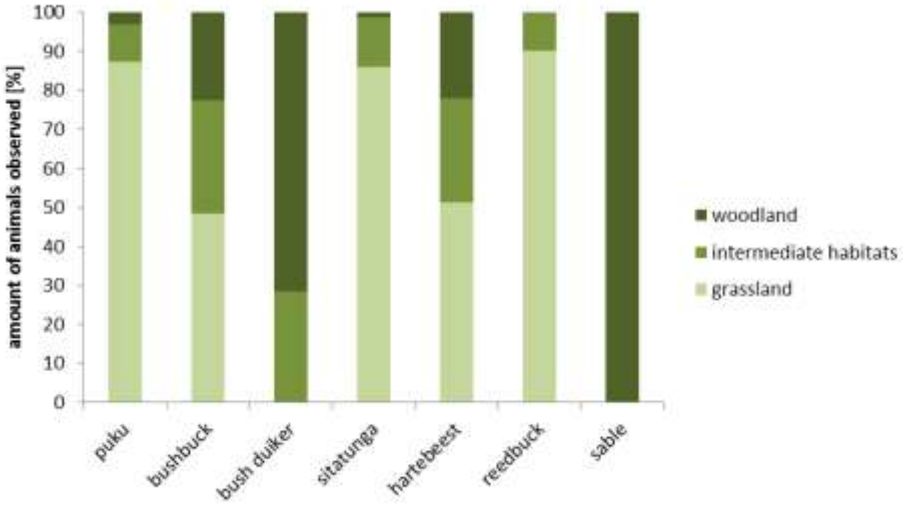


Figure 2-11: Amount of observed animals in the different habitat types in Kasanka NP. All surveys in Kasanka NP are shown. Differences in habitat choice were significant (see text); N=9,725 for puku, N=31 for bushbuck, N=7 for bush duiker, N=79 for sitatunga, N=41 for hartebeest, N=41 for reedbuck, N=19 for sable.

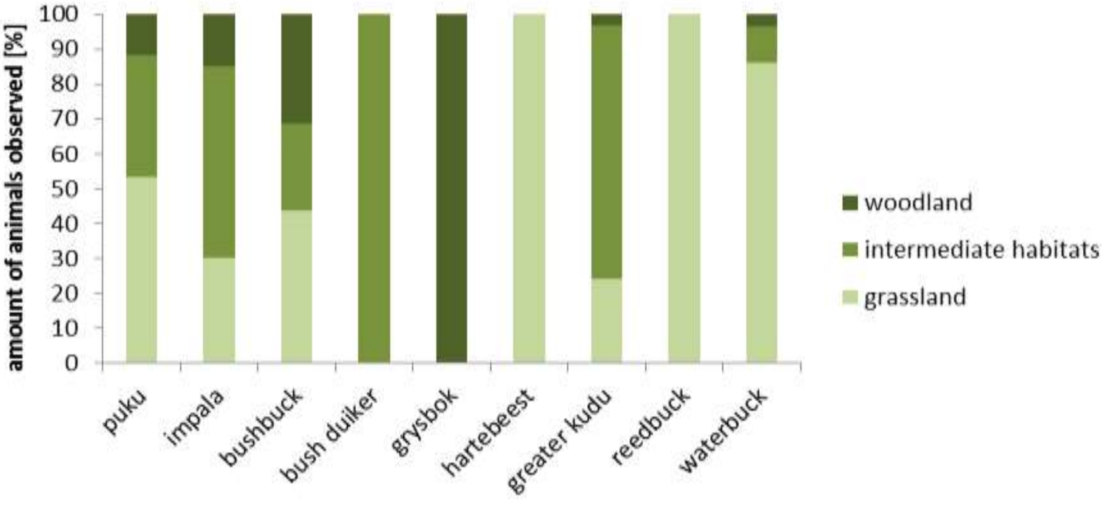


Figure 2-12: Amount of observed animals in the different habitat types in Kafue Region. Differences in habitat choice were significant (see text); N=845 for puku, N=1,129 for impala, N=16 for bushbuck, N=5 for bush duiker, N=1 for grysbok, N=3 for hartebeest, N=33 for greater kudu, N=1 for reedbuck, N=29 for waterbuck.

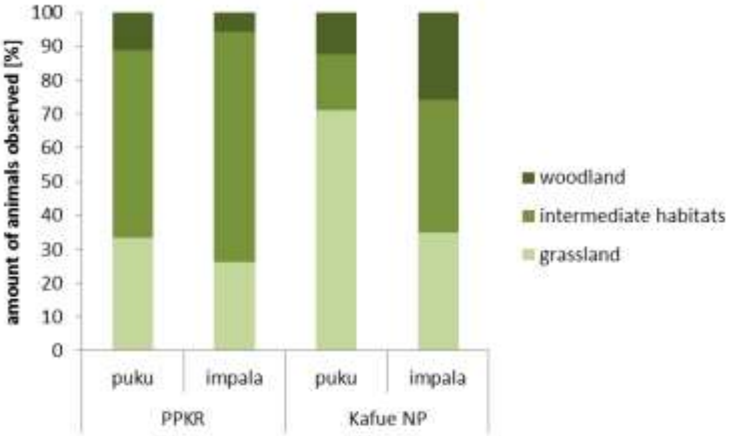


Figure 2-13: Amount of observed puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) in % in the different habitat types separated according to the subregions PPKR and Kafue NP. Differences were significant within puku, within impala, and between puku and impala in Kafue NP, they were not significant between puku and impala in PPKR; for puku N=397/448 in PPKR/Kafue NP; for impala N=607/522 in PPKR/Kafue NP.

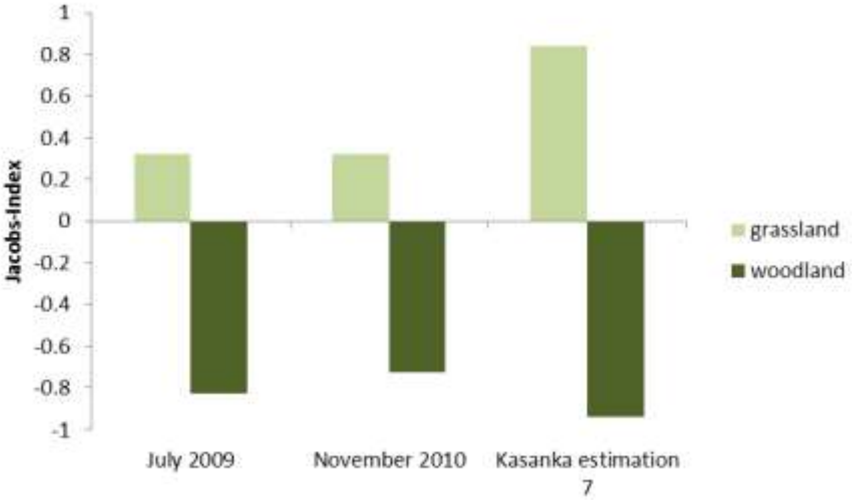


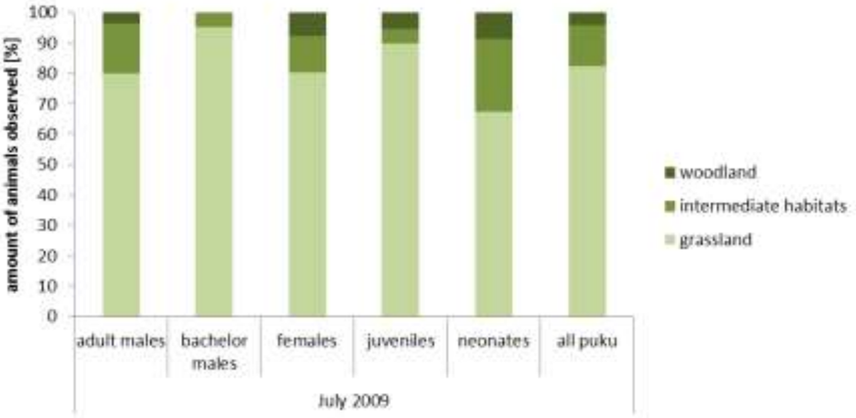
Figure 2-14: Jacobs-Index of habitat preferences of puku (*Kobus vardonii*) for grassland and woodland. It is based on the amounts of observed animals in the surveys of July 2009, November 2010 and on the results of Kasanka estimation 7, amount of available vegetation according to Kennedy et al. 2008.

Habitat preferences of puku in Kasanka NP were calculated via the Jacobs-index (Figure 2-14). Through all seasons and indifferent whether observed animals or estimated densities underlay the analysis, grassland was preferred and woodland was avoided (Figure 2-14). The amount was different: Based on the number of observed puku, grassland was preferred in July and November with a Jacobs-index value of about 0.32 in the two months. Woodland was rather strongly avoided in July with Jacobs-index value of -0.83 and less, but still avoided in November with -0.72. Based on the results of Kasanka-Estimation 7, the values of the Jacobs-index were higher in both directions.

In both Kasanka NP and Kafue region, the observations for puku in different habitat categories were split up to check for differences in sexes and age classes. The same was done with the observation of impala in Kafue region. As only two neonate puku were observed in Kafue Region this group is not presented here. In Kasanka NP, all classes of puku, adult males, bachelor males, females, juveniles and neonates were observed to a high extent in grassland (Figure 2-15). The only case when observations in grassland made up less than 70% were the observation of neonate puku in July 2009. Bachelor males were observed in fewer numbers in intermediate habitats and woodland. These differences in July were significant (Chi^2-test: $p<0.001$, $N=1,238$). Contrarily, the observations in November 2010: Differences between sexes and age classes concerning the observation in different habitat categories were less marked and were not significant (Chi^2-test: $p=0.107$, 1,862). In PPKR, all sex and age classes of puku distributed on grassland and intermediate habitats where about 90% of each class were observed (Figure 2-16). While more than 40% of the adult and bachelor males were observed in grassland, not even 30% of the female and juvenile puku were observed here. The differences in habitat use between sex and age classes of puku in PPKR were significant (Chi^2-test: $p=0.012$, $N=361$). In contrast, the observed distribution of the sex and age classes of puku over the habitat types resulted in no significant differences in Kafue NP (Chi^2-test: $p=0.052$, $N=436$). However, adult males were observed to a lesser extent in intermediate habitats and woodland than the other groups.

In Kasanka NP, generally, puku were observed to a higher degree in grassland at 10 am and at 4 pm (Figure 2-17). At 7 am and at 1 pm up to 30% of the puku were observed in intermediate habitats or woodlands. These differences were more exhibited in July 2009 and were only significant for this survey (Chi^2-test for July 2009: $p<0.001$, $N=2,135$; Chi^2-test for November 2010: $p=0.329$, $N=2,708$). In both subregions in Kafue Region puku were seen to high amount in grassland at 4 pm (Figure 2-18). In PPKR, puku were observed to less than 30% in grasslands during the other times of the day. These differences in habitat use at different times of the day were significant in PPKR (Chi^2-test: $p<0.001$, $N=397$). In Kafue NP, puku were observed to the highest amount in grassland at 7 am the amount of puku in grassland was decreased at 10 am and 1 pm. These differences during the day in habitat choice in Kafue NP were significant (Chi^2-test: $p<0.001$, $N=448$). For impala, differences were significant within both subregions as well (PPKR: Chi^2-test: $p<0.001$, $N=607$; Kafue NP: Chi^2-test: $p<0.001$, $N=522$). In both subregions impala were observed in intermediate habitats or woodlands especially at 1 pm. Further, impala were less frequent in the more covered habitat types at 4 pm, unlike puku. However, during the day the amount of woodland use is different between the study regions, these differences in the observations in the habitat categories between PPKR and Kafue NP were significant (Chi²-test: $p<0.001$, N=1,129).

A



B

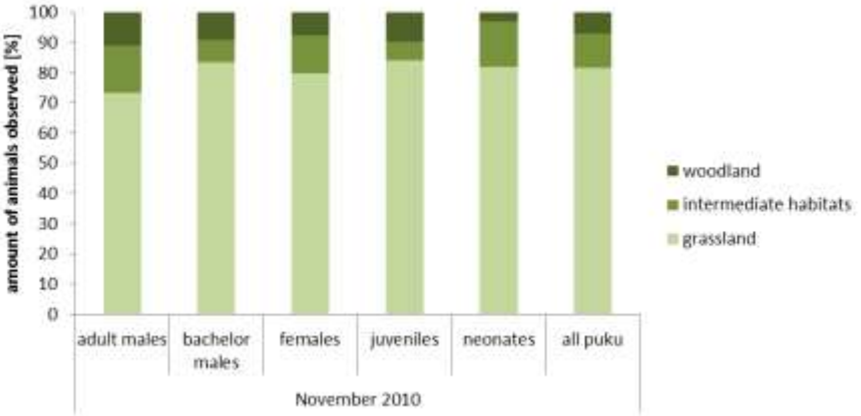


Figure 2-15: Observation of puku (*Kobus vardonii*) in Kasanka NP split up according to sex and age classes in the different habitat categories in July 2009 (A) and in November 2010 (B). Differences were significant in July only. In July 2009: N=344/209/364/275/46/2,135, in November 2010: N=495/164/963/207/33/2,708 (adult males/bachelor males/females/juveniles/neonates/all puku).

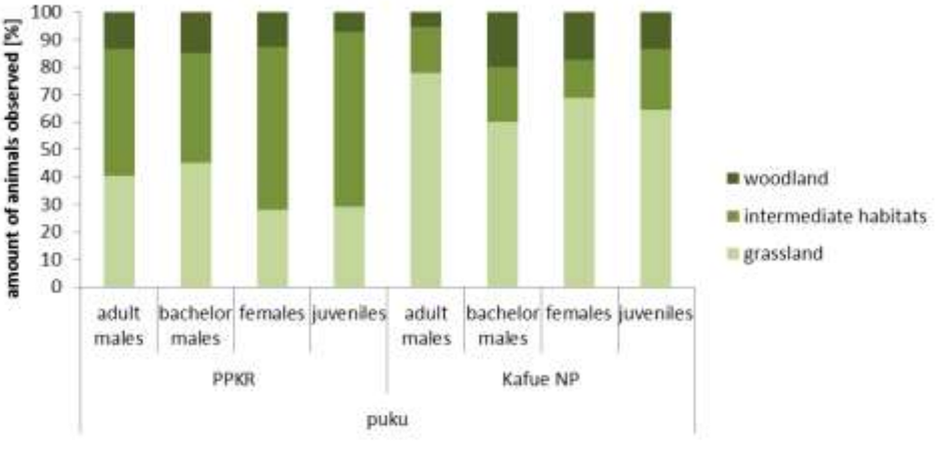


Figure 2-16: Observation of puku (*Kobus vardonii*) in Kafue region split up according to sex and age classes in the different habitat categories. Differences were not significant within puku in PPKR only. In PPKR: N=37/20/235/69, in Kafue NP: N=145/10/236/45 (adult males/bachelor males/females/juveniles).

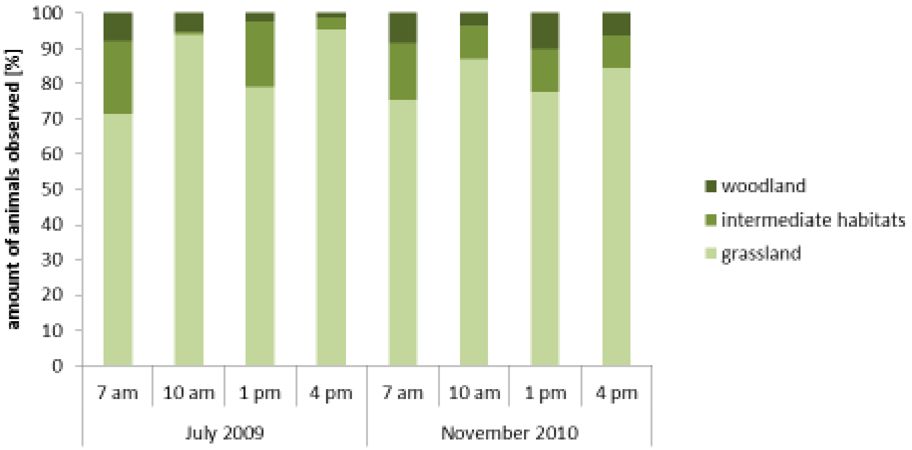


Figure 2-17: Habitat choice of puku (*Kobus vardonii*) in Kasanka NP at different times of the day during the survey in July 2009 and in November 2010. Differences were significant within July 2009 only. In July 2009: N=685/287/671/491, in November 2010: N=529/624/701/854 (7 am/10 am/1 pm/4 pm).

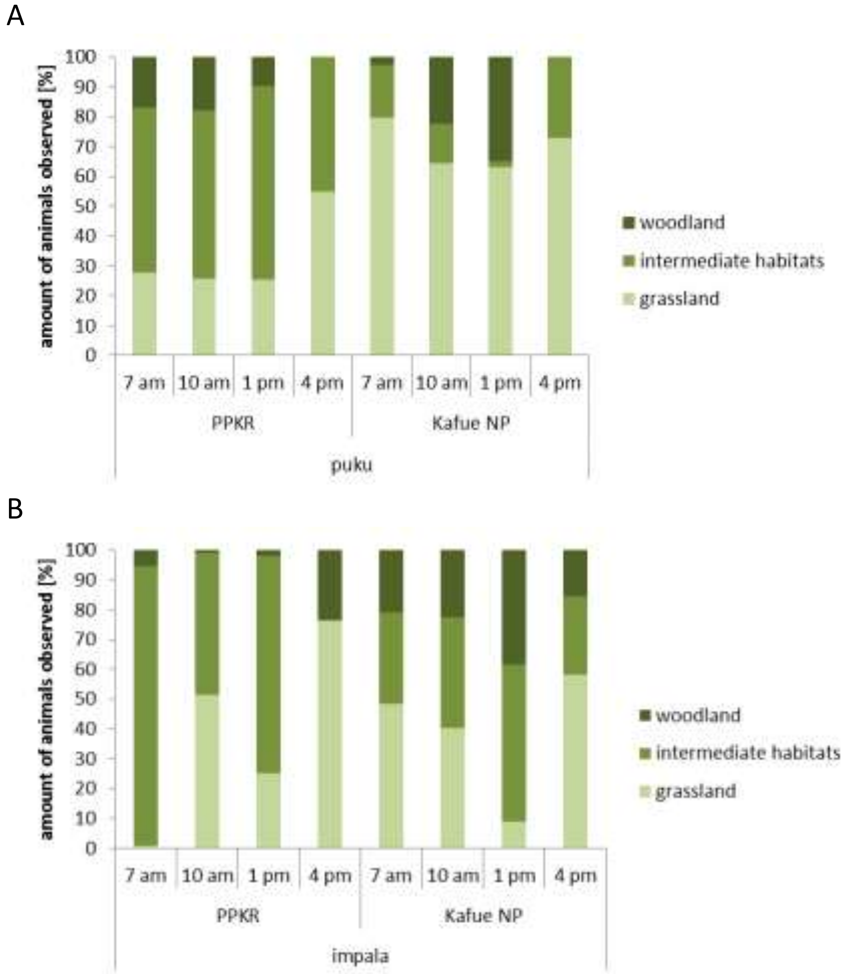


Figure 2-18: Habitat choice of puku (*Kobus vardonii*) (A) and impala (*Aepyceros melampus*) (B) in Kafue region at different times of the day. Differences were significant within puku in PPKR and Kafue NP as well as within impala in both subregions. For puku PPKR: N=94/101/102/100, for puku in Kafue NP: N=119/90/92/147, for impala in PPKR: N=240/105/190/72, for impala in Kafue NP: N=62/183/167/110 (7 am/10 am/1 pm/4 pm).

When comparing the observations of puku in different habitat categories at different times of the days between the three study regions (for Kasanka only observations in July are considered), the differences were significant (Chi^2-test: $p<0.001$, N=2,135). The pattern of puku in Kasanka NP and Kafue NP were more alike than habitat use of puku in PPKR and Kafue NP. In both Kasanka NP and Kafue NP, puku were observed to a higher extent in the more covered habitat, respectively, at 1 pm, whereas they were in grasslands at 10 am. In all three regions, puku were observed in higher numbers in habitat 1 at 4 pm, though less marked in PPKR.

2.3.3 Population estimates with DISTANCE

CDS as well as MCDS engine were tested for estimations based on the data of Kasanka NP and Kafue Region. Estimations of all antelopes, puku and impala based on the respective observations were compared for model fit and estimation characteristics. For all estimation the AIC were very close but they were lower for MCDS engine model fitting. The estimations computed with MCDS engine were more precise as they show smaller %CV values (see also Table A. 11, Table A. 12). The general model of the detection function showed no obvious differences in shape between the two estimations in puku (see also Figure A. 1, Figure A. 3). Only in MCDS engine, the detections are related to covariates which thus resulted in three different detection functions for puku estimation: one for each habitat type (see also Figure A. 2, Figure A. 4); the shape of the detection function remained the same whereas the scale changed. Compared to habitat 2 and especially habitat 3, for habitat 1, the detection probability diminished slowly towards higher the distances. The values of AIC and %CV were slightly better for the MCDS engine in the estimation for all antelopes and for puku and the MCDS engine is used.

All the resulting densities presented in this paragraph do not represent the species' densities in the entire national parks, but in the area surveyed by the transect lines. In Kasanka NP, based on all antelope sightings from all four survey periods, puku had an estimated density of 43.40 animals/km^2 along the transect lines and were by far the antelope with the highest density (Table 2-7, Kasanka-Estimation 2). All other antelopes reached estimated densities lower than 0.5 animals/km^2. These differences were significant (Chi^2-test: $P<0.001$, N=8). The D %CV (% coefficient of variation of the density) and the ER %CV (% coefficient of variation of encounter rate) are relatively low for puku, sitatunga and bushbuck – all under 40%. Contrastingly, the D %CV and ER %CV in the other antelopes

are high – especially in reedbuck, hartebeest, orebi and sable. Except for sable, the other antelopes reach low estimated group sizes between 1 and 2.56 animals. E(S) %CV (estimated group size variation) is generally low, reaching only high values for hartebeest. In Kafue Region, according to the pooled estimation of all antelopes (Kafue-Estimation 1), impala had the highest density of the antelope species, followed by puku. The differences between all antelopes were significant (Chi²-test: $p<0.001$, $N=9$). The estimations for puku and impala had relatively low D %CV. The estimation resulted in low densities for all other antelopes species and they reached high D %CV, especially for duiker and hartebeest. Considering ER all antelope species, except puku and impala, reached low values but high values in ER %CV. Except for waterbuck and hartebeest, the E(S) %CV was relatively low for the antelopes presented here.

Table 2-7: Estimation of population densities for antelope species in the area surveyed by the transect lines in Kasanka NP (Kasanka-Estimation 2) and in Kafue Region (Kafue-Estimation 1). The resulting densities do not represent the species' densities in the entire national parks, but in the area surveyed by the transect lines.

study region	antelope species	D	D %CV	E(S)	E(S) %CV	ER	ER %CV
Kasanka NP	puku (*Kobus vardonii*)	43.40	32.48	10.02	4.89	9.32	32.03
	sitatunga (*Tragelaphus spekii*)	0.39	40.46	2.11	9.07	0.40	39.36
	bushbuck (*Tragelaphus scriptus*)	0.14	36.06	1.14	5.37	0.26	35.58
	reedbuck (*Redunca arundinum*)	0.08	66.96	1.22	16.69	0.14	64.81
	Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*)	0.05	61.36	2.56	38.78	0.05	47.50
	orebi (*Ourebia ourebi*)	0.00	98.28	1.0	-	0.01	98.26
	bush duiker (*Sylvicapra grimmia*)	0.03	45.60	1.0	-	0.06	45.55
	sable (*Hippotragus niger*)	0.08	98.28	19.00	-	0.01	98.26
Kafue Region	puku (*Kobus vardonii*)	27.44	36.48	5.99	8.56	3.56	35.12
	impala (*Aepyceros melampus*)	34.95	35.92	10.91	13.86	2.49	32.76
	bushbuck (*Tragelaphus scriptus*)	0.55	62.42	1.23	13.50	0.35	60.74
	greater kudu (*Tragelaphus strepsiceros*)	1.10	64.29	4.57	20.17	0.19	60.84
	reedbuck (*Redunca arundinum*)	0.03	102.17	1.00	-	0.03	102.05
	waterbuck (*Kobus ellipsiprymnus*)	0.79	80.88	3.83	45.39	0.16	66.75
	Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*)	0.10	105.01	1.50	33.33	0.05	99.46
	Sharpe's grysbok (*Raphicerus sharpei*)	0.03	99.58	1.00	-	0.03	99.46
	bush duiker (*Sylvicapra grimmia*)	0.17	61.58	1.25	20	0.11	58.03

D: estimate of population density (density of individuals) [animals/km²]; D%CV: % coefficient of variation of D; E(S): expected cluster size [animals]; E(S) %CV: % coefficient of variation of expected cluster size; ER: Encounter rate [number of observed objects/total length of transect lines]; ER %CV: % coefficient of variation of ER

In Kasanka NP, puku reached different local population densities along the different transect lines that ranged between zero and 149.39 animals/km² (Table 2-8, Kasanka-Estimation 5). For all survey periods puku reached by far the highest local population densities along the Puku-Loop transect line along Kasanka River. Here, the local population density increased from July to August 2009 and from October to November 2010. Highest population density was reached in November 2010, 149.39 animals/km². The transect line with the second highest estimated densities was Fibwe. Remaining almost stable in 2009, local density was highest in November 2010, almost 80 animals/km². Along the Wasa transect line, the local population density was relatively high, too. Medium densities of puku were estimated for the transect lines Mulembo, Kafubashi and Katwa ranging up to 21.99 animals/km² for Katwa in November 2010. The local population density along Kafubashi was highest in October 2010. Luwombwa, Chikufwe and Nafulwe showed very low to zero population densities. Generally, local population densities increased towards November 2010 – except for the transect line Kafubashi. Kasanka Estimation 5 had a general low D %CV, 5.31, common for all transect lines. Expected cluster size, E(S) was 10.16 for all transect lines with 4.55 %CV. Encounter rates were different for each transect lines during each survey and thus result in zero %CV. Regarding the estimation of puku densities in the different habitat types (Kasanka Estimation 7, Table 2-8), it turned out that puku reached by far the highest density, 36.15 animals/km² in grassland. Puku occurred in the other habitat types, but in lower densities. Analyses with the aim of getting estimated densities per habitat in different survey periods turned out in very high D %CV and thus are not presented here.

Based on the population estimates for the habitat types, an extrapolation of the number and general population density of puku was possible for Kasanka NP. This resulted in an estimated population size of 5037.63 (3,267.59-7,237.53) puku. A general population density of 12.92 puku/km² was calculated (Table 2-9).

Table 2-8: Estimated population densities of puku (*Kobus vardonii*) in Kasanka NP for different transect lines, habitats and times of the day. Abbreviations see Table (Table 2-7), * transect line not surveyed at 4 pm, ** transect line surveyed twice

survey		D	D %CV	E(S)	E(S) %CV	ER	ER %CV	Kasanka-Estimation No.
	transect lines							5
2009-July	Luwombwa	1.20	5.31	10.16	4.55	0.31	0	
	Chikufwe	0	-			0		
	Nafulwe	0	-			0		
	Katwa	8.25	5.31			2.14		
	Kafubashi	2.40	5.31			0.63		
	Puku-Loop**	117.70	5.31			30.59		
	Mulembo*	11.15	5.31			2.90		
	Fibwe*	49.54	5.31			12.87		
	Wasa*	19.59	5.31			5.09		
2009-August	Chikufwe	0.61	5.31			0.16		
	Katwa	1.37	5.31			0.36		
	Puku-Loop	139.58	5.31			36.28		
	Fibwe*	47.77	5.31			12.41		
2010-October	Luwombwa	0	-			0		
	Katwa	10.99	5.31			2.86		
	Chikufwe	0				0		
	Kafubashi	6.01	5.31			1.56		
	Puku-Loop	113.17	5.31			29.41		
2010-November	Luwombwa	0	-			0		
	Chikufwe	0	-			0		
	Nafulwe	0	-			0		
	Katwa	21.99	5.31			5.71		
	Kafubashi	2.40	5.31			0.63		
	Puku-Loop	149.39	5.31			38.82		
	Fibwe	79.61	5.31			20.69		
	Wasa	37.78	5.31			9.82		
	different habitats							7
all surveys	grassland	36.15	36.00	10.86	5.09	8.23	35.42	
	intermediate habitats	4.27	32.68	7.06	11.19	1.29	29.70	
	woodland	2.96	38.30	5.80	16.11	0.53	32.42	

Table 2-9: Extrapolation of the population size of puku (*Kobus vardonii*) in Kasanka NP based on the estimated densities for different habitat categories.

	woodland	**grassland**	**total**
amount of area [%] KENNEDY et al. 2008	70	30	100
absolute area covered [km²] according to KENNEDY et al. 2008	273	117	390
population density of puku [animals/km²]	2.96 ± 1.16	36.15 ± 12.42	12.92 (8,386 – 17,867)
population size [animals]	808.08 491.31 - 1,124.85	4,229.55 2,776.28 - 5,682.82	5,037.63 3,267.59 - 7,237.53

Local population densities of puku in Kafue Region (Kafue-Estimation 2, Table 2-10) ranged between 0 on transects without any sightings and 110.64 animals/km². High local population densities were found along the transect lines Hippo, Kafue North or Camp. Kafue South, Plains or Dambo showed only low population densities. Zero population densities resulted for Miombo East, Miombo West and Kopje and low population densities were given for Main Road and Airstrip. ER was given for each line with a maximum of 13.33. As transects were treated separately, no variance was calculated. Thus, D %CV was low. In the repetition of the transect lines River and Plains in September, changes in local population densities were apparent (Kafue-Estimation 5, Table 2-10). Along the transect line River, the estimated population density of puku almost doubled. The estimated population density along the transect line Plains decreased. The overall D %CV was low.

Kafue Estimation 21 (Table 2-10) gave estimated densities for the different habitat categories. Grassland had the highest density of puku, 14.66 animals/km², followed by intermediate habitats. By far the lowest density was given for woodland. The D %CV was highest for woodland. It was lowest for grassland. E(S) %CV and ER %CV followed this pattern. ER %CV was especially high for woodland.

Table 2-10: Estimated population densities of puku (*Kobus vardonii*) in Kafue Region for different transect lines, the progression of the cool dry season and habitats. Abbreviations see Table (Table 2-7), *transect line sampled thrice in September 2010

	D	D %CV	E(S)	E(S) %CV	ER	ER %CV	Kafue estimation no.
transect lines in PPKR							3
Kafue North	110.64	10.85	6.10	8.54	13.33	0	
Kafue South	17.17				2.07		
Between	30.17				3.64		
Miombo East	0				0		
Miombo West	0				0		
River	21.41				2.58		
Main Road	8.03				0.97		
Plains	13.38				1.61		
Kopje	0				0		
transect lines in Kafue NP							
Dambo	18.74				2.26		
Hippo	100.58				12.12		
Camp	60.64				7.31		
Airstrip	6.92				0.83		
progressing cool dry season (September)							5
River *	38.33	10.34	6.02	8.04	4.78		
Plains	10.34				1.29		
habitats							21
grassland	14.66	35.19	8.40	12.45	1.28	32.23	
intermediate habitats	10.58	48.11	4.85	12.71	1.60	45.91	
woodland	3.60	61.62	4.50	18.94	0.59	58.25	

Table 2-11: Estimation of population density of impala (*Aepyceros melampus*) for Kafue Region for different transect lines, the progression of the cool dry season and habitats. Abbreviations see Table (Table 2-7), *transect line sampled thrice in September 2010

	D	D %CV	E(S)	E(S) %CV	ER	ER %CV	Kafue Estimation No.
transect lines in PPKR							7
Kafue North	60.84	16.09	11.02	12.79	5.42	0	
Kafue South	30.98				2.76		
Between	10.21				0.91		
Miombo East	2.87				0.26		
Miombo West	4.88				0.43		
River	32.61				2.90		
Main Road	3.62				0.32		
Plains	32.61				2.90		
Kopje	7.49				0.67		
transect lines in Kafue NP							
Dambo	68.84				6.13		
Hippo	108.91				9.70		
Camp	8.64				0.77		
Airstrip	9.36				0.83		
progressing cool dry season (September)							9
River *	19.46	14.52	12.31	12.35	1.30	0	
Plains	62.56				4.19		
habitats							22
grassland	9.49	37.89	11.41	21.76	0.72	29.65	
intermediate habitats	18.06	35.78	12.74	20.58	1.23	27.82	
woodland	5.24	75.16	7.08	18.67	0.64	72.23	

Impala had their highest local density along Hippo where they reached almost 109 animals/km², thus 9 animals/km² more than puku (Figure 2-19). Interestingly, along the other transect line that parallel Kafue River, along Kafue North, impala density reached about 61 animals/km² only, whereas puku reached 111 animals/km², a density almost twice as high as those of impala. Along Between and especially along Camp, puku reached higher densities than impala. Impala were especially abundant along Dambo reaching a density of almost 69 impala/km² (versus about 19 puku/km²), but also along Plains, and to lesser extent along Kafue South and River. The observed differences between puku and impala concerning the local densities along the transect lines were not significant (Wilcoxon test: p=0.552, N=26).

Regarding the estimated density in the habitat categories, impala were most abundant in intermediate habitats (18.06 impala/km²), i.e. in long grass, the edge of woodlands, in light scrub- and woodlands (Figure 2-20). Here, they were more abundant than puku, and vice versa in grassland (9.49 impala/km²), the open grasslands. Impala were slightly more abundant than puku in woodland. However, only impala were observed, in low densities though, along Miombo East, Miombo West and Kopje that lead through miombo woodland.

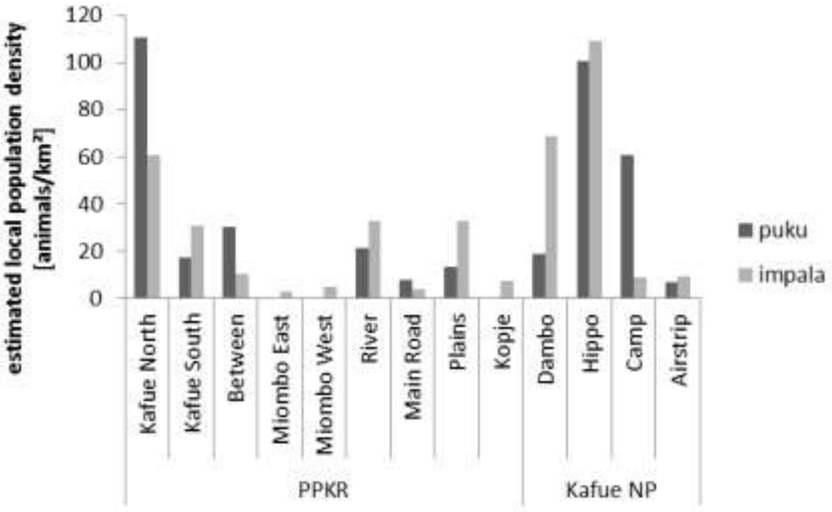


Figure 2-19: Comparison of estimated local densities for puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) along the transect lines in Kafue Region. The differences were not significant between antelope species (see text).

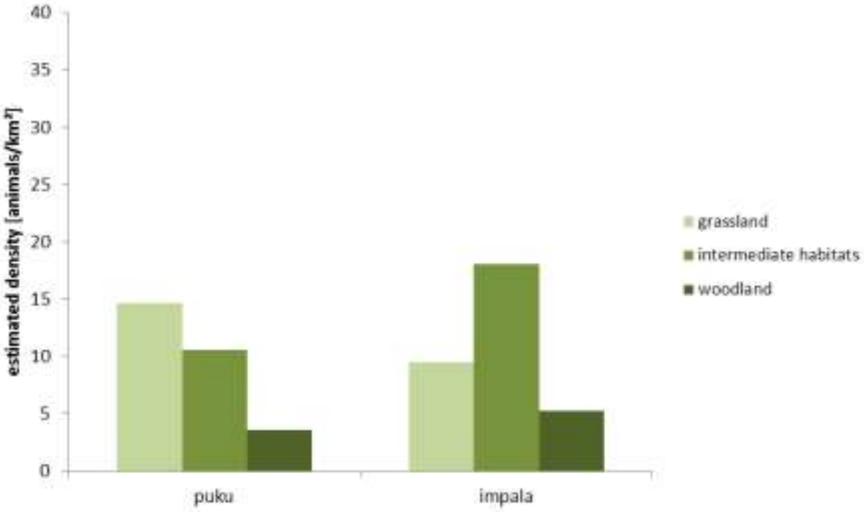


Figure 2-20: Comparing estimated densities of puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) in the three habitat categories in Kafue Region.

In Kasanka NP, the amount of observed animals and the resulting density of puku was by far highest in grassland, reaching 36.15 animals/km² (Figure 2-21). This was much more than in the other habitat categories. Contrastingly in Kafue Region, the gap between grassland and intermediate habitats concerning estimated density was not that big. Puku reached 14.66 animals/km² in grassland and 10.58 in intermediate habitats. Only the estimated value for woodland was about the same, about 3 to 4 animals/km², in the two study regions.

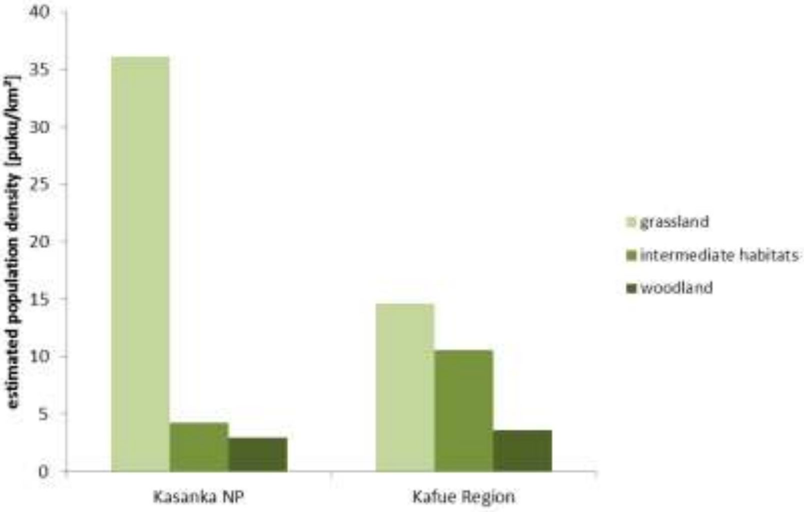


Figure 2-21: Comparing estimated density of puku (*Kobus vardonii*) in the three habitat categories in the two study regions.

2.3.4 Results of the camera-trap survey

The entire survey resulted in a Total TN of 924. 40 different camera-trap stations recorded a total number of 709 independent photographs showing mammals. Considering each study site, these numbers split up into a Total TN of 748 at 28 camera-trap stations for Kasanka NP; and a Total TN 176 at 12 different camera-trap stations for PPKR.

In Kasanka NP, the puku antelope had the highest RAI value (1.00) of all antelopes and all captured mammals (Table 2-12). The bushbuck reached a RAI of 0.54 half of the puku's value. All other antelope species, i.e. Lichtenstein's hartebeest, sitatunga and bush duiker reach RAI values below 0.10. In PPKR (Table 2-12), three antelope species reached relatively high RAI: these were the impala (RAI of 1.99), the puku (RAI of 1.35) and greater kudu (RAI of 0.83). Bushbuck reached a RAI of 0.51 as well as waterbuck. Differences in antelopes captured are visible: While impala were captured to a high number in PPKR, they were not seen in Kasanka NP at all. The same applies to waterbuck, greater kudu and sable antelope. The captures of Lichtenstein's hartebeest and sitatunga only took place in Kasanka NP.

In Kasanka NP, the puku antelope occurred in most of the focal areas and reached relatively high RAI (3.79 to 20.00) (Table 2-13). Only at Chikufwe, puku reached low RAI (0.26) and in Fibwe-Forest they were even absent. This opposes the puku to the reedbuck and hartebeest which both were only captured at Chikufwe and reached low RAI (0.09 and 0.26). In the two Fibwe focal areas, the RAI for bushbuck reached high values Fibwe-Forest, RAI reached 12.50. Bushbuck were not photographed at Katwa and Chikufwe. Sitatunga were only seen on camera-traps in the two Fibwe focal areas and their RAI reached 0.58 and 0.61. Bush duiker were detected at Kabwe and Katwa, reaching RAI of 1.55 and 0.76.

Table 2-12: RAI of bovid species detected by the camera-trap survey in the different study regions. The carnivore species detected and their RAI are presented in chapter 4.

mammal species	Kasanka NP	PPKR
puku (*Kobus vardonii*)	1.00	1.35
waterbuck (*Kobus ellipsiprymnus*)	-	0.51
common reedbuck (*Redunca arundinum*)	0.01	-
impala (*Aepyceros melampus*)	-	1.99
Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*)	0.01	-
bushbuck (*Tragelaphus scriptus*)	0.54	0.51
sitatunga (*Tragelaphus spekii*)	0.05	-
greater kudu (*Tragelaphus strepsiceros*)	-	0.83
bush duiker (*Sylvicapra grimmia*)	0.09	0.06
sable antelope (*Hippotragus niger*)	-	0.05
undetermined antelope, Bovidae	0.10	0.26

Table 2-13: RAI for bovid species at different focal areas within Kasanka NP

mammal species	Fibwe-Forest	Fibwe-Area	Kabwe	Puku-Loop	Katwa	Chikufwe
puku (*Kobus vardonii*)	-	4.73	11.09	20.00	3.79	0.26
common reedbuck (*Redunca arundinum*)	-	-	-	-	-	0.09
Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*)	-	-	-	-	-	0.26
bushbuck (*Tragelaphus scriptus*)	12.50	4.19	1.36	1.11	-	-
sitatunga (*Tragelaphus spekii*)	0.58	0.61	-	-	-	-
bush duiker (*Sylvicapra grimmia*)	-	-	1.55	-	0.76	-

Table 2-14: RAI of bovid species at the artificial saltlick and waterhole.

mammal species	saltlick	waterhole
puku (*Kobus vardonii*)	-	220.00
waterbuck (*Kobus ellipsiprymnus*)	-	-
impala (*Aepyceros melampus*)	120.00	240.00
bushbuck (*Tragelaphus scriptus*)	-	60.00
greater kudu (*Tragelaphus strepsiceros*)	120.00	10.00
bush duiker (*Sylvicapra grimmia*)	-	-
sable antelope (*Hippotragus niger*)	-	-

The camera trap stations at the artificial saltlick and at the waterhole near Kaingu Lodge (Table 2-14) were turned on for the same amount of trap-nights, i.e. 11 camera trap days. With a RAI of 120, both impala and greater kudu were most abundant at the saltlick. The impala reached the highest RAI at the waterhole with 240, followed by the puku reaching a RAI of 220. There was no antelope that would only be detected at the saltlick. Only the other way round, during the survey the bushbuck and the puku used the waterhole but not the saltlick.

2.3.5 Social organisation of the puku

A first general approach (Table 2-15) shows that groups of puku were larger in Kasanka NP than in Kafue Region. Maximum and average of observed group sizes were much larger in Kasanka NP. When comparing different survey periods in Kasanka NP (Table 2-15, Figure 2-22 A), the largest group size was recorded in November 2010. But generally, more large groups were encountered in July, resulting in a mean group size being larger. These differences were not significant (KS-test: p=0.382, N=534). In Kafue Region (Figure 2-22 B), the distribution of group sizes was similar in PPKR and Kafue NP but not significant (KS-test: p=0.999, N=154). Although the largest group size was recorded in Kafue NP, group sizes in PPKR were slightly larger, as also shown by the mean values (Table 2-15). In the cool dry season, larger group sizes were observed in Kasanka NP than in Kafue Region (Figure 2-22 C). When considering the mean value in July in Kasanka NP it was almost double the mean values in Kafue Region. These differences between the study regions concerning the observed group sizes were significant (KS-test: N=349, p=0.018).

Table 2-15: Statistics about the observed group sizes of puku (*Kobus vardonii*) in the study regions

study region	**Kasanka NP**		**Kafue NP**	
			PPKR	**Kafue NP**
survey period	**July 2009**	**November 2010**	**July/August 2010**	**August 2010**
mean value (± SE)	10.47 (± 0.95)	8.21 (± 0.67)	5.93 (± 0.68)	5.74 (± 0.67)
minimum value	1	1	1	1
maximum value	104	169	25	37
modal value	1	1	1	1

Generally, small group sizes of 1 to 5 animals were observed most often in all study regions and during all survey periods and made up 50% or more of the sighted groups (Figure 2-23). Modal value was 1 in all study regions. Single puku made up more than 20% of the encountered groups; in Kasanka NP single puku were observed at 18%. Other group sizes were encountered in generally less than 10% of the sightings; only in Kafue NP, groups of two puku were observed in about 17% of the sightings. Large group sizes of more than 25 puku were observed only once in Kafue Region. These large group sizes were observed in both July and November in Kasanka NP and made up about 14% and 10% of the sighted groups, respectively. Speaking about the amounts of puku observed in the specific group sizes, the image is different: Less than 5% of all puku observed along the transect lines in each study region and survey period were encountered as single animals. In Kafue Region, most of the puku, more than 78% in the subregions, were encountered in groups of up to 15 animals. Less than 50% of the puku in Kasanka NP were encountered in the respective groups of up to 15 animals in the survey periods. Contrarily, 41% and 25% of the puku were encountered in group sizes with more than 25 animals.

Groups of puku encountered in the grassland (habitat category 1) showed the tendency of being larger than those in intermediate habitats of woodlands (habitat 2 or 3) (Figure 2-24). This was visible especially from the data collected in the survey carried out in July 2009 in Kasanka NP (Figure 2-24 A), where very large groups were observed in grassland only. Concerning group sizes observed in Kafue NP (Figure 2-24 D), the median value was higher in grassland than in the other habitat types. Differences were only significant for Kafue NP (KW-test: N=78, p=0.002) but not for the other surveys (July 2009: KW-test: N=204, p=0.093; November: KW-test: N=330, p=0.335; PPKR: KW-test: N=67, p=0.919).

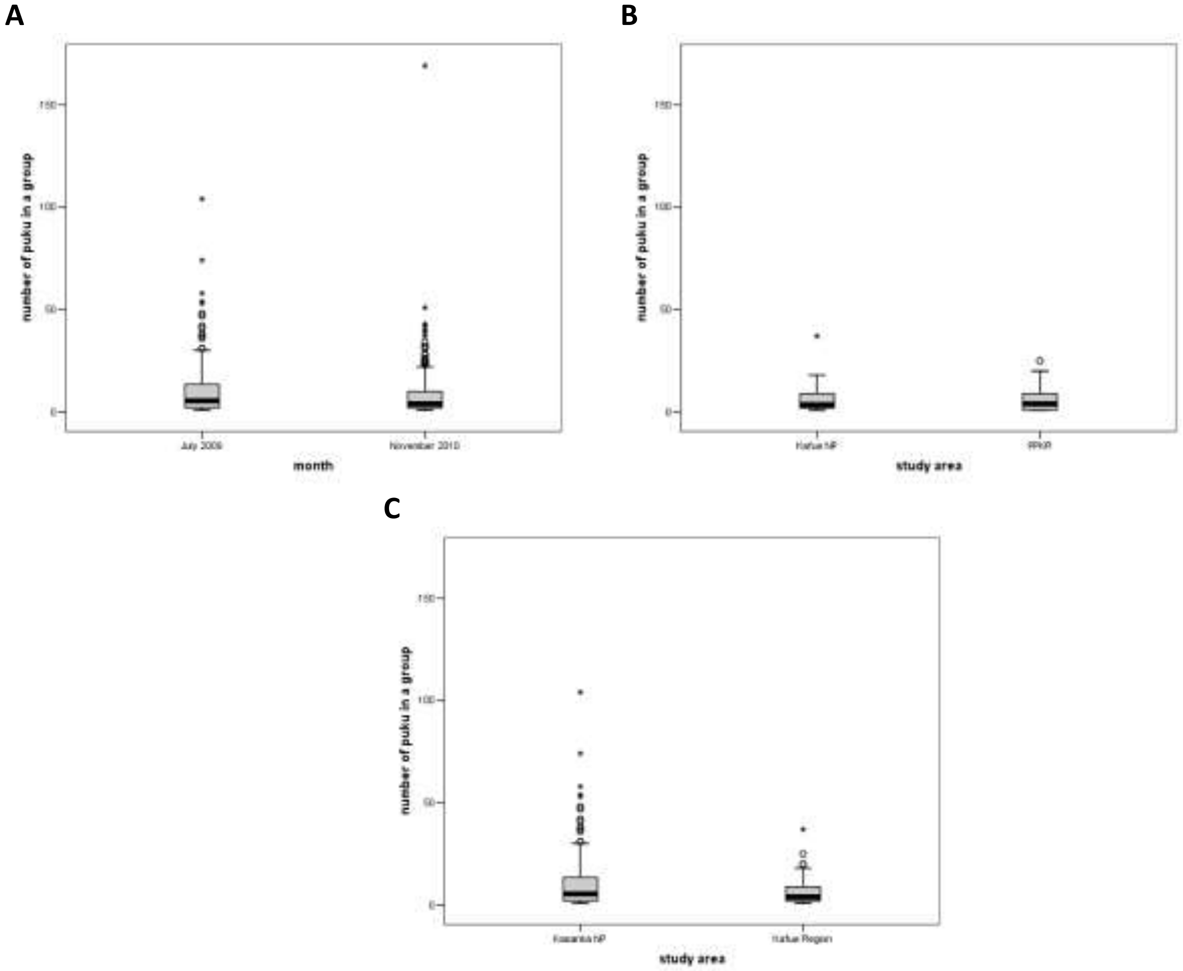


Figure 2-22: Boxplot comparing group sizes of puku (*Kobus vardonii*) in different surveys. They were observed during the surveys in July 2009 and in November 2010 in Kasanka NP (A), in Kafue NP and PPKR in the cool dry season 2010 (B) and in Kasanka NP (survey in July 2009) and Kafue Region (survey from July to August 2010) in the cool dry season (C). Differences are significant comparing Kasanka NP (July 2009) to Kafue Region (see text).

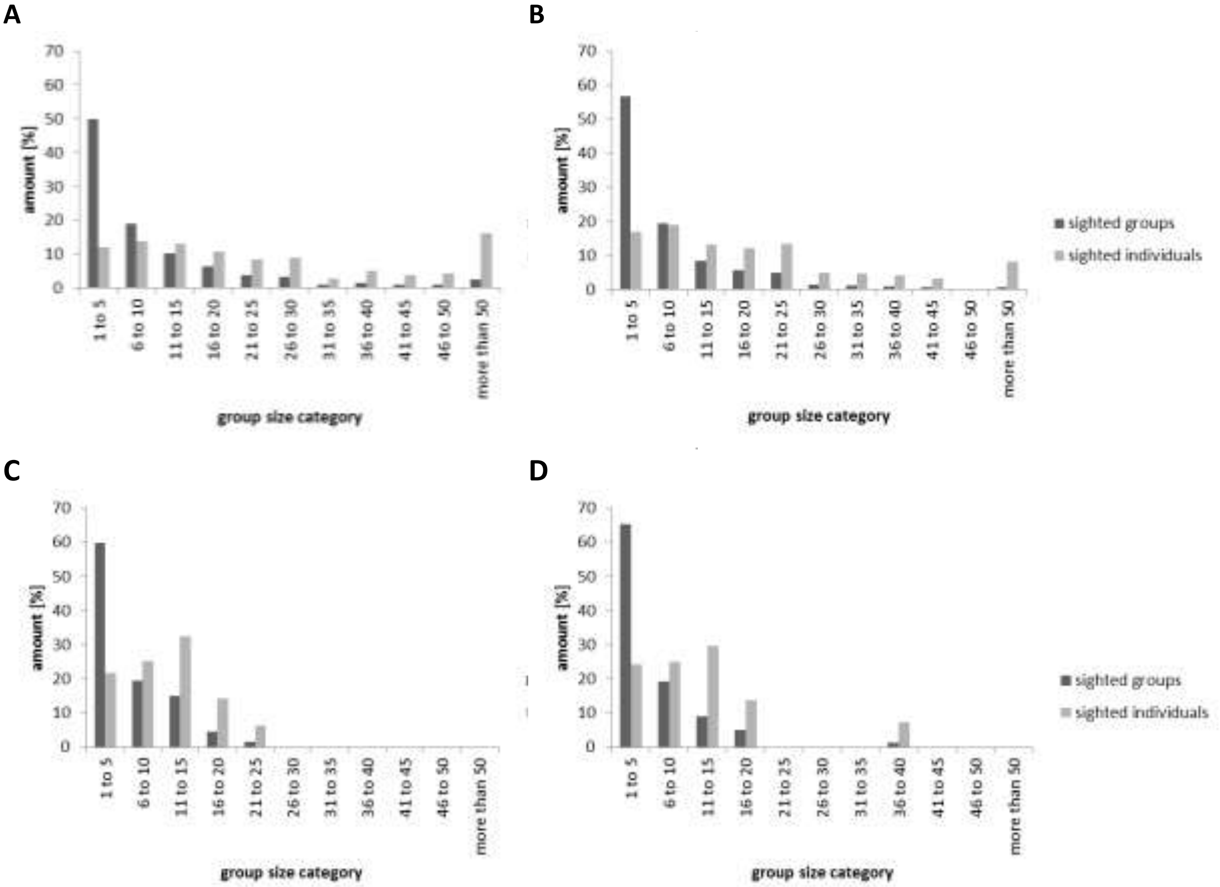


Figure 2-23: Group sizes of puku (*Kobus vardonii*) shown as the amount of sighted groups and the amount of sighted individuals in the respective groups in different surveys: in the cool dry season (July 2009) (A) and in the hot dry season (November 2010) (B) in Kasanka NP; in PPKR (C) and Kafue NP (D) in the cool dry season 2010.

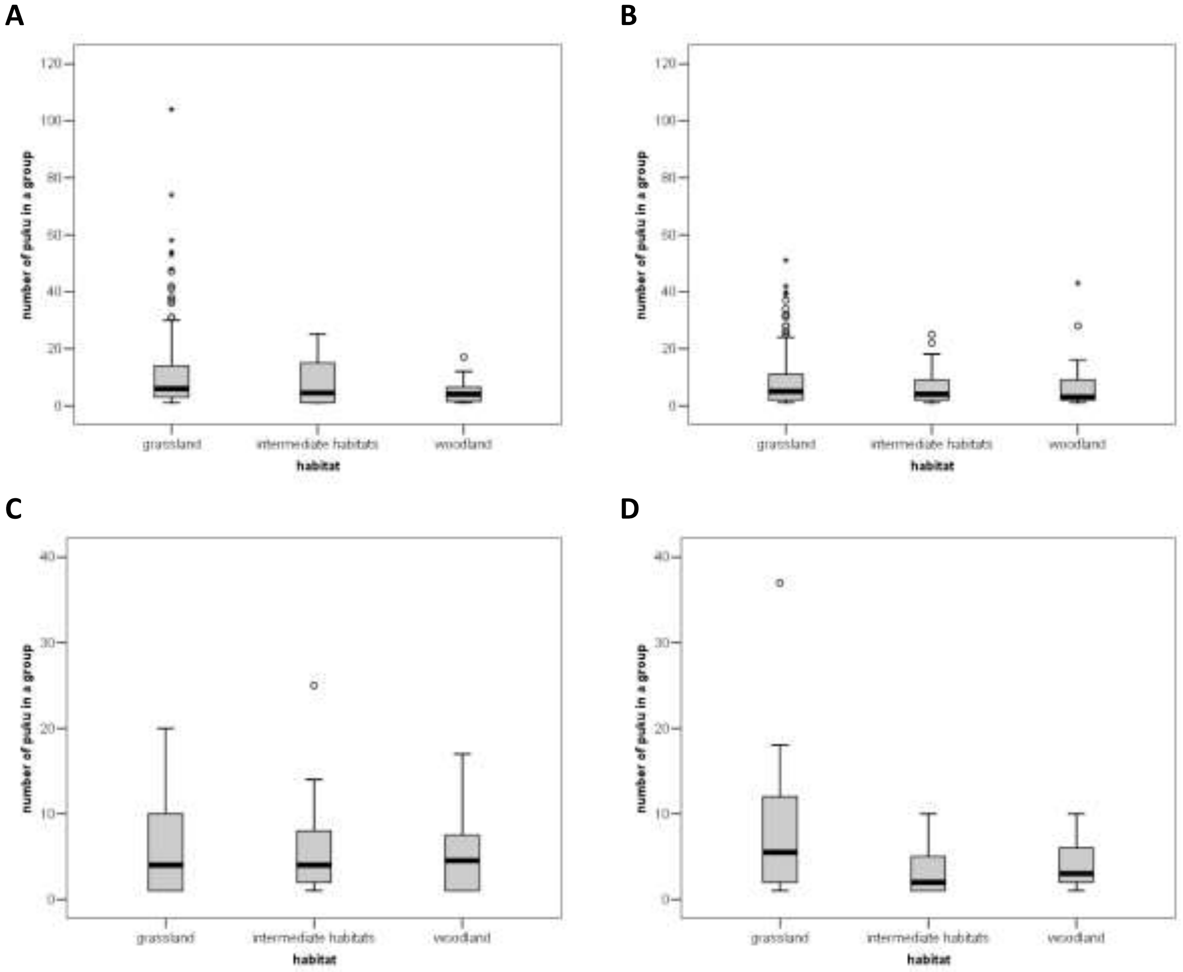


Figure 2-24: Boxplot comparing group sizes of puku (*Kobus vardonii*) observed in the different habitat categories during different surveys: during the survey in the cool dry season (July 2009) (A) and in the hot dry season (November 2010) (B) (the largest group in grassland is not shown in the figure) in Kasanka NP, in PPKR (C) and in Kafue NP (D) in the cool dry season 2010. Differences in each case are not significant (see text).

The general aspect of the group compositions sighted in the two study regions was similar (Table 2-16). Common observed groups were females, eventually accompanied by juveniles and/or neonates. These groups were especially frequent in PPKR. Adult males can and do accompany females and young puku; this was the second most frequent group composition observed. In Kafue NP, this was the most common group composition encountered. Except for Kafue NP, single adult males made up the most common group form. Single subadult males as well as groups of only subadult males were encountered in Kasanka NP, only. Groups comprising males only were not observed in PPKR at all. Groups of adult males, subadult males and juveniles were not encountered in Kafue Region contrary to Kasanka NP. Group compositions encompassing only juveniles and/or neonates were not observed in Kafue Region. The number of groups whose members could not all be classified into age and sex classes leading to groups with unknown group composition is higher in Kasanka NP than in Kafue Region. According to Wilcoxon-test, the differences observed were not significant neither within the study areas (Kasanka July 2009 vs. November 2010: N=17, p=0.687; PPKR vs. Kafue NP: N=17, p=0.433) nor between the study areas (Kasanka July 2009 vs. PPKR: N=17, p=0.234; Kasanka July 2009 vs. Kafue NP: N=17, p=0.619).

Table 2-16: Group compositions observed in puku (*Kobus vardonii*) in Kasanka NP and Kafue Region. The frequency of occurrence [%] refers to all groups whose members could be all determined according to the sex and age classes used in this study. The amount of unclassified groups refers to all groups sighted. Differences between seasons and study regions are not significant (see text). Juv = juveniles, Neo = neonate.

study region		**Kasanka NP**		**Kafue Region**	
				PPKR	**Kafue NP**
survey period		**July 2009**	**November 2010**	**July/August 2010**	**August 2010**
group composition		**Frequency of occurrence [%]**			
males	single adult male	24.77	25.84	25.45	20.83
	single subadult male	2.75	0.48	0	0
	2 or more adult males	8.26	7.18	0	9.72
	2 or more subadult males	5.50	1.44	0	0
	adult + subadult males (2 or more)	7.34	4.31	1.82	4.17
	adult + subadult males (2 or more) +juv	6.42	4.78	0	0
	1 adult male + 1 or more juv	3.67	0.48	1.82	5.56
females	single adult female	4.59	1.91	5.45	2.78
	single adult female + 1 juv/neo	0	1.44	0	1.39
	1 adult female + 2 or more juv/neo	0.92	0	1.82	2.78
	2 or more females (+ juv/neo)	13.76	20.10	34.55	13.89
juv/neo	single juv/neo	0.92	2.87	0	0
	2 or more juv/neo	6.42	0	0	0
pairs	adult male + adult females	0.92	2.39	0	5.56
	adult male + adult females + juv/neo	0.92	0.48	1.82	0
breeding group	1 adult male + 2 or more females (+juv/neo)	9.17	17.22	23.64	26.39
others	other group compositions	3.67	9.09	3.64	6.94
amount of all groups sighted that could not be classified		46.57	36.67	17.91	7.69

In Kasanka NP, when evaluating about the survey of all transect lines in July 2009, the ratio of females to males was biased towards the males (0.66), considering all males, and only slightly biased to the females, when considering adult males only (Table 2-17). Both values were more biased toward the females in November 2010 and were then similar to the values observed in Kafue NP. Looking closer at the situation along Puku-Loop, the sex ratio was very much biased towards all males in July and especially in August 2009 with 0.82

and 0.57 females to all males, respectively. Considering adult males, the ratio was biased towards females. This was similar in October 2010. Only in November 2010 the sex ratio was biased towards the females when considering all males and only adult males. The ratio of females to juveniles and neonates decreased from July to November, considering all transect lines as well as along Puku-Loop. In both cases the ratio dropped from about 1 to about 4.

In Kafue Region, the ratio of females versus males was biased towards the females (Table 2-17). The ratio of females to all males was 1.52 in Kafue NP and it was more biased to the females in PPKR with 4.12. The ratios were higher if only adult males were considered. Where there were about 3 young puku per females in PPKR, there were only about 5 young puku per female in Kafue NP, the lowest overall value of this ratio.

Table 2-17: Ratio of female puku (*Kobus vardonii*) versus all males (adult males and subadult males), adult males and versus juveniles and neonates in the study regions, for Kasanka NP in July 2009 and November 2010 and a more detailed look to the transect line Puku-Loop during all four surveys.

		ratio			**amount[%]**
		females:			
study area	**survey**	**all males**	**adult males**	**juveniles and neonates**	**unclassified**
Kasanka NP	July 2009	0.66	1.06	1.13	68.20
	November 2011	1.46	1.95	4.01	48.12
Kafue Region	PPKR	4.12	6.35	3.31	10.47
	Kafue NP	1.52	1.63	5.24	2.29
Puku-Loop	July 2009	0.82	1.49	1.11	61.33
	August 2009	0.57	1.19	1.42	38.76
	October 2010	0.86	1.50	2.18	44.33
	November 2010	1.37	1.86	3.65	50.79

In Kafue Region, two neonates were encountered in Kafue NP (Table 2-18). In Kasanka NP, neonate puku were encountered in different numbers and thus amounts during all surveys. Generally in Kasanka NP, but also along Puku-Loop, the highest number and the highest amount of neonates was encountered in July 2009. For Puku-Loop, numbers and the respective amounts of neonates were low in August and October. They increased in November, but were lower than in July 2009; this applies for Puku-Loop as well as entire Kasanka NP. While the amount of juvenile puku (Table 2-18) was about the same, about 20%, in PPKR and in Kasanka NP in July, the amount of juveniles was about half that value in Kafue NP. In Kasanka NP, the amount of juveniles decreased to about half values from July to November visible in the overall observation as well as along Puku-Loop only.

The amount of puku that could not be classified according to sex or age classes was much higher in Kasanka NP than in Kafue Region. While in Kafue Region the amount of unclassified puku did not exceed 11%, in Kasanka NP it did not fall below 48% for the survey of all transect lines or 38% along Puku-Loop, respectively.

Table 2-18: Number of observed neonate puku (*Kobus vardonii*) during the surveys in Kafue Region and for different survey in different seasons in Kasanka NP.

		neonates		juveniles
study area	**survey**	**observed number**	**amount of all classified puku [%]**	
Kafue Region	PPKR	2	0.55	19.01
	Kafue NP	0	0	10.32
Kasanka NP	July 2009	46	3.71	22.20
	November 2010	33	1.77	11.12
Puku-Loop	July 2009	40	3.93	25.02
	August 2009	6	0.34	20.00
	October 2010	7	0.55	16.97
	November 2010	26	2.41	11.29

In Kasanka NP, puku were observed in mixed groups with sitatunga and bushbuck, only. In 2009, during the two surveys along the transect lines, only one sighting resulted in a mixed group of puku and sitatunga along Fibwe. In 2010, during the two surveys along the transect lines, mixed groups were observed on 21 occasions along Puku-Loop only. Thus, in 6% of the sighted puku groups, another bovid species occurred in the same group. Puku were observed with sitatunga or bushbuck, on two occasions a group of puku, sitatunga and bushbuck was sighted. Puku were observed with sitatunga for another 17 times and with bushbuck on another two occasions. Mixed groups of puku and sitatunga contained 1 to 42 puku (mean 15.58 puku) and 1 to 4 sitatunga (mean 2.21).

In Kafue Region, groups of two bovid species were observed at 29 occasions – once a group composed of 3 bovid species (puku, impala and waterbuck) was sighted. 17 of the mixed groups were observed in Kafue-NP and 12 in PPKR. Mixed groups of puku and impala were observed most often. Regarding other antelopes, puku were seen together once with waterbuck and with bushbuck. Additionally, impala were observed two times with kudu. Concerning the amount of observed groups, in 21% of the sighted puku groups, another bovid species was observed in the same group, in 15% of the sighted puku groups this group was complemented by one or more impala. The mean group size of mixed groups of puku and impala was 17 animals, ranging from 2 to 71 animals. Mixed groups of puku and impala had very different amounts of both species (Figure 2-25): the amount of puku ranged from 1 to 20 animals (mean: 6.06 puku), the amount of impala from 1 to 67 animals (mean 10.91 impala). The number of puku and the number of impala in one mixed group did not correlate (Spearman-Correlation: r=-0.013, p=0.955, N=22). A number of 9 of the 22 groups of puku and impala were observed along Hippo.

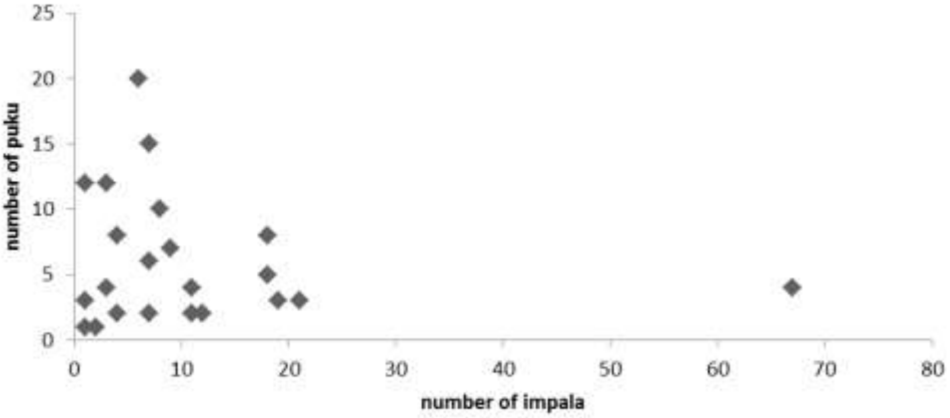


Figure 2-25: Scatter Plot showing the numbers of puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) in mixed groups of these bovid species.

2.3.6 Body condition of puku

In all study regions, the amount of puku that were in a good body condition was about 80% (Figure 2-26) and slightly higher in Kafue NP, closely followed by the observations in July 2009 in Kasanka NP. While the remaining evaluated puku in Kafue Region were almost exclusively characterised by a medium body condition, a poor body condition was observed in about 5% of the puku in both July and November in Kasanka NP.

Looking closer at the evaluated puku along Puku-Loop (Figure 2-27) a decrease in body condition was visible between July and August 2009. While about 80% of the puku evaluated had a good body condition, only slightly more than 60% were in this class in August. Especially the amount of the puku having a medium body condition increased whereas the amount of puku with poor body condition remained stable at about 5%. In October 2010 the body condition of the evaluated puku was generally better than in July 2009, especially visible by the low amount of puku in poor body condition. In November 2010, the distribution was similar to the observations from July 2009.

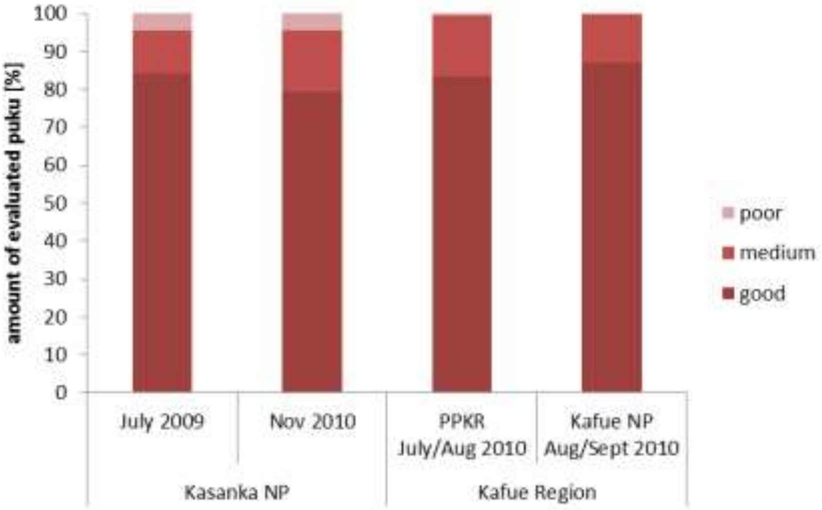


Figure 2-26: Body condition of puku (*Kobus vardonii*) in the different study regions and for Kasanka NP in the different survey periods.

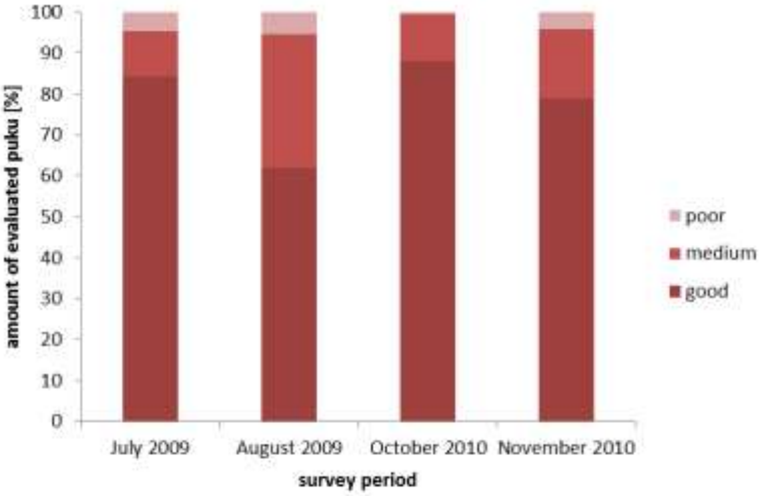


Figure 2-27: Body condition of puku (*Kobus vardonii*) along Puku-Loop during the four surveys.

In PPKR, the body condition of about half (48%) of the sighted puku could be evaluated. In Kafue NP, in only 40% of the puku an evaluation of the body condition was possible. The amount of puku whose body condition was not assessed was far higher in Kasanka NP. In July 2009 an evaluation was not possible in 85%; in November 2010 the amount of unevaluated puku was 76%. Along Puku-Loop, the amount of puku with unevaluated body condition was about 83% in July and August 2009 and 74% and 76% for October and November 2010, respectively.

2.4 Discussion

2.4.1 General remarks to line transects and DISTANCE analyses

A number of 60 to 80 sightings are supposed to be needed for reliable distance analyses (Barraclough 2000, Greenwood & Robinson 2009). Concerning the number of sightings of puku, this condition was largely fulfilled for all four surveys of puku in Kasanka NP. The number of sightings for each survey ranged from 163 to 375 and summed up to 1,082 for the entire study period. A total of 146 sightings of puku were made in the Kafue Region. Thus, the number of sightings lay within that recommended span. Other antelope species in Kafue Region as well as all other antelopes in Kasanka NP did not reach the minimum of 60 sightings.

The scatter plots, plotting the group size against the perpendicular distance, done as recommended by Buckland et al. (2001) lead to the following conclusion: Generally, for both Kasanka NP and Kafue Region, the observations of small groups and single animals were made at high perpendicular distance from the line. This is a sign for a good data collection. Largest perpendicular distances were 349 m in Kasanka NP and 590 m in Kafue Region. Thus the 1 km minimum distance between the transect lines was enough for Kasanka NP – but generally speaking for Kafue Region as well. The observation at 590 m perpendicular distance was one of the few observations above 400 m. Possible overlap of sightings between transect lines could thus be avoided; the area covered by the transect lines did not overlap.

By using the MCDS engine I counteracted the possible changes in detection probability in different habitat types. In MCDS engine, every sighting was related to one of three habitat categories, which means that the habitat composition – more or less patchily – of both study regions was taken into account. This covariate as described by Thomas et al. (2009) affected the scale of the detection function that dropped earlier for habitat 2 and especially for habitat 3 – in both study regions. Thus, detectability was not only assumed but verified to decrease from open habitat 1 to dense habitat 3: For both study regions the MCDS engine resulted in detection functions different in scales for the three habitat categories. The estimations based on MCDS were slightly more precise than those of the CDS engine and hence preferred. Because of the patchily composition of different habitats in the study regions, a stratification based on the situation of entire lines in specific habitat types, then analysed separately via CDS, was not carried out. This represents the basic difference in data analysis between Rduch (2008) and the current study.

Puku were less frightened compared to other antelope species so that they could be observed relatively easy and close to the line, although some observations were made far from the line. But due to sometimes high numbers of puku difficulties arouse in determining herd size and the centre of the herd. This fact was already stated by Ogutu et al. (2006) about surveying loose aggregations of Thomson's gazelle (*Gazella thomsoni*), wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) in south-western Kenya.

Unfortunately, variation in encounter rate and group size affected negatively the estimations. General estimations pooling all observations to generate the detection function resulted in relatively precise estimations for puku, bushbuck and perhaps sitatunga in Kasanka NP and for puku and impala in the Kafue Region. Estimations for other antelopes resulted in high D %CV due to low numbers of sightings; generally, neither group size estimation nor encounter rate estimation were very precise. High variance in encounter rate might explain high variance in estimations. Sightings were distributed very unevenly over the different transect lines which might be the reason for high ER %CV (Cassey & McArdle 1999, Fewster et al. 2009). Fewster et al. (2009) described that the variance in encounter rate is the main cause for variance in estimations. Nevertheless, pooling data of different species and using one detection function for all antelopes might be a useful tool to get precise estimates of rare antelopes as shown for bushbuck in Kasanka NP.

Precision in estimates is given by the D %CV. The smaller this value is, the more precise is the estimation; and the more precise the estimation the better is its use for wildlife conservation and management (Ogutu et al. 2006, Fewster et al. 2009). Generally, for puku in Kasanka NP and Kafue Region, the estimations were precise as well for puku and for impala. The assessment of puku at Lake Rukwa, Tanzania, resulted in a D %CV of 28.9 (Waltert et al. 2009). Thus, the precision of the estimations in this study were generally higher along the transect lines (D %CV of 5.31 in Kasanka NP and 10.85 in Kafue Region), and slightly lower for the habitat categories. The only estimations marked by high D %DV were those of the habitat category 3 in the Kafue Region for puku and impala, 62 and 75 D %CV, respectively. They resulted in both cases from a high ER %CV as E(S) %CV was low.

Precise and unbiased estimates of densities are important to understand population dynamics, to serve conservation purposes (Shorrocks et al. 2008) e.g. to make reliable decisions in wildlife conservation and management (Ogutu et al. 2006).

2.4.2 Distribution patterns of puku in the dry season

Many animal species are unevenly distributed across the landscape (Fryxell et al. 2004). On the one hand some localities within a certain region can contain dense animal concentrations and on the other hand there are areas nearby that are virtually unoccupied (McNaughton 1988). Grazing distribution patterns of herbivores species are affected by abiotic and biotic factors (Bailey et al. 1996). Abiotic factors like slope or distance to water determine large-scale distribution patterns; biotic factors act within the constraints of abiotic factors (Bailey et al. 1996). Water availability, energy-optimising (Fryxell et al. 2004), general quantity and quality of forage (Bailey et al. 1996, McNaughton 1988), competition and predation (McNaughton 1988) influence the herbivores distribution. But these factors are not stable: they change between regions and between years. Another important factor affecting the distribution of herbivores is bushfire: it reduces the available food, and also cover. But after a while, depending on soil characteristics and time during the dry season, grasses are freshly sprouting, depending on soil characteristics and time during the dry season, though. Location and timing of bushfires can natural and hence at random, or less random, if set by poachers or planned by the park management. Not to forget, the distribution of animals is influenced by all kind of human activities as well: positively or negatively, directly or indirectly. It is sometimes difficult to isolate one or more factors that allow a distinct explanation for the observed patterns.

The surveys along the transect lines showed a patchy distribution of puku in both Kasanka NP and in Kafue Region. This was revealed initially by the sightings on the transect lines and then by the estimated local population densities along the transect lines as well as in the different habitat categories in the study regions. This heterogeneity in the puku's distribution has been stated by several authors (Goldspink et al. 1998, Starkey et al. 2002, Rosser 1992, Rodgers 1984, Rduch 2008) and this fact challenges surveys of puku (Starkey et al. 2002).

Estimated local densities along the transect lines ranged up to 149.39 puku/km² in November 2010 in Kasanka NP and up to 110.64 puku/km² in Kafue Region. By this, especially the densities in Kasanka NP were higher than local densities reported by other studies. Rosser (1992) gave a maximum local population density of about 105 puku/km² in South Luangwa NP which is close to the densities found in Kafue NP. In Luambe NP puku reached 54.78 animals/km² along transect lines or local densities of up to 96.61 puku/km², respectively (Rduch 2008). All these local densities are lower than the results of this study from Kasanka NP and Kafue Region. Only Goldspink et al. (1998), in a previous study in Kasanka NP, presented local densities of up to 126 puku/km² that are thus in the range of the results of this study. They already stated that the densities of puku in Kasanka NP are in parts superior to other African sites as also reported by the findings of this study.

General habitat choice of puku

Grassland covers most of floodplain areas and dambos, even though some parts are characterised by long grass. Both cover short, mostly green, presumingly nutrient rich grassland and swale vegetation. The use of these habitats by puku was reported from South Luangwa NP in eastern Zambia (Rosser 1992), from Kilombero Valley in Tanzania (Starkey et al. 2002, Jenkins et al. 2002), from Chobe NP in northern Botswana (Dipotso & Skarpe 2006, Child & von Richter 1969), and during previous studies from Kafue NP (de Vos & Dowsett 1964) and Kasanka NP (Goldspink et al. 1998). The use of open grassland areas was also reported from Luambe NP (Rduch 2008). Puku reached a density of 27.65 animals/km² in grassland areas in the western half of the NP. That is the area between Luangwa River and about 25 km distance upcountry (Rduch 2008). Rosser (1992) reported from South Luangwa NP that the larger the patch of swale, the higher the puku’s density. Large grasslands, relatively shallow floodplains, like along the meandering Kasanka River, were less represented in the areas covered by the transect lines in Kafue Region. Especially in PPKR they were lacking, explaining the low amount of puku observed in grassland. As the population densities along Kasanka River, sampled on the transect line Puku-Loop, were extremely high, large floodplain areas might be the puku’s most preferred habitat, at least in the dry season. The floodplain areas are supposed to be the lechwes prime habitat (de Vos & Dowsett 1964, Child & von Richter 1969). But no lechwe occurred in Kasanka; only a couple of individuals were observed from 2007 to 2009 (Kasanka 2013). The absence of lechwe might enable puku, restricted to the borders of floodplains when those are sympatric with lechwe (Child & von Richter 1969), to move on the exposed floodplain in Kasanka NP.

Intermediate habitats still provide a considerable grass layer in open woodlands and at the edge of woodlands. In other words this habitat category represents the crossover between open grass and woodlands. This crossover can represent a kind of conversion resulting from elephant activities. Dipotso & Skarpe (2006) reported from Chobe NP where elephants opened the woodlands. As in Chobe, this might create habitat for puku in Kafue Region. These activities positively affect habitat of puku and also their number (Dipotso & Skarpe 2006). Elephants were less common in Kasanka NP than in Kafue Region (own obs.) making the described type of habitat less available for puku. Thus, it appears that elephants influence the amount of suitable area for puku.

Woodland, dense woodlands, miombo and thickets were marginally used by puku. The use of light woodlands was reported (Ansell 1960a, Rosser 1992), as well as low densities in riverine thickets (Rosser 1992). Data from Luambe NP revealed a density of 6.726 puku/km². Mopane woodlands, riverine thickets but also dambos within these woodlands were included in this figure (Rduch 2008) what might explain the higher density compared to the findings of this study. Rosser (1992) reported mopane woodlands to be used only by bachelor males. The use of miombo woodlands by puku was not observed by Starkey et al. (2002) in Kilombero Valley. However, for Kilombero Valley Jenkins et al. (2002) reported pellets and tracks of puku in the wet season. The observations in this study about the use of miombo by puku come from the dry season, though! Thus, this might be a difference between puku in Tanzania and Zambia. The use of miombo by puku needs generally further investigation, not only in the dry season (see Chapter 2.4.3).

The patterns of habitat use in Kasanka NP remained stable when comparing July 2009 to November 2010. Nevertheless, in November, the amount of puku observed in woodland increased slightly. The first rains and rising hot temperatures might induce grass and vegetation growth, causing changes in the distribution of animals. This might indicate the shift of habitat use towards woodlands in the rainy season, observed also by Jenkins et al. (2002) in Tanzania (see also Chapter 2.4.3). As the amount of grass- and woodland was available for Kasanka NP, the preferences of puku for grassland or woodland could be assessed via the Jacobs-Index. Thus, the preference was not only concluded from the amount of observed animals and the respectively estimated densities, but the latter were weighted by the relative amounts of the area covered by the habitats. The puku's preference for open, short grasslands was underlined for July and November by similar, positive values of the Jacobs-Index. The avoidance of miombo and woodland habitats decreased in November, because of the aforementioned reasons. Based on the estimated densities, this pattern of avoidance and preference for the two habitat categories was more distinct.

Females were reported to use woodlands less frequently than males (Dipotso & Skarpe 2006). But this could not be confirmed by the data of this study. Differences in habitat use between sex and age groups of puku were significant in July. Especially neonate showed relative high amount of intermediate habitats and woodland. Neonates hide during the first weeks of their life (Estes 1991, Ansell 1960a). The denser vegetation of these habitats provides cover and is supposed to protect from predators (Rosser 1989). The territories of male puku attract females, among others, by a reduced likelihood of predation for themselves, but also for their offspring (Rosser 1992). On the one hand, this might explain the similar patterns of habitat choice by adult males, females and neonates, on the other hand, it explains the differences in habitat choice observed for bachelor males, presumably chased to other areas. In November, habitat choice of sex and age classes assimilates. It should also be mentioned that it is not exactly clear in which manner territories are maintained through the year in Kasanka NP. By assembling in high numbers along Kasanka River, pressure from bachelor males on the territories for feeding purpose, is probably higher in November. Interestingly, the results in habitat choice showed a similar pattern between sex and age classes of puku in PPKR. This contrasted to the findings from Kasanka NP, but also to those from Kafue NP. This difference might be due to the lesser amount of large open areas in PPKR.

In the dry season, puku showed a significantly different habitat choice during the day in all study regions. The only common feature between all study regions was the high amount of puku observed in the grassland at 4 am. In PPKR, the pattern of habitat choice of puku remained rather stable during the remaining time of the day, contrasting to the other study regions. In both Kasanka NP and Kafue NP, puku were encountered to considerable amounts in intermediate habitats and woodland at 1 pm. In this hottest time of the day, they tend to use cover in order to escape from the sun, although they have the reputation to occur in the sun at midday (Mills & Hes 1999), which was supported by the observations on the puku's activity (Chapter 5). Probably, due to the general aspect of more scrubland in PPKR, puku might not need to change their location during the day.

The occurrence in intermediate habitats and woodland reduces detection probability. Following this, different amount of puku might have been sampled which also influences the estimated population densities based on data from different times of the day (unpubl. data of this study). It is important to survey at different times of the day, as detection probability of animals might change, possibly as a consequence of differences in habitat use. This has to be considered during surveys since resulting estimated figures of abundance of animals can be affected both positively and negatively.

Estimated local densities for the cool dry season

A comparison of the results of both Kasanka NP, collected in 2009, and Kafue Region, collected in 2010, was possible. However, as the study regions were sampled in different years, inter-annual differences might affect the puku's distribution.

The Puku-Loop transect is situated in the middle of Kasanka NP, along Kasanka River. This area provides green floodplain areas near or in the meandering river, the puku's preferred habitat (Goldspink et al. 1998, Rosser 1992, Child & von Richter 1969). Furthermore, puku occurred in the termitaria area along this transect line, situated between the floodplain and the miombo, where the grass was very much grazed (own obs.; unpubl. data of this study). This transect line had by far the highest population density of puku, about 118 puku/km² in July. The same kind of habitat, the floodplain along Mulembo River, marks most of the northern side of the transect line Mulembo. Nevertheless, only a few puku were observed along that line and the local density was relatively low, only 11.15 puku/km². This was similar for Katwa leading next to Mulembo River, where few puku only were observed on the floodplains. The question arises if puku avoid these areas because of their proximity to the Kasanka NP's border which increases the risk of poaching, as also concluded by Goldspink et al. (1998).

Fibwe and Wasa are situated in the middle of the park and close to touristic facilities. The transect Fibwe was the transect line with the second highest local population density of puku in Kasanka NP, 50 puku/km² in July 2009. Fibwe leads through Fibwe Plain, a vast grassland area, generally dry but with moist spots. Wasa transect line goes south of the Wasa Lakes. Puku were recorded to moderate numbers directly along the line and thus in the miombo but mostly at a certain distance to the line on dambos and near the lakes. Grassland areas with high number of puku lay at the northern edge of the area that could be surveyed from the transect line Wasa. That side, the transition from miombo to the water is less abrupt and thus leading to larger areas of floodplains, termitaria or other open areas (own obs.) which would explain the abundance of puku.

The transect line Luwombwa leads through miombo woodland; only one single male was observed, probably vagrant. Other parts of transect lines in miombo revealed puku, but in low numbers: the western side of Kafubashi, most of Nafulwe, some area along Katwa, Mulembo, the northern end of Fibwe or Wasa. This reduced the estimated densities for Wasa or Fibwe and resulted in general rather low densities, zero to 11 puku/km², for the other transect lines. However these observations of few puku underline the marginal use of woodlands (Ansell 1960a, Starkey et al. 2002), but disagree with the observations of Starkey et al. (2002) who never found puku in miombo.

Although the transect line Kafubashi is marked by a dambo going along at the eastern side of the transect line, as well as by some termitaria and grasslands, this did not stand for a lot of sightings or high densities, respectively. The transect line Chikufwe goes around Chikufwe Plain, a large area of grassland, marked by termitaria and a water hole in the north as well as a smaller waterhole in the southern part. A similar kind of grassland marks the northern end of the transect line Nafulwe. Only once a small group of vagrant puku was observed, at Chikufwe. Although the waterholes provided water in the dry season (own obs.) they are neither as big as the Wasa lakes nor rivers with floodplains. Thus, although Rodgers (1984) reported puku to be observed close to water, they are not automatically at any surface water in the area of their occurrence. Ansell (1960a) considered puku to not use isolated water holes; nevertheless, he reported them to do so along the Lushimba, west of the Kafue NP boundary.

Concludingly, the area at Chikufwe, Nafulwe and to some extent along Kafubashi appears to be unsuitable for puku. They are grassland areas but situated at certain distances to rivers or lakes. Chikufwe was the only transect line where reedbuck were observed during this study. Hartebeest were seen at Chikufwe and Nafulwe only. Competition can influence a species distribution as well as a variety of other factors (Pulliam 2000), e.g. the mineral content of food (McNaughton 1988). The grass species *Loudetia* was observed on Chikufwe Plain, on the grassland at Nafulwe and along Kafubashi (see chapter 3). Does this grass stand for inappropriate habitat for puku?

Nafulwe is situated at the Kasanka NP's southern border, less covered tourist activities. Human settlements reach close to Kasanka NP (Figure 2-4). As for Mulembo and Katwa, situated at the northern border, the risk of poaching might be increased in this southern park area as well.

The next villages are at some distance from the transect lines in Kafue Region from both PPKR in the GMA and the study area in Kafue NP. Very high densities of puku, more than 100 animals/km², occurred at Kafue North and Hippo. These transect lines are parallel to Kafue River at small distance. They provide open areas as well as dambos. Kafue North experienced more bushfire. Hippo provides more areas of dense riverine vegetation that did not influence the high numbers of puku. Also providing riverine vegetation, River had a density of 21 puku/km² only.

Kafue South is situated at some distance parallel to Kafue River and Camp leads away from it. Situated next to water, the survey of these two lines resulted on different local densities of puku: 17 puku/km² along Kafue South and 61 puku/km² along Camp. The latter begins near McBrides' Camp on an open grassland where puku were observed and leads through an open woodland with sparse undergrowth. This missing undergrowth could be the difference to Kafue South where grasslands but also rather abundant scrubs could be found. However, puku can occur in scrublands as also reported from Chobe NP (DIPOTSO & SKARPE 2006). The area on the eastern side of the transect line had a high, dry grasslayer, whereas most parts of the western side were burnt. This was the result of management implementations by the Puku Pan Lodge. By carrying out early burning, they intend to prevent heavy fires in the late dry season and to establish a firebreak to prevent the lodge from possible fires. Trying to not interfere too much in the whole ecosystem, and also in order to keep animals favouring cover near the lodge for Safari tourists, they let the grass on the eastern side (LUWAMYA KANCHEYA, pers. comm.). Dry grass in combination with scrubs and trees is not likely to attract puku.

At some distance from Kafue River puku were observed in medium densities along Between that leads along a small dambo and into miombo. This is in accordance with the findings of DE VOS & DOWSETT (1964) who found puku in small areas within woodlands. The question raised here is what are the physical differences (e.g. soil characteristics, distance to water) of Between in PPKR, 30 puku/km², and Kafubashi in Kasanka NP, 2 puku/km², leading to such obvious differences in occurrence. They are situated at some distance from rivers, both are dambos, narrow strips of open areas surrounded by miombo except that Between is narrower.

The transect lines Plain and Dambo cover grassland areas, dambos, at a certain distance to Kafue River and lead away from it. Puku were observed at medium densities, 13 and 19 animals/km², respectively. Dambos are one of the puku's preferred habitats (ANSELL 1960a, SKINNER & CHIMIMBA 2005). Thus, the general occurrence of puku was not surprising, although puku did not occur at high densities either, probably because of the certain distance to Kafue River.

Generally, Dambo and Plains can be compared to the transect lines Chikufwe or Nafulwe in Kasanka NP. In contrast to the lines of Kasanka, not only reedbuck, hartebeest or sable (for Plains during ad libitum observations) were seen, but also impala, kudu, waterbuck, bush duiker as well as puku. Thus, Dambo and Plain showed a higher diversity of antelopes. On the one hand when considering kudu or impala, this might be explainable by the difference in overall geography and situation: they did not occur or, as for impala, their former occurrence is doubtful in Kasanka NP and its surroundings (Ansel 1960a). Bush duiker were observed at Chikufwe by camera traps. Waterbuck are observed, rarely though, in Kasanka NP (Frank Willems, pers. comm., Kasanka 2013).

The transect lines Miombo East, Miombo West, Airstrip and Main Road go through miombo woodland. The puku were rarely observed in the miombo itself, but at small stripes of grassland along Airstrip and Main Road. In this context, the observations from Kafue Region and Kasanka NP generally agree. Along transect lines within miombo woodlands few to zero observations of puku were made. If the transect line goes along miombo with grassland on the other side or through miombo close to grasslands, this aspect sometimes changed. Then, puku were observed in the miombo as well. Furthermore, puku did not only go through it but rested or fed in it (own obs.). Examples of these areas are: Fibwe, Wasa, Katwa in Kasanka NP or Between in Kafue Region. Thus, puku do on occasions use miombo habitats, albeit, not too frequently, but it can be said that they appear generally not to occur in miombo far away from their main habitats. However, this general pattern of low numbers of puku in miombo woodland might change in the rainy season (see Chapter 2.4.3).

Estimated local densities for the progression of the cool dry season

The estimated local population densities changed within the progression of the cool dry season. Underlining observations were made in the two study regions. After a first general survey in the cool dry season in July 2009 in Kasanka NP, some selected lines were resurveyed at the end of August 2009. Here, the one and only observation of puku at Chikufwe was made. Nevertheless, the general aspect remained stable. Whereas the density of puku dropped along Katwa, it increased along Puku-Loop. In Kafue Region, the transect lines River and Plain were resurveyed. While the density of puku almost doubled along River, it dropped along Plains. Puku-Loop and River are located along permanent water supplies. Although there is a waterhole along Plains, this area, as well as probably the entire area apart from permanent water got drier. The puku assembled in the floodplain of Kasanka River, where green grass was readily available. Similarly, they converged along the banks of Kafue River in order to get closer to water, even though there are only some dambo areas instead of a large floodplain. Jenkins et al. (2002) observed similar patterns of distribution in Kilombero Valley, where puku assemble in the floodplains in the dry season.

Estimated local densities for the hot dry season

Only the transect lines in Kasanka NP were surveyed in the hot dry season. Selected transect lines were surveyed in October 2010 and all transect lines except Mulembo were sampled in November 2010. Some first rains fell in November, yet no big rainfalls that mark the real beginning of the rainy season, before the line transects were surveyed.

Generally, the patterns of the puku's distribution along all transect lines was similar to the observation in the cool dry season. Similar to the observation in the progressing cool dry season, the local population densities along Puku-Loop increased with the progression of the hot dry season. They reached the maximum local population density during this study: 149.39 puku/km²! Consequently, data collection along this line of 5.1 km repleted with puku sightings took about 2.5 hours and required a lot of concentration, barely feasible. Decreasing water levels, exposing more floodplain area for the puku as well as probably decreasing availability of food and water in other regions might be the main reasons attracting the puku even more than in the cool dry season. This was supported by statements of Monique Helvert (pers. comm.): the shrub layer has the highest biomass increase from November to December and the Puku-Loop is one of the most productive areas in Kasanka NP in terms of vegetation. Nevertheless, inter-annual differences in the factors affecting the puku's distribution and may have led to a lower population density in October 2010 than those observed in August 2009. In this context Frank Willems (pers. comm.) reported the very high rainfall in Kasanka NP in the rainy season 2009/2010. This might assemble the puku at Kasanka River at later time during the year than the year before. The same might explain the general higher densities along Katwa.

2.4.3 The puku's distribution in the late rainy season

Due to partial inundation of almost each of the transect lines, line transect sampling could not be carried out in the late rainy season, neither in Kasanka NP nor in PPKR. Ad libitum observations could be made in Kasanka NP during almost three weeks in April 2011. In the late rainy season, puku were scattered all over Kasanka NP. Furthermore, they were found in miombo woodlands at sometimes fairly long distances from open areas. However, they still occurred, but in much lower numbers compared to the previous surveys in the dry season, along Kasanka River that inundated much of the floodplain. These movements of puku away from inundated floodplains were also observed by Dipotso & Skarpe (2006) in Chobe NP. There puku move into scrublands (Dipotso & Skarpe 2006). In Tanzania, habitat changes of puku during the rainy season were also observed (Jenkins et al. 2002). By moving into rice fields, the puku might cause human-wildlife conflicts (Jenkins et al. 2002). Assessments of puku in the wet season are largely neglected (Jenkins 2013). Muddy or inundated areas counteract surveys on line transects by car and by foot. Dense vegetation and the presumed occurrence of puku in miombo woodlands go against aerial surveys (Jachmann 2002). As line transect surveys appear not to be adequate, other tools have to be found: e.g. tracking individuals by GPS-collars.

Puku in Kasanka NP show shifts in distribution and habitat use during the wet season that still requires further investigation!

2.4.4 The development of the puku's population in Kasanka NP

The distribution of the estimated local densities of puku observed during this study in July 2009 can be compared to the findings of Goldspink et al. (1998) who surveyed puku in Kasanka NP in the cool dry season 1994. The distribution patterns of puku show common features as well as differences (Figure 2-28). The two surveys resulted in zero densities for puku at Chikufwe and Nafulwe. Slight differences can be detected along Katwa and Kafubashi area, where Goldspink et al. (1998) found no puku, dissimilar to the results of July 2009, where estimated densities of puku were small. Further, differences can be found in the eastern part of the transect line Wasa. Probably, they result from the different methods applied. The density at eastern end, where a lot of puku were seen, merged with the overall density along the Wasa transect line in this study. The area of Puku-Loop, along Kasanka

River, and Fibwe were the only places where the estimated densities were much higher in 2009 than in 1994. It needs to be said that GOLDSPINK et al. (1998) sampled Luwombwa floodplain areas, unlike this study that covered miombo woodland in this area.

Generally, the distribution patterns of puku remained similar in the two surveys, although separated by 15 years. The puku increase in local population densities towards the centre of Kasanka NP and despise apparently suitable areas elsewhere. For the survey in 1994 as in 2009/2010 this pattern is suggested to be a response to poaching (GOLDSPINK et al. 1998). Nevertheless, competition might play an additional role (see Chapter 2.4.6).

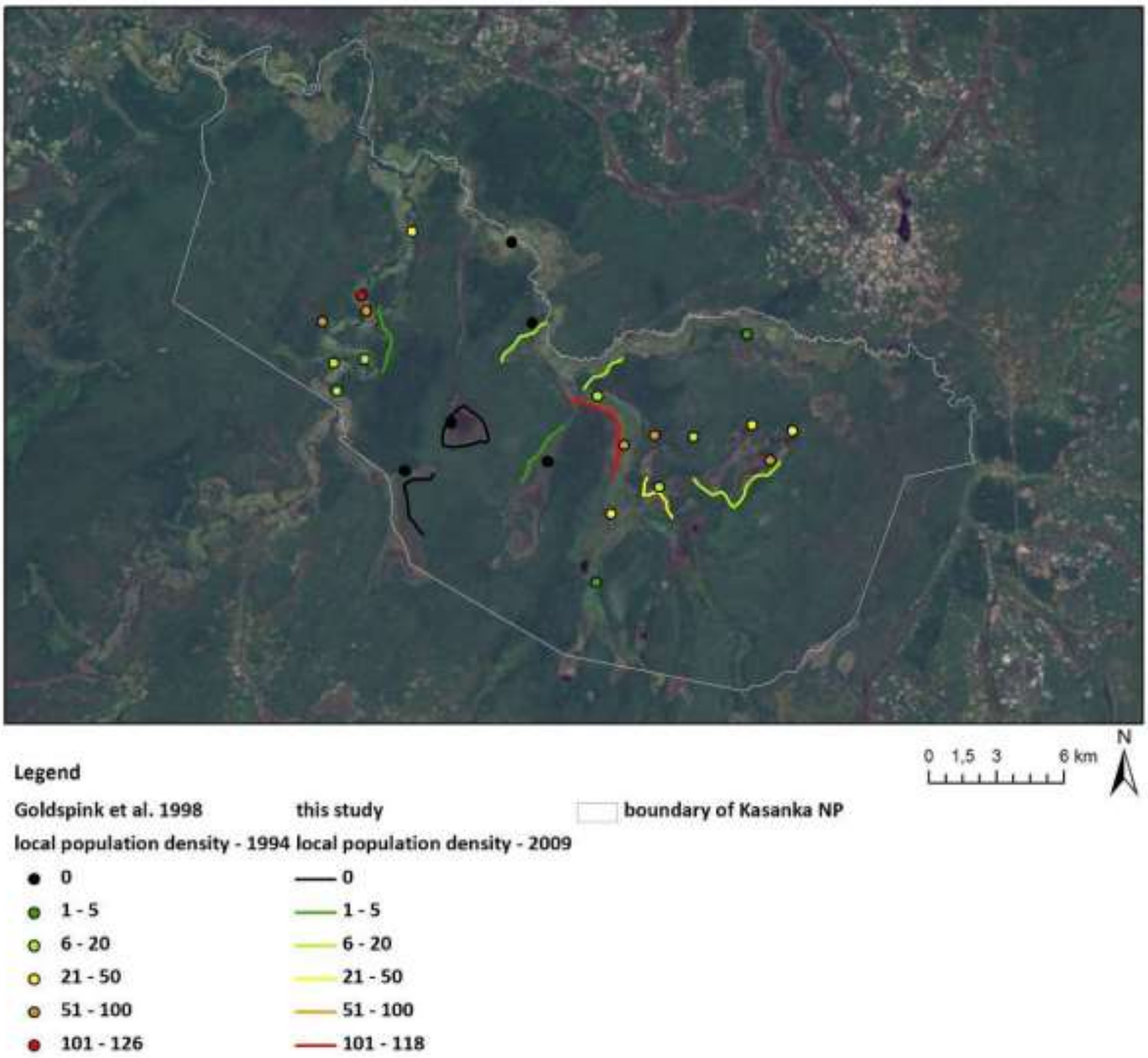


Figure 2-28: Comparison of the findings of GOLDSPINK et al. (1998) to this study: Spatial distribution of estimated local population densities of puku in Kasanka NP in 2009 and in 1994. The data compared were collected in the dry season, from July to September 1994 and in July 2009.

The extrapolation of puku densities and numbers to the entire area of Kasanka NP was based on the relative amount on woodland given by Kennedy et al. (2008). Only by involving the area covered by the habitat categories, the extrapolation was considered reliable.

The general population density of puku in Kasanka NP was calculated at 12.92 animals/km². It is difficult to compare these figures as most studies do not cover and consider entire protected areas. The total population size of puku in Kasanka NP resulted in a rounded figure of 5,038 individuals with calculated confidence limits from 3,268 to 7,238 individuals based on the %CV of the population densities in the respective habitats. The survey of Goldpink et al. (1998) resulted in a population size of 613.1 (confidence limits 413.6 to 967.2) in 1994. This is an eightfold increase of the puku's population within 15 years which is due to the ongoing conservation work of Kasanka Trust Ltd. established in 1990 (Goldpink et al. 1998). Only long term surveys in the next years can reveal the future development of the population of puku in Kasanka NP.

2.4.5 The camera-trap survey

This survey was based on a survey effort 924 trap-nights. They split up unequally over the study regions: in Kasanka NP 748 trap-nights were performed. A comprehensive survey requires a survey effort of more than 1,000 trap-nights (Giman et al. 2007) not reached by this study. Furthermore, the camera trap stations did not cover the entire study regions but rather specific spots. The choice of the spots in Kasanka NP was a result of the reflection about where captures of predators might be more possible or more probable than in other areas and was based among others on information of Frank Willems. Hence, a considerable amount of camera traps was mounted at Fibwe. Placed further as a complement to the line transects in Kasanka NP, the information gathered by the camera traps were comparable to the results of line transect sampling. In the study regions, results have to be considered as trends or additional information, not as a stand-alone survey. However, photos collected by less statistically sampling designs may still provide useful data (Jenks et al. 2011).

Especially for the abundance of non-individually identifiable species, indices can be problematic because a distinction between cases of single individuals with numerous records and cases of numerous individuals with single records is difficult (Trolle et al. 2008). Therefore, a determination of independent captures as done by O'Brien et al. (2003) and as performed for this study is very important, also in order to reduce the risk of overestimation mentioned by SILVEIRA et al. (2003). The RAI does not give actual numbers or densities in the study areas, but relative abundances; however, it facilitates comparison (JENKS et al. 2011). Further, this relative abundance can be compared amongst animals in the study regions.

According to the RAI, the puku was the most abundant antelope in Kasanka NP. This agreed with the observations of the line transect survey, the resulting observations and estimated densities. Contrastingly for bushbuck: this antelope was ranked second and half as abundant as puku according to the RAI, but reached only a fraction of the puku's densities according to the data from the line transect survey. The RAI underlines that bushbuck were common in Kasanka NP. This might be similar but less pronounced for bush duiker. During line transect sampling, reedbuck and hartebeest were detected, but their abundance was calculated low. Although observed during line transect sampling, sable and orebi were not captured by the camera-traps. None of the antelope species was observed by camera-traps only.

In PPKR, as a supplement to the observations during line transect sampling, the camera-traps captured the sable antelope. Hartebeest, reedbuck and grysbok were not photographed, although recorded on transects. In order to capture hartebeest and reedbuck, the camera-traps should probably have covered rather grassland at a certain distance to Kafue River than the area close to its boarders, and it might be that this is the reason why none of these animals were photographed. However, the camera trap at the waterhole on the transect line Plains, where hartebeest and reedbuck were seen during line transect sampling, did not capture these antelopes either. In PPKR, according to the RAI, the puku was the second most common antelope. Impala were most abundant in this region. This was also the result of the transect line sampling. Concerning bushbuck, as in Kasanka NP, the results of the RAI, in contrast to the results of the line transects, might fit better to its actual abundance. Similarly, relative abundance between puku, waterbuck and greater kudu was less biased towards the puku as in the DISTANCE estimations. Results of the RAI might fit better to the actual situation; they suggest a higher relative abundance of these antelopes than the results from the line transects in the study region.

In general, detectability of species is higher for habitat generalist, terrestrial and large-bodied species (TREVES et al. 2010). This explains low RAI values of the small carnivores, but also of sitatunga. Further, this statement might explain the difference in RAI values of bushbuck and bush duiker, although bush duiker might not have been less abundant than bushbuck.

The RAI values of puku in different areas underlined the findings of the line transect surveys. Concerning RAI and estimated population densities, puku were very abundant at Puku-Loop. The area at Kabwe, partly covering the northern end of Puku-Loop transect line, resulted in a high abundance of puku as well. The area at Fibwe and Katwa provided medium densities of puku; they were similar concerning RAI, but based on the line transects, Fibwe had a higher density of puku. This might be caused by the position of camera traps and transect line: while the transect lines led through Fibwe plain, most of the camera trap stations were in or at the border of miombo woodlands. Puku did occur here, but at lower abundance than on grassland. Camera traps revealed a low occurrence of puku at Chikufwe as did the observations of the line transect. However, they both might indicate a rather vagrant status of puku on that site. The rather dense evergreen forest at Fibwe was not covered by the transect lines. Although occurring in miombo woodlands, puku were not detected in this dense evergreen forest.

Bushbuck were found at high abundance in the evergreen forest at Fibwe which underlines their general habitat preferences (Leslie Jr 2011b). Sitatunga were detected at the two focal areas at Fibwe. This area around Fibwe, characterised by a high amount of swamps, wetland areas and thickets matches with the habitat choice of this antelope (May & Lindholm 2013). The western part of the park around Chikufwe provides less waterbodies. Reedbuck and hartebeest were detected only at Chikufwe, similar to the observations on the line transects.

Although occurring at high abundance at the artificial waterhole near Kaingu Lodge, puku were never observed at the saltlick at about 50 m from the waterhole. Beside the observation during this study, puku were generally not seen at the salt (Tom Heinecken, pers. comm.), but at the waterhole only. like bushbuck, while impala and kudu used both sites. Impala, especially in the dry season, browse to a considerable amount, comparable to kudu (Gagnon & Chew 2000), whereas the puku’s food is composed almost entirely of grasses (Chapter 3). Analyses of mineral content of the actual food plants might reveal more information. Nevertheless, puku’s food might be richer in minerals and sufficient for the puku’s requirements. However, these observations need to be intensified.

Generally, more cameras, installed for longer periods, placed at more stations and perhaps following a more standardised study design could provide more detailed information about the species and their abundances within the study areas. By this way, the occurrence of rare species might be proven and the relative abundance of all (larger mammal) species in the study regions could be assessed.

2.4.6 Spatial overlap between puku and other antelopes

In **Kasanka NP**, the antelope species syntopicly occurring with puku on the floodplains was the **sitatunga**. Nevertheless, sitatunga were observed on much lower occasions than puku, only next to the transect lines Puku-Loop, Wasa and Fibwe. The sitatunga's estimated population density in the area covered by the transect lines was only a very small fraction of the puku's density. Other estimations of local population estimates along the transect lines were performed but were not presented here, as they were considered unreliable due to the relatively low number of sightings. The sitatunga in Kasanka NP was certainly more common than the sightings indicated (May & Lindholm 2013). During the observations along the line transects, the sitatunga were observed most often in grassland. They were discovered in intermediate habitats and woodlands by the camera-traps. These observations were most probably biased. Sitatunga are reported to have a cryptic nature and favoured habitats with tall and dense vegetation as swamps, marshy clearings, riverine thickets and monospecific stands of papyrus (May & Lindholm 2013). All kind of habitats are difficult to sample during line transect sampling, especially from a car, and also insufficiently covered by the camera-traps. The sitatunga's occurrence in these areas might be underrepresented. Thus, although the results of the habitat choice indicated a high spatial overlap between puku and sitatunga in Kasanka NP, the sitatunga might occur additionally in habitats not used by puku (e.g. dense swamps and evergreen forests). Furthermore, if observed at the same places, sitatunga were detected in much lower numbers than puku. Overlap existed but it is considered low. In Kafue NP, sitatunga were observed once in November 2011 in the swamp near Hippo Lodge (own obs.).

In Kasanka NP **reedbuck**, **hartebeest** and **sable** were observed on and near Chikufwe plain and, only hartebeest, along Nafulwe. On one occasion a single **orebi** was observed at Chikufwe, a species not listed at the Kasanka Mammal List (Kasanka 2013)! Except for one sighting, puku were never observed in the same area. These antelopes do occur not only at Chikufwe (Frank Willems, pers. comm.), but the other places might be rather apart from the puku's area of occurrence as well. In Kafue Region, reedbuck were observed along Between and Plains, where also puku were observed. Hartebeest were observed along Plains. Accordingly, here both, hartebeest and reedbuck occurred rather together with puku. Additionally ad libitum observations from both PPKR and Kafue NP showed hartebeest, reedbuck and also orebi syntopic at grassland areas at some distance from Kafue River not covered by transect lines. Impala or puku were not observed at these places. Due to the low number of sightings, the estimated densities of reedbuck, hartebeest, sable and orebi species resulted in high D %CV. However, they probably reach much lower population densities than puku in the two study areas.

Reedbuck were observed almost exclusively in open grassland in the study regions. Reedbuck are reported to use grasslands at a time when the vegetation is at its greatest height when other herbivores leave these areas (Jungius 1971). This cover is an important refuge for them (Huffman 2011). As long as a certain cover is provided, reedbuck remain in these areas after burns and use dry vegetation that has been left or freshly sprouting grass (Jungius 1971). Only when not completely hidden, reedbuck are visible; this might explain the results of the habitat choice. Nevertheless, they were never observed in dense wooded habitat that they are reported to avoid (Kingdon & Hoffmann 2013b). By this, it appears that reedbuck and puku have similar habitat requirements, but they were seldom seen together. The exact reasons that lead to this spatial separation need further investigation.

Miombo woodland is the habitat related to **Lichtenstein's hartebeest** (Groves 2011). Generally, hartebeest species are associated with grasslands and they occur on grassland clearings (Gosling & Capellini 2013). Following this, observations on habitat choice can show the use of open habitats as well as of dense habitats, as in this study. Other hartebeest species in other regions in Africa may be outcompeted by open grassland species. The latter change the grasslands into the way they like while hartebeest no longer can use it (Gosling & Capellini 2013). This leaves the question about how high numbers of puku might affect hartebeest. Generally, there was little spatial overlap between the two species.

Beside Lichtenstein's hartebeest, **sable** antelopes are closely identified with the miombo woodlands; no large mammal is closer related to this ecosystem than these two antelopes (Estes 2013). Occurring inside the woodlands in the wet season, they move onto the grasslands in the dry season (Estes 2013). Only once sable antelopes were observed during line transect sampling. They were discovered in the miombo, but in close proximity to grasslands. Several ad libitum observations from groups of sable in Kasanka NP complemented and underlined this observation. In Kafue Region, sable antelopes were detected by the camera-traps and they were seen during ad libitum observations in both miombo as well as at the margins of woodlands. The observations made during this study were probably too few to give reliable statements, but sable antelopes appear to exhibit little spatial overlap with puku.

The **Bushbuck** prefers areas with cover like woodlands, forest edges or thickets (Leslie Jr 2011). This was reflected by the high amount of bushbuck discovered in intermediate habitats and woodland during this study, although also observed to a high degree in grassland. Occurring mostly alone and in habitats providing cover (LESLIE JR 2011) bushbuck might be better surveyed by camera-traps than by line transects. This might also apply for **bush duiker** and **Sharpe's grysbok**, although the first is also reported to use open country (WILSON 2013). Bushbuck and bush duiker are probably among the antelopes with high abundance in the two study regions, underlined for the bushbuck by the results of the camera-trap study and also outlined by the Kasanka Mammal List (KASANKA 2013). As all aforementioned antelope species occupy rather dense habitat and thickets, the spatial overlap between those and puku is regarded as small.

Waterbuck, **greater kudu** and especially **impala** were observed in Kafue Region only. Nevertheless, waterbuck are reported from Kasanka NP, yet not abundant, though (KASANKA 2013), but occur at sites not covered by the transect lines (FRANK WILLEMS, pers. comm.) which were rarely visited during this study. In Kafue Region, a number of 28 waterbuck was observed along the lines at 7 occasions, too few to get precise estimates. However, the estimated density of waterbuck (0.79 animals/km²) lay within the span of estimated densities in areas where waterbuck are common, 0.4-1.5 animals/km² (SPINAGE 2013); and the waterbuck's abundance can be regarded as common in both PPKR and Kafue NP supported by the results of the camera-trap study. The same applies to the greater kudu, which also not achieved enough sightings for reliable estimate. The camera-trap study revealed them to be the third common antelope in PPKR.

Greater kudu are reported to occur in arid scrubland and in thickets, but are rather absent from closed forests (OWEN-SMITH 2013). This was supported well by the results of the habitat choice in this study, where kudu were observed above all in intermediate habitats, rather than in open areas or in dense vegetation. Based on the differences in habitat choice of puku between PPKR and Kafue NP, spatial overlap between puku and kudu existed especially in PPKR.

The habitat choice of **waterbuck**, pooled for the entire Kafue Region, showed a high amount of grassland, which was more than for puku in the two subregions. Generally, habitat choice of puku and waterbuck appeared similar, especially in Kafue NP. These observations are supported by HUFFMAN (2011a) who described waterbuck as most common in grasslands. Nevertheless, open forest and scrub habitats are used as well (HUFFMAN 2011, SPINAGE 2013). The most important feature of the waterbuck's habitat is the proximity of permanent water during the dry season (SPINAGE 2013). Nevertheless, they tend to live on higher ground than puku in Chobe NP, occurring in well wooded habitats and along the edge of the floodplain (Child & von Richter 1969). Despite of some spatial separation, some competition for space was presumed to happen between puku and waterbuck in Chobe NP (Child & von Richter 1969) and it might happen in Kafue Region, too. Estimated numbers of waterbuck were not very precise, but indicate, as well as the raw observations, much lower numbers of waterbuck than the puku in Kafue Region. However, the RAI of waterbuck is only half of that of puku suggesting higher abundance of waterbuck than estimated by the data from the transect lines. It might be interesting to find out which of two antelope species exercises the stronger competition pressure. It appears that in Kasanka NP, where no waterbuck could be observed during this study, puku occupy the waterbuck's habitat. This might indicate an influence of waterbuck on the distribution and habitat choice of puku.

The highest spatial overlap between antelopes in Kafue Region occurred between puku and **impala**. Sightings and observed animals were higher for impala. The estimated density in the area covered by the transect lines in Kafue Region was about 7 animals/km² higher for impala (34.95 impala/km²) than for puku (27.44 puku/km²). Due to the high number of observations, precise estimates for impala could be carried out for transect lines as well as for habitat categories which allow a more detailed look at the situation.

The spatial overlap between puku and impala was considerably high and covered with the exception of miombo the entire study area in Kafue Region. The occurrence of impala biased towards close vegetation was found for Luambe NP as well (Simon 2008). Pooled in two vegetation classes during that specific study, impala reached 8.394 animals/km² in open vegetation and 19.391 animals/km² in close vegetation (Simon 2008). Characterised as well by the proximity of a big river, Luangwa River, these densities are comparable to the findings of this study. Many other studies have been carried out on population densities of impala. Unfortunately, due to different techniques applied they are hardly comparable (Fritz & Bougarel 2013). Furthermore, densities refer to whole protected areas rather than to local variations. This study does not cover the population of impala of the whole Kafue NP.

Impala occur in a variety of habitats: open scrub- and woodland and savannahs (Fritz & Bougarel 2013, Jarman 2011). In miombo areas, they are associated with riverine habitat and flooded grasslands (Jarman 2011). This underlined the findings of this study: Impala were observed on dambos, to a lower extent in miombo, and to the highest extent in scrubland and light woodland. The dambo covered partly by the transect line Dambo, represented one of the largest open and grassy areas in the study. Here impala were most abundant. This could be related to the impala's preference for short grasses, either close to lakes or, as in this case, after bushfires (Fritz & Bougarel 2013). Impala like to feed on freshly sprouting grasses, that grow after bushfires and decrease their amount of browsing (WRONSKI 2003). This could have been the reason for the high densities of impala along Dambo that provided large burnt areas. Impala need to drink during the dry season, when the water content of the plants falls below 30% of the plant's dry weight (JARMAN & SINCLAIR 1979). This agrees with the congregation of impala especially along the transect lines near Kafue River. The impala's density was highest along Hippo that might provide the best combination of habitats for impala consisting of some dambo areas, riverine woodland and the proximity to water. Although not resulting in such high densities, impala were abundant along Kafue North as well, which provides some scrublands as well as burnt areas. Thus, like puku impala occurred near water in the dry season but occurred to higher extent along transect lines situated in the miombo.

Resurveying the transect lines River and Plains in the progressing dry season, the impala's density increased along Plains, certainly influenced by one sighting of a huge group walking through this area. This might explain the high density along Plains, although a higher density along River, closer to permanent water, was expected.

Within the resident species of the Serengeti, JARMAN & SINCLAIR (1979) observed an incomplete separation with regard to the habitat preferences. Each species prefers a particular habitat, but there is overlap with other species (SINCLAIR 1983). This overlap is greatest in the late dry season (JARMAN & SINCLAIR 1979), potentially because food is in short supply at this time of the year (SINCLAIR 1983). In the hot season in Kasanka NP, overlap increased above all between the puku as they assembled to very high numbers along Kasanka River, but also along Fibwe or Wasa. The fact that more sitatunga were observed along Puku-Loop in October and November, indicating a potentially higher overlap in the hot dry season, might rather have been related to reduced cover for this antelope than to increased abundance. The progression of the dry season did not increase or induce overlap between puku and reedbuck, hartebeest or sable, respectively. In other words, all but puku were observed to overlap in space at Chikufwe during both the cool and the hot dry season. In the late rainy season, none of these species was sighted at Chikufwe (own obs.), but might have been overseen due to increased cover, which might apply especially to reedbuck. Unfortunately, no data from the hot dry season were gained from Kafue Region and the study period during the late rainy season was too short to provide reliable statements.

Antelopes overlapping in their occurrence show associations of many species (Sinclair 1983), as also observed during this study. Interference competition meaning a behavioural exclusion of one species is considered relatively unimportant, although not well studied (Sinclair 1983). Despite the fact that antelopes occurring together exert a kind of competition for resources, exploitation competition (Sinclair 1983) e.g. for food, water or shade, these associations of animals can also result in benefits. Regardless of whether the associations are intra- or interspecific they can facilite grazing and reduce predation risk (McNaughton 1988). Furthermore, with regard to the food resource, syntopic antelope species can use the same grass but at different growth stages which thus leads to niche separation (Murray & Brown 1993). Another possibility to avoid competition is to use the habitats in different areas or at different times of the day (Sinclair 1983). This might also be the case for puku and impala in Kafue Region. In the two subregions they showed tendencies to utilise habitats at different extent through the day. In PPKR, while puku were not seen at all in habitat 3 at 4 pm, impala were observed there to a higher amount than at the other times of the day. For Kafue NP, differences in habitat use were visible at 4 pm as in the case for 1 pm.

2.4.7 Looking inside the puku's populations

"Puku are gregarious in small to large herds" Ansell (1960a). This common opinion about the puku's social organisation can be supported by the findings of this study. Most of all the data about the puku's social organisation were collected during the dry seasons in the different study areas: generally in Tanzania (Rodgers 1984), from Kilombero Controlled area, Tanzania, (Corti et al. 2002), from Chobe NP, Botswana, (Child & von Richter 1969) and from Zambia: from Luambe NP (Rduch 2008), from Kafue NP and Luangwa Valley (de Vos & Dowsett 1964) and from Kasanka NP (Goldspink et al. 1998). The two latter studies can be compared directly with the results of this study, also based on observations in the dry season, to evaluate possible changes over the passage of time.

Many of the groups in Kasanka NP could not be classified for group composition. The same applies to the evaluation of sex and age ratio and body condition. This is certainly be related to the fact that the amount of sightings during each survey in Kasanka NP was much higher than in Kafue Region. Although overall sighting distance is larger in Kafue Region, fewer sightings occurred above 200 m in contrast to Kasanka NP.

The non-territorial adult and subadult males assemble at specific places more or less apart from the territorial males and females (own obs.). The transect lines in Kasanka NP lead along some of the ‘male-only’-sites situated along Puku-Loop (southern and northern end) or on Fibwe Plain. Others of these sites were not covered e.g. at the northern border of Wasa Lakes (own obs.). In Kafue NP, the transect lines Airstrip or Dambo covered areas with males. In PPKR only Between covered a patch occupied by some males. But another site with more adult and subadult males was situated about halfway between Puku Pan-Lodge and the airstrip of the lodge and not covered by the transect lines. This might have influenced the results of the overall group composition amount as well as of the sex ratio. This small-scale influence of study sites within the study regions might also explain the differences between the studies reported from Chobe NP by Child & von Richter (1969) and Dipotso & Skarpe (2006). Furthermore, as the study regions were sampled different years, inter-annual differences might affect the results of the population characteristics and thus influence the comparison.

Average values of group sizes are difficult to compare as not always given as a mean for all observed groups in the respective studies. In Luambe NP, a mean group size of 3.56 puku was found for July and 4.22 for September (Rduch 2008) which is lower. De Vos & Dowsett (1964) gave a mean group size of 6 which corresponds almost exactly to the values of Kafue Region from this study, and is lower than the mean group sizes of Kasanka NP.

Although large groups occurred, puku appear to prefer small groups. Especially single animals were encountered often, the modal group size during all surveys. The modal group size of one puku was described for other areas, too, as in Kilombero Valley (Corti et al. 2002), in Chobe NP (Dipotso & Skarpe 2006) or Luangwa Valley (Rduch 2008). Small groups of up to 5 puku were sighted most frequently in the study regions. This agrees with the findings of other studies in Chobe NP (Dipotso & Skarpe 2006), Tanzania (Rodgers 1984) or Luambe NP (Rduch 2008). Group sizes of puku in Kasanka NP reached 104 in the cool season and 169 the hot dry season, respectively. They were larger than those observed in Kafue NP which were ranging up to 37 puku. Other studies give a maximum group size of 28 (Child & von Richter 1969) to 46 (Corti et al. 2002); these are in the range of the maximum group sizes of Kafue Region. In Kasanka NP, maximum observed group sizes in the cool dry season were large and increased dramatically from 39 in 1996 (Goldspink et al. 1998) to 104 in 2009. These larger groups are rather uncommon; although groups of up to 100 individuals were recorded in Zambia (de Vos & Dowsett 1964). But in Kasanka NP they made up 14% of the sightings in

July and comprised about 40% of the observed individuals. This was less in November but still more than in other regions. While selective browsers, in particular if they are small species, are likely to occur in smaller and very small groups, unselective grazers have a potential for larger groups (Jarman 1974, Wirtz & Lörscher 1983, Brashares et al. 2000). Relating group size to feeding style, Jarman (1974) classified puku in one group with lechwe, waterbuck, springbok, most gazelles, impala, greater kudu: "although adult males may be found singly, young males and females very rarely occur singly except when sick or giving birth. Most individuals find themselves in groups between 6 and 60 animals, sometimes as many as 200." This was supported by the findings of this study: although single animals were encountered and small groups made up high amounts of the sightings, most of the individuals were encountered in groups between 6 and 25 individuals in Kafue region and between 6 and 169 individuals in Kasanka NP, respectively. Thus, for puku, it makes a difference if one looks at the occurrence of group sizes or individuals encountered.

Puku in open habitat tended to occur in larger groups than in dense habitat. Variation in social behaviour is observed for other bovids: e.g. buffalo (*Syncerus caffer*), Grant's gazelle (*Gazella granti*), impala or common reedbuck; each form smaller groups in mixed woodlands, scrub or tall grass habitats than they do in short grasslands (Brashares et al. 2000). While keeping sensory contact with conspecifics is more difficult in dense habitat, hiding is less feasible in open habitat and grouping becomes the main anti-predator defence (Wirtz & Lörscher 1983). This generally applies for antelopes but as well for the same species in different types of habitat (Wirtz & Lörscher 1983). The groups of puku split up and merge; nothing indicates a closer relationship between the animals (de Vos & Dowsett 1964). Especially these open groups of puku are likely split up when entering denser habitat (Wirtz & Lörscher 1983), in contrast to cohesive family groups.

Lastly, group sizes of antelopes are a subject of population density (Gerard et al. 2002, Wirtz & Lörscher 1983), especially if they live in open groups (Wirtz & Lörscher 1983) like puku. If groups are non-permanent units, often flushing and splitting up, any increase of the distance at which animals perceive one another could increase the rate of group fusion and thus group size (Gerard et al. 2002). The puku's population densities were higher along the transect lines in Kasanka NP than in Kafue Region, reaching the highest population density along Kasanka River, where most of the observations were made, also on group size. Furthermore, puku reached higher densities in the two study regions in open habitat. These higher population densities, at the scale of the overall study region as well as locally along specific transect lines or in the habitat categories, thus might influence group sizes.

This relation of density and group size as presented by Gerard et al. (2002) might also explain the formation of mixed groups between puku and impala, the kind of mixed group observed most often in Kafue Region. Already de Vos & Dowsett (1964) and Ansell (1960a) stated that puku have more tendencies to mix especially with impala, than waterbuck or lechwe. The two species reached similar densities, which made the formation of mixed groups between these species more probable than any combination with other bovid species. Thus, mixed groups, both in Kafue region and in Kasanka NP, might form rather at random. This was also supported by the variation in number of the two species within mixed groups. However, interspecific association can additionally facilite grazing and reduce predation risk (McNaughton 1988).

Generally, the share of different group compositions of all classified groups was similar in the study regions and reflected the findings from other regions in southern central Africa.

The amount of male groups, including single males, was higher in Kasanka NP, especially in July 2009 (Figure 2-29 A), and rather low in PPKR. While male groups made up 39% in Chobe NP (Dipotso & Skarpe 2006), in July 2009, they reached about 48% of the groups in Kasanka NP. However, in the observation of Child & von Richter (1969) these groups made up about 61%, which is even more than in Kasanka NP. With an amount of 35%, 36% and 40%, respectively, the amount of observed male groups was similar in Kafue NP (this study), in Luambe NP (Rduch 2008) and in Kafue NP and Luangwa Valley reported by de Vos & Dowsett (1964). With 39%, the observed amount of male groups in Kasanka NP in November 2010 fell in this range, too.

The amount of single males is the most often observed group composition in Chobe (Dipotso & Skarpe 2006, Child & von Richter 1969), in Zambia as observed by de Vos & Dowsett (1964) and Rduch (2008), as well as generally during this study, except for Kafue NP. As a compensation, during this study, the amount of breeding groups (Figure 2-29 B) was highest in Kafue NP (26%). Only in Chobe NP, Dipotso & Skarpe (2006) observed a higher amount (36%). Thus, apparently the males observed singly in the other regions were accompanied by females and eventually young puku in Kafue NP. The amount of breeding groups in Kasanka NP was comparable to the values given by de Vos & Dowsett (1964), Child & von Richter (1969) or Rduch (2008), but lower in Kafue Region or in Chobe as given by

Dipotso & Skarpe (2006). Surprisingly, these low amounts of breeding groups in Kasanka NP were not compensated by higher amounts of groups of females with young puku (Figure 2-29 C).

Nevertheless, in all study region, beside male groups, female groups, possibly accompanied by young puku with or without the presence of an adult male, were very common if not the most important group composition of puku. The differences in the amounts of group composition observed in Kasanka NP might be due to the differences in sex ratio when comparing Kasanka NP to Kafue Region.

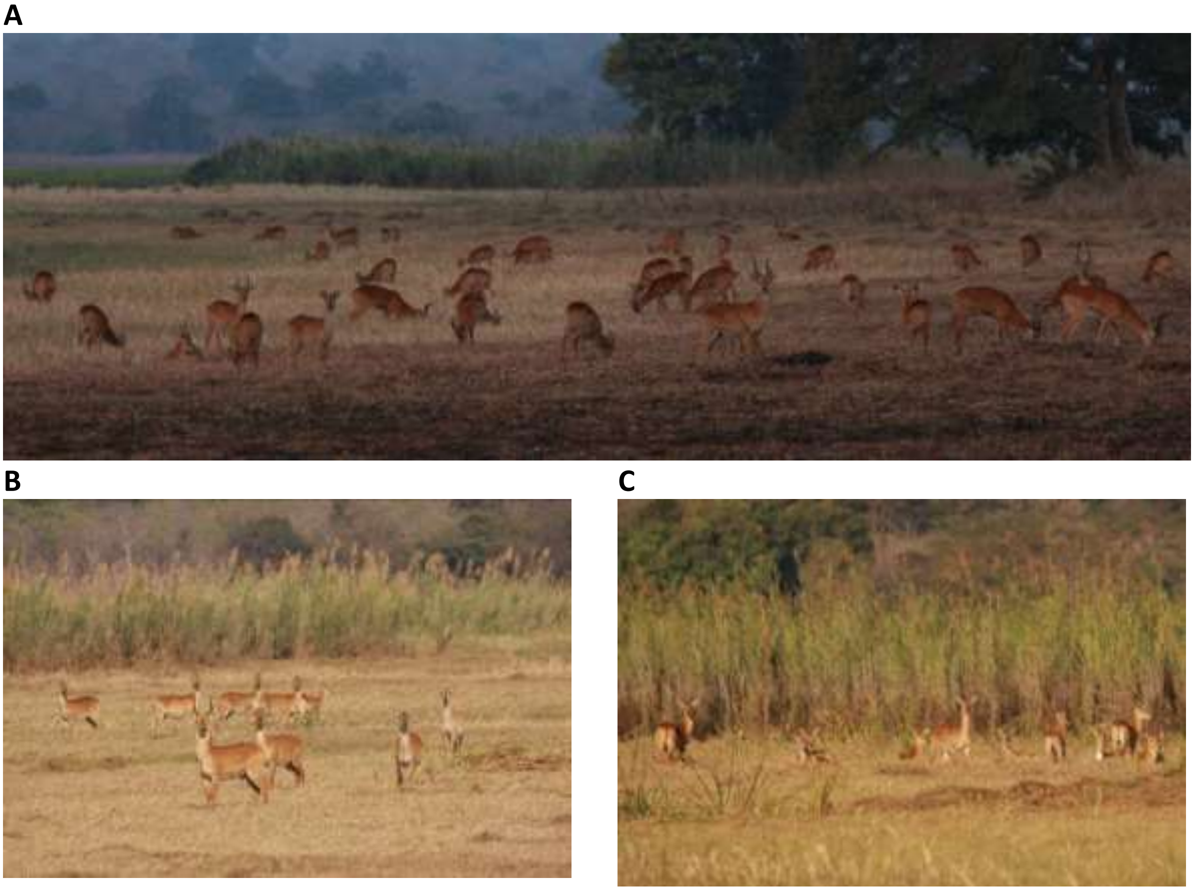


Figure 2-29: Pictures of group compositions of puku (*Kobus vardonii*) observed in Kasanka NP (all taken in the cool dry season 2009): a large of adult males, subadult males and juveniles (A), a breeding group of one male with females and juvenile puku (B) and females with juveniles (C).

In Kafue Region as in other areas in southern Africa, the sex ratio of the puku was biased towards the females. The ratio of females to all males of 1.63 in Kafue Region agrees very well with the findings of other studies. For Chobe NP, Dipotso & Skarpe (2006) reported a sex ratio of 1.42 and Child & von Richter (1969) gave 1.3. In Kilombero Valley, a ratio of 1.21 females per male was found (Starkey et al. 2002). Even higher are the sex ratios from Luambe NP, with 2.7 females per male in open habitat and 1.9 females per male in closed habitat (Rduch 2008). De Vos & Dowsett (1964) presented a sex ratio even higher from Kafue NP: 4 females per male. This is high but supporting the very high observed sex ratios in PPKR of 4 females per all male and 6.35 females per adult male.

Sex ratios biased towards the males were given only by Goldspink et al. (1998) while presenting the range of 0.4 to 6.6 females per male from different sites over Kasanka NP in the cool dry season 1994 with an average of 3.4. The average sex ratio in the cool dry season 2009 was 0.66 (females to all males) and 1.06 (females to adult males), respectively. This is a shift towards a male biased or less female biased population of puku in Kasanka NP. The high amount of males was generally visible through the survey in July, August and October along Puku-Loop. If including the subadult males, the ratio got biased toward the males. In November, this shift was less visible concerning both the entire Kasanka NP and Puku-Loop only. This might be the reason for more groups of adult and subadult males in Kasanka NP, and vice versa of the very occasionally observed adult and/or subadult male groups in PPRK.

The sex ratios in Kasanka NP concerning adult males were in the range of the values cited above from other areas. This difference in sex ratio concerning all males or adult males only was less exhibited in Kafue NP; it was rather exhibited in PPKR, but the sex ratio was still very much biased toward the females in PPKR. Apparently, especially the higher amount of subadult males in Kasanka NP is unusual for populations of puku.

The general statement that births can take place at any time of the year (Skinner & Chimimba 2005, Huffman 2011) can be supported by the observations in Kasanka NP. When speaking about neonate puku, it has to be mentioned that they hide and already Rosser (1989) noted that calves were rather difficult to find. Nevertheless, during all surveys, neonate puku were observed, yet in different amounts; and numbers are rather tendencies than facts. Highest numbers and also amounts of all classified puku of neonates were found in July and November. This might indicate that puku in Kasanka NP avoid the time of the year, which provides less food for the lactating females, e.g. , August and October, as also reported from South Luangwa NP (Rosser 1989). In November, the close rainy season and first rains induce new growth of grasses and thus births. For Kafue Region, as only a total of two neonate puku was observed, the cool dry season is not the time of most births, and that births are more likely to happen in other periods of the year, unlike in Kasanka NP. However, it might be that the puku born during the cool dry season are more likely to be killed by predators (see also Chapter 4).

In Kasanka NP, the amount of juvenile puku was generally decreasing from July to November. At this time of the year, most former juveniles probably had a shoulder height high enough to be classified as females or subadult male, respectively. Despite when comparing the amount of juveniles in the study regions during the cool dry season, the amounts were smaller in Kafue Region, especially in Kafue NP. This result points towards a higher survival rate of young puku in Kasanka NP. The survival of young antelopes as also of zebra affects the development of their respective populations (Sinclair 1979b, Grange et al. 2004). This fact might explain the very high population densities of puku in Kasanka NP, generally along the transect lines, pooled or when considering Puku-Loop local densities only, and in open habitat compared to Kafue Region. This high survival rate of young puku, due to conservation measures of Kasanka Trust Ltd and probably also due to low densities of large predators (see also Chapter 4), might also be the cause of the increase of the puku's population size in Kasanka NP from 1994 to 2009/2010.

The body condition of the puku can provide information on the puku's populations in the study regions. Body condition of puku in Kasanka NP was generally poorer than in Kafue Region; on each survey, 5% of puku showed a poor body condition. Poor body condition was rarely observed in both PPKR and Kafue NP, respectively. Thus, it appears that puku in Kafue Region cope better with the present conditions; resources seem to be available sufficiently for the amount of puku. The surveys in 2009 and 2010 in Kasanka NP have to be considered separately in order to find out about trends throughout a year. Differences in rainfall in the respective preceding rainy seasons might have caused differences in food availability. Indeed the rainy season 2009/2010 resulted in very high precipitations in Kasanka NP (Frank Willems, pers. comm.). In 2009, it appears that less food (of good quality) was available for the puku than in 2010. In August 2009 the general aspect of the body condition in the population of puku was poorest indicating a general 'bad' year for puku. In 2010 apparently more or better food was available. Nevertheless, body condition of puku decreased with the progression of the dry season in the two years, although body condition was generally poorest in August 2009.

However the data on body condition were not collected within the same dry season, though. Thus, the question arises if in Kafue Region, as in Kasanka NP, rainfall in 2008/2009 was lower than in 2009/2010 and if so how puku were affected in Kafue Region.

Furthermore, only in Kasanka P, puku with damaged limbs (Figure 2-30 A), slow or not-healing wounds (Figure 2-30 B) or other injuries were observed to a noticeable amount (own obs.).

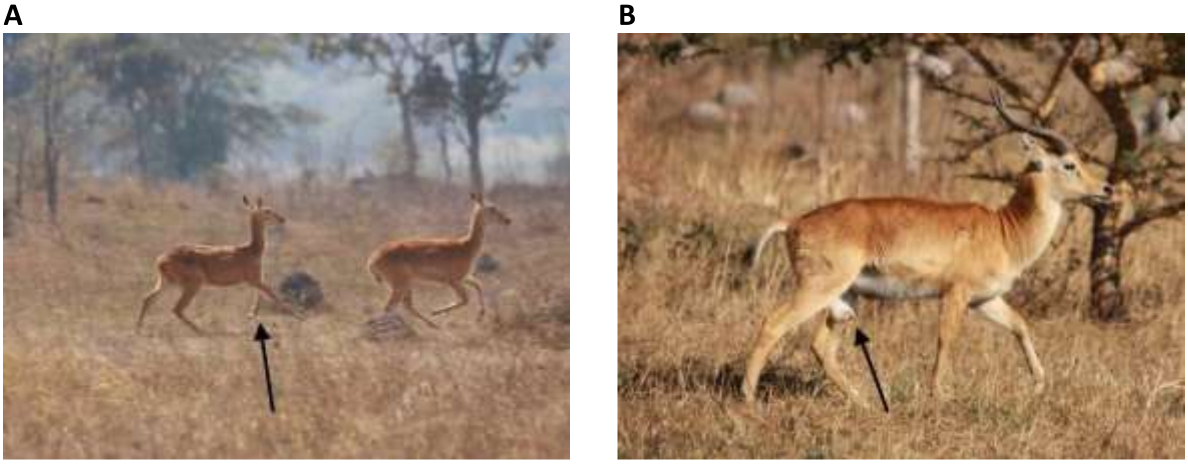


Figure 2-30: Physically disabled puku (*Kobus vardonii*) in Kasanka NP (pictures taken in the cool dry season 2009): a puku with a stiff limb (A) and a puku with an abscess-like injury (B).

2.4.8 Conclusions

Observations during the dry season found puku to prefer in open grasslands near water. Puku in Kasanka NP showed the higher density in open habitats than those in Kafue Region. Estimated local population densities of puku reached almost 150 animals/km². In Kasanka NP, little spatial overlap was observed between puku and other antelopes during both the cool and the hot dry season. A high spatial overlap was observed between puku and impala in Kafue Region in the cool dry season. Waterbuck and greater kudu reached low to medium abundances, the slight overlap between those and puku was present. By integrating the resource use see (Chapter 3), the evaluation of the competition might be improved, since that is by far the most important process and determines relative abundance of bovids (Sinclair 1979a).

Higher amounts of juvenile puku in Kasanka NP than in Kafue Region suggest an increased survival of young puku in the first mentioned region. Thus, Kasanka NP apparently offers perfect conditions for successful reproduction of puku. Generally, juvenile survival, beside age of first reproduction, is a parameter most sensitive to environmental variation and density-dependence (Bolger et al. 2008). Howsoever, survival of young puku is facilitated in Kasanka NP, this leads to density-dependent effects: the social structure of the puku in such a way that sex ratio is biased towards males; especially subadult males were more present in Kasanka NP than in Kafue Region. The observed group compositions showed higher amounts of male-groups and the high numbers lead to large group sizes in Kasanka NP. Lastly, the body condition of puku in Kasanka NP was poorer than the populations of puku observed in Kafue region. The results based on data from the cool dry season 2010 concerning the social structure agreed mostly with the findings of other studies.

The population size of puku in 1994 was reported to be 613.1 (413.6-967.2) puku (Goldspink et al. 1998). This study describes a population size of 5,038 (3,268-7,238) puku for the survey period 2009/2010. This is an eightfold increase within 15 years and a proof for the ongoing purposeful conservation work of Kasanka Trust Ltd. Kafue NP is much larger; not all areas and habitat types were covered by this study. But further investigations are needed in all areas of this huge area in order to get reliable figures of the population of puku in entire Kafue NP.

Unfortunately, the surveys that lead to comparisons between study regions were not undertaken at the same time. Parallel survey in different study regions might increase the reliability of the comparisons of the puku's populations in different areas and decrease the influence of rainfall or other parameters on the results.

In the two study regions, although aimed at, a standardised data collection along line transects was not possible in the late rainy season. The roads used for the line transect were still inundated, at least partly. Thus, observations from the rainy season, based on more than ad libitum observations, are still lacking. This should challenge future research work on the puku. The puku's distribution and habitat use in the rainy season might affect their degree of vulnerability by human activities (Jenkins 2013). Only the knowledge of their entire range of occurrence through the course of a year can assure continuous, purposefully conservation work.

Observations made during the data collection for this thesis indicated differences in distribution and habitat use from day to night-time in the two study regions. In PPKR, it was observed that during night-time puku left the area covered by the transect lines Kafue North, characterised by a high population density at daytime, though. The same was observed for the puku at the artificial waterhole at Puku Pan Lodge (see Chapter 5): they left this area at night-time. Furthermore, in this case they moved eastwards to the more wooded areas, increasing the distance to Kafue River. In Kasanka NP, observation at night could be made along Kasanka River (Puku-Loop transect line). These data still have to be analysed. Nevertheless, it was observed that puku numbers increased along Kasanka River at night.

Data collection at night is difficult, vision is poor and it is not without risk (e.g. possible encounters with hunters, poachers or elephants). That is why, although intended, extensive data collection along the transect lines at night during this study was abandoned. But for a complete view on the puku's ecology these data are needed.

The data about habitat choice of puku give a rough picture only. In order to give more details about the habitats occupied or not by puku, data about habitat characteristics (e.g. greenness or height of grass, soil moisture) were collected at points situated about 250 m away from each other along the transect lines. The envisaged data analyses will relate the observations of puku (and other antelopes) to these points and thus to the habitat characteristics if not situated more than a specific distance from it. By this the habitat used by puku will be described in more details. Furthermore, it should be interesting to relate the puku's forage sites to nutrients in the soil and especially in the plants. Attempts therein have been made during this study and need further evaluation. Nevertheless, it is generally difficult to get plant material in areas where a lot of animals graze. All that could lead to a more detailed picture of the puku's foundation, about food and habitat; this might lead to information which habitat is suits to puku. In this context it is interesting to know that species can be common in unsuitable habitat or absent in suitable habitat (PULLIAM 2000); and it has to be detected which habitat is suitable, difficult to measure, though (PULLIAM 2000). Generally organisms can occur and also be more common in unsuitable habitat that acts as sink, if in source habitat local reproduction is more than sufficient (PULLIAM 2000).

The populations of puku in the study regions should be assessed regularly in order to detect changes in the populations. This study is only a first step in giving actual information about the puku's population status in Zambia; recent data about the puku's population status in whole Zambia are hardly available. Thus, in other (protected) areas in Zambia puku should be surveyed. It is recommended to not only collect data about the numbers of puku but also data of the social structure and the puku's body condition. Only by doing so, as shown in this study, a real assessment of the puku's population status is possible in order to improve and adjust purposeful natural conservation measures.

3 Diet and dietary overlap of puku and other bovids

Abstract

Resource partitioning of food enables sympatric occurrence of bovids in Africa. Diets of puku (*Kobus vardonii*) and selected other bovid species were assessed to evaluate the competition status. Data comes from both Kasanka NP and Kafue Region and were collected in different seasons. For puku, sexes were evaluated separately.

A reference collection of the epidermis of grasses was compiled in order to perform microhistological analyses of bovid dung samples in the study regions. Diets composition was assessed and preferences were calculated via the Jacobs index, based on the relative abundance of the grasses. Via the Pianka Index and principal component analyses the diets were analysed for potential overlap.

Through all seasons and study regions puku, confirmed as hypergrazers, fed on *Panicum* spp., *Brachiaria* sp., *Sporobolus* spp., *Hyparrhenia*/*Andropogon* grasses and *Eragrostris* spp., in different amounts. Differences between sexes were observed, especially in the cool dry season in Kasanka NP. Probably diets of bachelor males differed from both territorial males and females. The results of PPKR suggest a similar diet for puku females and territorial males. The amounts of grass species changed between seasons. The puku’s dietary niche was broadest in the cool dry season and narrowest in the late rainy season. In Kasanka NP, the analysis of puku dung from different sites revealed a high spatial variation in the puku’s diet which suggests an opportunistic food choice.

Reedbuck (*Redunca arundinum*), sable antelope (*Hippotragus niger*), hartebeest (*Alcelaphus lichtensteinii*) and buffalo (*Syncerus caffer*) in Kasanka NP as well as impala (*Aepyceros melampus*) and waterbuck (*Kobus ellipsiprymnus*) in Kafue Region fed mainly on the same grasses as puku, but took only very low amount of *Brachiaria sp*. and *Sporobolus spp*. Reedbuck and hartebeest consumed *Loudetia* sp.; sable, impala and waterbuck considerably added browse to their diet. Sitatunga (*Tragelaphus spekii*) fed differently from puku and even more from other bovids. While there was a slight overlap in the cool dry season, there appeared virtually low to zero dietary overlap in the hot dry season between puku and other bovids in Kasanka NP.

In Kafue Region, due to changes in the impala’s diet that increased the amount of grasses in the late rainy season, the dietary overlap between this antelope and puku increased in the late rainy season, and was rather low in the cool dry season.

Sympatic occurrence of puku and impala at similar population densities in Kafue Region might be explained by dietary differences especially in the cool dry season. Thus, generally low dietary competition might be one reason for high densities of puku.

“Animals are not always struggling for existence, but when they do begin, they spend the greater part of their lives eating. Feeding is such a universal and commonplace business that we are inclined to forget its importance. The primary driving force for all animals is the necessity of finding the right kind of food and enough of it. Food is the burning question in animal society, and the whole structure and activities of the community are dependent upon questions of food-supply.”

Elton 1927

3.1 Introduction

Herbivore populations can be regulated by predators (top-down) (see Chapter 4) or the resources i.e. the plants limit the herbivores by low forage and/or constitutive and inducible plant defences (bottom-up) (Sinclair et al. 2003, Terborgh et al. 2001). Intense grazing can affect the ratio of palatable to unpalatable grass species, increasing the resistance of the vegetation and reduce the carrying capacity for grazers (Terborgh et al. 2001). Beside the direct influence of these factors, resources can also be used by other herbivore species which leads to competition. This study is the first that attempts to assess the puku’s (*Kobus vardonii*) diet and of possibly competing bovid species via microhistological analyses of dung samples in Zambia:

- Which plants constitute the diet of puku in the study areas? Are there any differences between sexes? Do the diets change within the course of a year? Generally puku are suggested to graze to high amounts. Food plants in the study region might be alike as the two lie within the miombo ecoregion.

- What about the overlap between puku and other bovid species concerning their diets? The dietary overlap between bovid species is generally higher during the times of food scarcity, i.e. greater overlap in the hot dry season than in the cool dry season (the middle of the dry season) where every species withdraws to its food refuge. Generally, sympatric occurrence with other antelopes might be favoured by different diets.

Puku are classified as grazers (e.g. Child & von Richter 1969, Gagnon & Chew 2000). Gagnon & Chew (2000) reveal a proportion of 93% monocots and 7% dicots in the food plants of the puku and classify it as “obligate grazer”. Puku are reported to browse on the shrubs only sometimes; otherwise, they will also graze in woody areas (Dipotso & Skarpe 2006). But apart from the general classification of the puku's food preferences, regarded as not reliable by Gagnon & Chew (2000), there is a high need to assess their diets. Most of the grazers are said to be choosy, as it is known for a lot of browsers and often attributed to them only (Hofmann 1989). Studies of Child & von Richter (1969) and Rosser (1992) on the food plants of puku – based direct observations and the use of vegetation communities – are available. A PhD thesis provides information about the diet of puku in Chobe NP based on both direct observations and faecal analysis (O'Shaughnessy 2010). All studies were carried out along Luangwa and Chobe River and thus in the big valley regions. Up to now, Rosser's study is the only one that gives information about the diet of puku in Zambia. For Tanzania, some information is provided by Vesey-FitzGerald (1965) and by Jenkins (2013).

It is the first time that the puku's diet is evaluated in Kasanka NP and at sites in Kafue NP and adjacent GMA. Down to the present day, no study reveals the diet of puku within the miombo ecoregion. As shown by transect line sampling and camera trapping other bovid species occurred in the study regions (Chapter 2). Aiming at evaluating the competition status between puku and other bovid species in their distribution areas, the assessment of diets of several other bovid species might reveal interesting information. Still focussing on the ecological niche of the puku and its competition status in Zambia, only bovid species having a reported average proportion of monocotyl plants of more than 65%, as reported by Gagnon & Chew (2000), were considered as potential competitors and selected for the analysis. The only exception was the impala (*Aepyceros melampus*), first because it reached similar overall and local population densities (Chapter 2) and second because it is reported to have variability in its diet (Gagnon & Chew 2000). Food plants might influence occurrence of animals (Barthlott & Martens 1979) and both can vary over space and time (Jarman & Sinclair 1979). Dietary analyses reveal overlap in food resource use and thus competition (Gray et al. 2007, Capello et al. 2012). The understanding of resource use and partitioning among species is of direct relevance to private ranches (Gray et al. 2007) and of national parks (Jarman & Sinclair 1979, Barthlott & Martens 1979) in matters of conservation and management.

No attempt is made to incorporate the diets of other animals as other ungulate species like zebras *Equus* or the hippopotamus *Hippopotamus amphibibus*, rodents (Rodentia) or insects (Insecta) like termites (Isoptera) or grasshoppers (Orthoptera); the results of this study will give insights into bovid society only.

Concerning African bovids competition for food resources is one key to understanding sympatric occurrence. It is supposed to be one if not the most important factor for bovid radiation in Africa (Estes 1991, Sinclair 1983, McNaughton 1979). Bovids have subdivided the African ecosystem into small segments: by adapting their size, their feeding apparatus, their digestive system and their dispersion patterns, they are able to specialise more narrowly and efficiently than other ungulates (Estes 1991). While some species go more for the plant cell contents, some are adapted to the fermentation of the plant cell wall (Hofmann 1989). Several attempts have been made to classify feeding types of bovids: e.g. Hofmann (1989), who rejects the classical “browser” and “grazer” classification, proposes “concentrate selectors”, “intermediate types” and “grass/roughage eaters”. Gagnon & Chew (2000) present a classification of six dietary strategies, depending on the amount of monocots, dicots and fruits in the diet. Ruminants are able to profit nutritionally from what is useless to humans: they can use cellulose, hemicellulose and pectin that seem indigestible (Hofmann 1989). The ruminant digestive system is characterised by a “complicated morphological master plan” that varies between species (Hofmann 1989). Ruminants are characterised by what the layman calls four stomachs, which is in fact one stomach divided into four compartments: the rumen, the reticulum (sometimes referred to as a single organ: the reticulorumen), the omasum and the abomasum (van Soest 1994). The morphological features of the puku’s ruminant digestive system match with the typical characteristics of a bulk and roughage eater as presented by Hofmann (1989). Puku have a large subdivided rumino-reticulum, the pillars lack definite papillae, the rumen papillae are unevenly distributed, the reticulum is medium-sized and the omasum is large (Skinner & Chimimba 2005). Pillars divide the rumen into pouches and papillae absorb nutrients (van Soest 1994). Indeed, in the reticulorumen, the main parts of fermentation and absorption take place (van Soest 1994). A large rumen allows more time for fermentation of fibrous food (Sinclair 1983). In addition to the variation between species, this digestive system is very flexible: individuals can adapt to different diets and nutrient requirements; also seasonal adaptations to changing forage availability are possible (Hofmann 1989). Fermentation and digestion of food depend on microorganisms in the digestive system. The exact composition of the microorganism alters according to the diet. It takes some time for the bovids to deal with new food – especially after abrupt changes (van Soest 1994). As a consequence, not every food item is digested the same way all the time (Putman 1984).

Direct observation of the animals, although requiring minor equipment, lacks accuracy in species identification and quantification of the amount of consumed plants (Holechek et al. 1982). Thus a detailed determination of the food plants is hardly possible (Barthlott &

MARTENS 1979). Furthermore, wild animals are often difficult to locate and to observe (HOLECHEK et al. 1982). Other commonly used methods in determining the animals' diet are the analysis of the stomach or of the intestinal tracts, but this requires to sacrifice an animal (HOLECHEK et al. 1982). Otherwise fistulae are employed, but they are not suitable for wild ruminants (HOLECHEK et al. 1982).

In order to find out more about the food plants of bovids in the study regions I used microhistological analyses of faeces. Plant epidermises – coated with cuticula and thus soaked with cutin – are very robust (BARTHLOTT & MARTENS 1979). They withstand the passage through the digestive system of herbivore species: in consequence, fragments of epidermal tissues of plants can be found in the faeces of animals (STEWART 1967, BARTHLOTT & MARTENS 1979) which makes the analysis of the relative importance of different grasses in the diet possible (STEWART 1967). Some main advantages are summarised by HOLECHEK et al. (1982): Faecal analyses do not restrict the normal habits of the animals nor theirs movements; it is the only way to get to know about the diet of secretive and/or endangered animals; the diets of two or more animals at the same time can be compared; and the sampling is practically unlimited and requires very little equipment. But HOLECHEK et al. (1982) also give disadvantages: there is no information about where the food was consumed; the identification of faeces might be a problem; an extensive plant collection is required; training and time are needed to identify the plant fragments; not all species might be identified; and fragmentation may differ between species during digestion. To counteract the latter disadvantage, STEWART (1967) proposes to give the proportion of the consumed plants as a proportion of the area of the fragments. According to MÜHLENBERG (1983), faecal analysis and rumen content analysis agree mainly in their results.

To assess the diet of bovids via microhistological analyses, knowledge of the grasses in the study areas is indispensable. Grasses occurring in the study areas have to be determined and a reference collection of their epidermal cell patterns has to be established. Up to my knowledge, this is the first time that such a reference collection is compiled for grasses in Zambia.

3.2 Material & Methods

3.2.1 Assessment and collection of grass species

Grasses were sampled at sample points that extend along the transect lines in Kasanka NP (Figure 3-1) and in Kafue Region (Figure 3-2, Figure 3-3). There sample points are situated at a distance of approximately 250 m from each other and about 15 m from the transect line, i.e. from the road. At each point, the grasses were checked; inflorescences facilitated the identification. This resulted in presence/absence information of grass species at each point. New grasses were photographed (habitus and inflorescence), their leaves were collected and air-dried and stored either in plastic zip bags or in plastic tubes. In the field, grasses were collected and sampled under 'field names'.

Figure 3-1: Sample points along the transect lines in Kasanka NP that were checked for presence/absence of grasses in all survey periods.

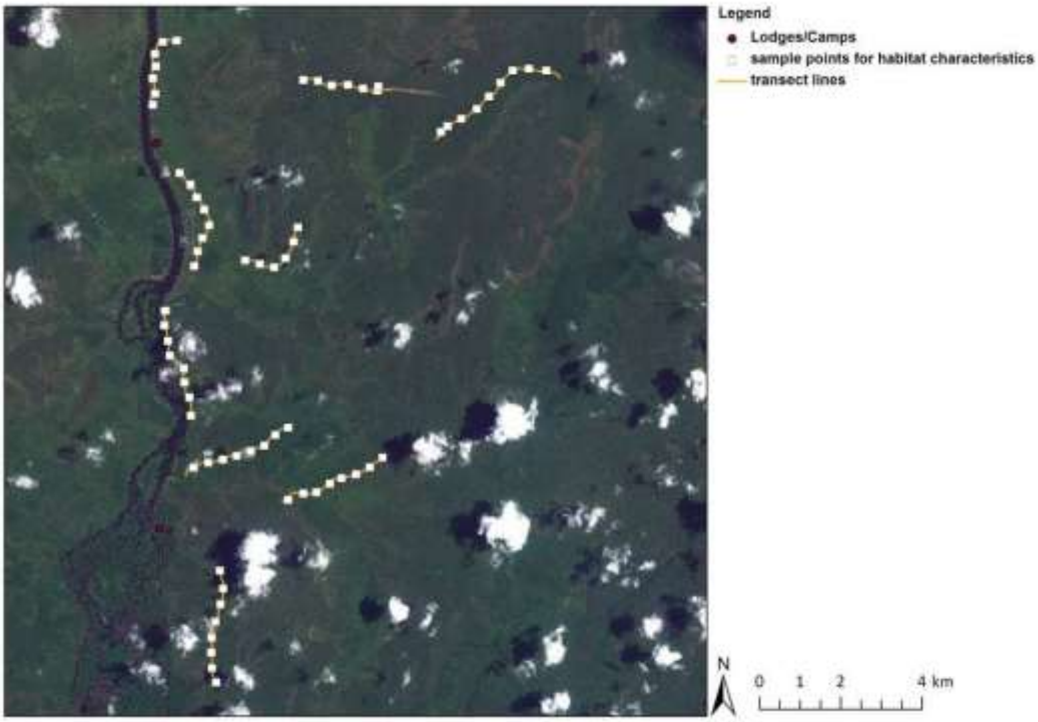


Figure 3-2: Sample points along the transect lines in PPKR that were checked for the presence/absence of grass species.

Figure 3-3: Sample points along the transect lines in Kafue NP that were checked for the presence/absence of grass species.

In Kasanka NP, these points were checked three to four times: in the cool dry season 2009 (from 11th July to 7th August 2009) in the hot dry season 2010 (from 7th to 12th October 2010, for the transect lines Luwombwa, Chikufwe, Katwa, Kafubashi and Puku-Loop; from 8th to 12th November 2010, for all transect lines except Mulembo) and in the late dry season 2011 (from 15th to 21th April 2011, except Mulembo). In Kafue Region, the points were checked only once during the cool dry season 2010 (from 23th July to 22th August 2010 in PPKR and from 29th August to 3rd September 2010 in Kafue NP).

Grasses were determined mainly afterwards at the ZFMK, with the help of the photographs and some collected inflorescences. For an initial determination approach, I was assisted by Fritz Van Outshoorn. Further determination was carried out using the following references: Van Outshoorn (2009), Bingham et al. (2012), Watson & Dallwitz (1992 onwards). Additionally, the epidermal layers were compared with the figures and descriptions given by Barthlott & Martens (1979) or Gutbrodt (2009). Thus, identification of species was done with the help of the inflorescences and growth habit as well as epidermal characteristics. Then, the determined grasses were pooled with identical grasses still bearing different 'field names'. Maps created using ESRI ArcMap 10.0 showed the distribution of grass-genera, the same taxa as for the reference collection. Thus, a comparison of the diets of bovids with the distribution of grasses was possible. This was done for Kasanka NP only, as one season was felt to be insufficient to evaluate the distribution of grass species in Kafue Region. With respect to grazing, fire and the growing cycle, for Kasanka NP, the exact grass species composition at many sample points could only be assessed as a result of all field-trips.

3.2.2 The reference collection of grasses

The epidermis cells of dicotyledons are arranged in a scattered, unlinear way. In dicotyledon leafs, the stomata follow this scattered arrangement, whereas stomata in fruits are rare (Mühlenberg 1983) (Figure 3-4 A). In the monocotyl epidermis, leaf veins, general arrangement of cells as well as stomata are parallel (Figure 3-4 B-F). The structures and arrangements of differently shaped cells in the epidermis are specific for each plant species, especially the Poaceae have very variable epidermal structures (Barthlott & Martens 1979) that can be discriminated by checking the following characteristics (after Barthlott & Martens 1979): i) the general patterns of cells in the epidermis, i.e. the arrangement of cells in the costal and intercostal, the undulation of the cell walls of long cells in the intercostal

and the abundance and situation of short cells; ii) shape, abundance and situation of silica bodies in the short cells, stomata, papilla and trichomes (long hairs, pickle hairs and micro hairs).

The epidermal layers of the grasses were gained by mechanical isolation. Using a scalpel, the cellular layers above the epidermis were removed. The isolated tissues were fixed with nitrocellulose (i.e. transparent nail polish) on microscope slides and covered with a cover slip. The reference slides were viewed and photographed with a microscope (Olympus BX41) and a microscope camera (Olympus DP21). All pictures for reference purposes were taken at 200fold magnification to allow direct comparison of the proportions in each grass. Generally, both sides were prepared and viewed. The abaxial side of the grass leaves showed differentiated epidermal structures – and in most cases it was easy to prepare. This was not the case in the adaxial sides of the leaves: they were difficult to isolate, showed low structural differences and mostly lacked features for identification, a fact already stated by Barthlott & Martens (1979). In consequence, this reference mainly refers to the abaxial epidermal structure of the grasses.

As it was found that epidermal structures of closely related grasses resemble each other, a differentiation between species was considered to be inconclusive and hence was not conducted. Thus, some genera were represented by more than one species in the study areas e.g. *Eragrostis*, *Hyparrhenia* or *Panicum*. Additionally, due to their similar structure of the epidermis, the genera *Hyparrhenia* and *Arthropogon* were pooled into one group. The only non-Poaceae plant that could be clearly identified to species level and prepared for this reference collection is *Cyperus papyrus*. Other plants were further determined as Cyperaceae. It was discovered that they lack a lot of those diagnostic features which would have been needed in order to obtain a good determination in the dung samples. Thus, they were not further determined to species level and excluded in the reference collection.

The two study regions belong to the Miombo ecoregion. Therefore, the entire reference collection was applied for the two study regions although not all grasses were recorded in both study regions. The complete reference collection with descriptions of the epidermal layers is provided in the Appendix (Figure A. 6 to Figure A. 11).

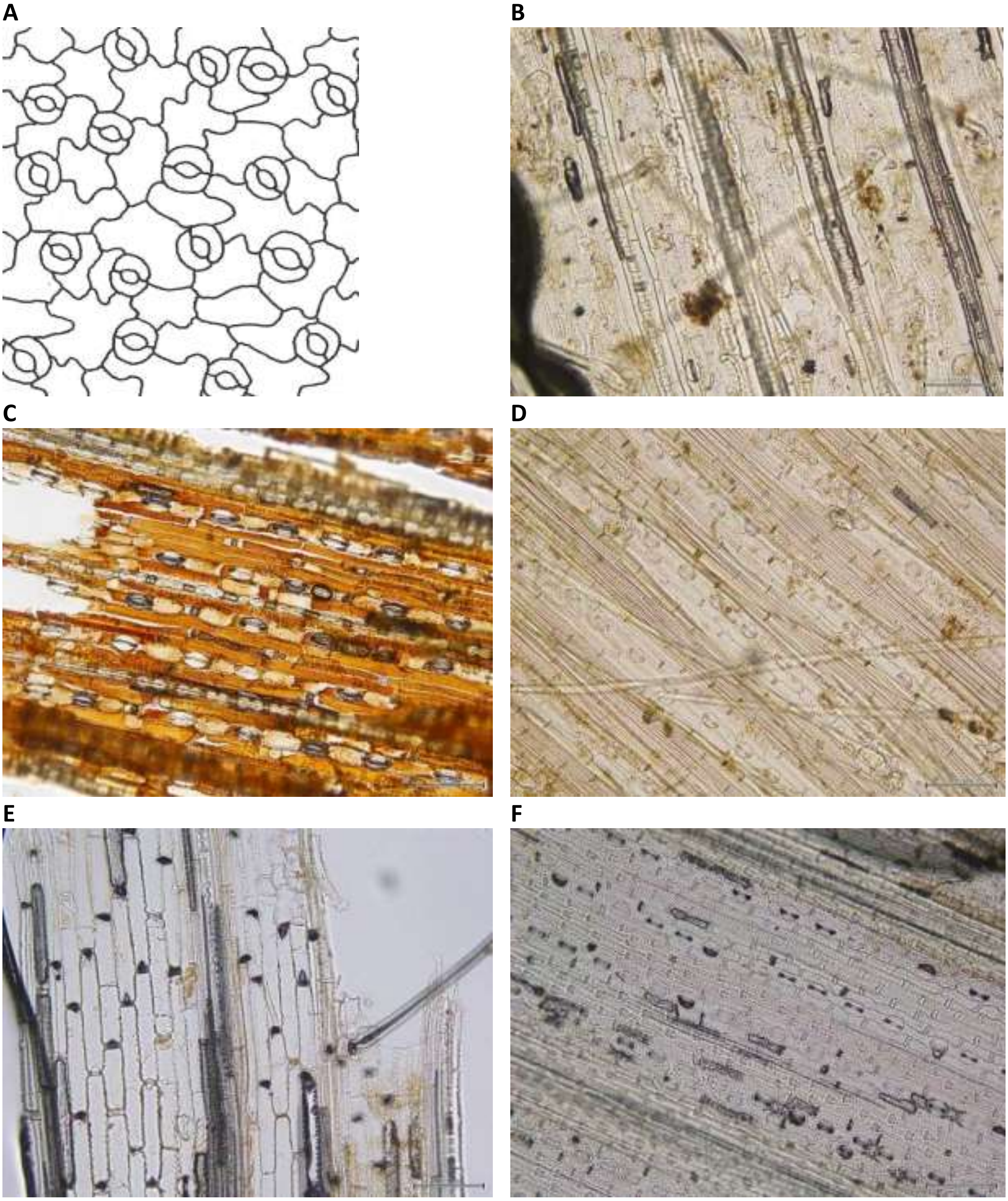


Figure 3-4: Examples of epidermal layer in plants: epidermal layer in dicotyledon leaf (A) (Modified after Mühlenberg 1983). Epidermal layer from the reference collection: *Brachiaria sp.* (B), *Hyparrhenia nyassae* (C), *Eragrostis congesta* (D), *Panicum maximum* (E) and *Sporobolus africanus* (F). All scales give 100 µm, magnification: 200fold.

3.2.3 Collection of faecal samples of bovid species

In Kasanka NP, the general collection of puku dung took place along the transect lines Puku-Loop, called the “Kasanka River puku” and meant when puku in Kasanka NP are not further specified. Additionally, I collected dung of puku at further sites in Kasanka NP (called puku-regional, see Figure 3-6 for locations and labels); 6 dung samples were taken from the ground. In Luwombwa Area (P-0) only 4 dung samples were found and entered the analysis. This was done only during the cool dry season 2009. Dung of reedbuck (*Redunca arundinum*), sable antelope (*Hippotragus niger*) and Lichtenstein’s hartebeest (*Alcelaphus lichtensteinii*) was found at Chikufwe Plain only. Dung of buffalo (*Syncerus caffer*) was found at Chikufwe and near the confluence of Kasanka and Mulembo River. Dung of Sitatunga *Tragelaphus spekii* was found by WPO in the Fibwe Swamp in 2009 and in the Kasanka River floodplain in 2010 (Figure 3-5). Dung samples were collected in all seasons: during the cool dry season 2009 (3rd July to 29th August 2009), during the hot dry season (between 5th and 17th October 2010 for puku and between 13th October and 5th November for other bovids), after the first rains (from 15th to 17th November 2010) and during the late rainy season (16th April 2011).

Figure 3-5: Localities of dung samples of different bovid species in Kasanka NP. The puku-regional samples are shown in Figure 3-6.

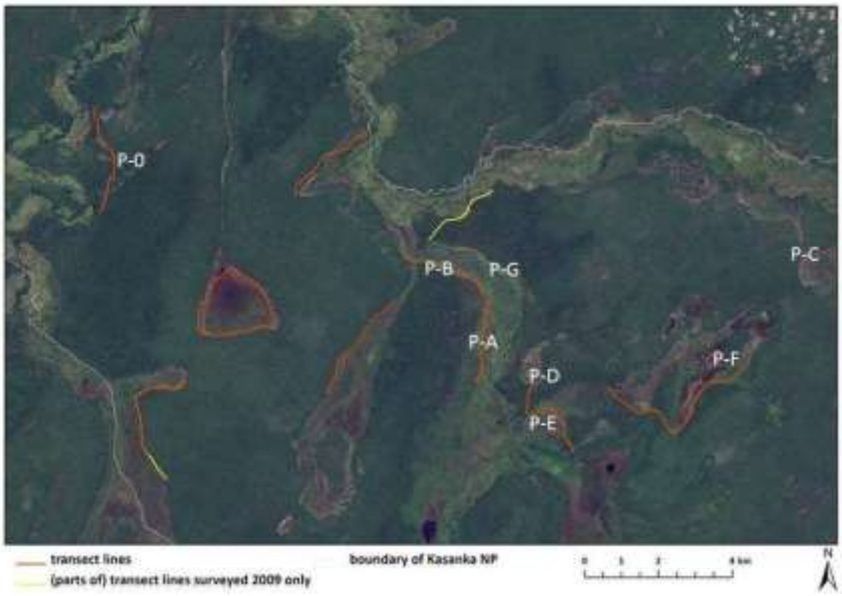


Figure 3-6: Location and labels of puku-regional samples. P-O: Luwombwa Area, P-A: Puku-Loop, southern end, P-B: Puku-Loop, northern end, P-C: New Airstrip, P-D: Chisamba Waponde, P-E: Fibwe-Plain, P-F: Wasa Area, P-G: Kasanka River, eastern border.

In Kafue Region, the collection of puku dung was spread over the study areas along all transect lines (Figure 2-4, Figure 2-5) – with a slight focus on the area around the artificial waterhole at PukuPan Lodge for PPKR especially in the late rainy season, for safety reasons. Dung of impala (*Aepyceros melampus*) and waterbuck (*Kobus ellipsiprymnus*) was collected. Data collection took place during the cool dry season in PPKR (from 10th July to 27th August 2010), during the cool dry season in Kafue NP (from 27th August to 6th September 2010) and during the late rainy season (from 5th May to 7th May 2011) in PPKR around PukuPan Lodge only

Although intended, dung could not be collected from all all possible competitors of puku occurring in the study regions. Collected dung was labelled, if necessary air-dried, and stored in plastic bags. If possible, six dung samples were collected per species, per sex in puku only, per season and per study area. Generally, dung of puku was taken only if an animal was observed while defecating, which allowed a differentiation between males and females. Only dung of adult puku was taken. For the first mentioned condition, two exceptions were made: In the late rainy season, as puku were scattered over Kasanka NP (see Chapter 2.4.3), and while taking the puku dung samples of different regions in Kasanka NP, droppings were taken from the ground. For other bovid species, taking the dung from the ground was the adopted method in most cases. Attention was paid to collect the freshest dung samples. WPO escorted and assisted the search for dung sample; they shared their knowledge of the identification of dung from different antelope species. Antelope species only show slight differences in shape and size of their dung pellets and resemble each other in many ways (Figure 3-7 A-D). Only the dung of buffalo is quite characteristic (Figure 3-7 E).

Figure 3-7: Dung from different bovid species. A: puku (*Kobus vardonii*), B: Reedbuck (*Redunca arundinum*), C: sable antelope (*Hippotragus niger*), D: Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*), E: African buffalo (*Syncerus caffer*), F: midden of impala (*Aepyceros melampus*). Pictures A-E from Kasanka NP, picture E from PPKR. (Pictures B and C taken by JUDITH KROBBACH)

3.2.4 Analysis of faecal samples

About 5 to 7 g of each dung sample, i.e. about 8 to 10 pellets, was taken for preparation and entered the analyses. The dung of puku-regional was pooled into one subsample per site: two pellets from each dung sample were mixed into the subsample. The procedure for the preparation of the dung samples for analysis generally followed the methods presented by Hooimeijer et al. (2005), Gutbrodt (2006), Suter et al. (2004) and de Jong et al. (1995). The samples were first ground in a mortar to crush up the pellets. Secondly, the samples were put into glass containers. Tap water was added, the lid was put on. These containers were processed at 100°C for 70 minutes in an oven. Then, they were left to soak overnight (Hooimeijer et al. 2005, Gutbrodt 2006). Thereafter, the samples were mixed for 1 minute in a household blender and some more tap water was added (Gutbrodt 2006, de Jong et al. 1995). The sample was washed with tap water over a plankton sieve (Hooimeijer et al. 2005) with a mash size of 200 µm. As the samples were to be analysed at a later date, the sample was washed and transferred into 70% alcohol (Gutbrodt 2006, Hooimeijer et al. 2005).

For the analysis, some drops of the sample were put on a microscope slide. They were spread out evenly, a few drops of water were added when necessary and all was covered with a cover slip. By scanning the slides on transects, 100 fragments (Gutbrodt 2006, Hooimeijer et al. 2005, de Jong et al. 1995) were examined for each sample. This was done with a microscope Olympus BX41 at 200fold magnification. Only fragments recognised as epidermal tissues were considered. Furthermore, they had to be characterised by a minimum of 4 visible cells. Fragments were categorised according to their origin of monocotyl and dicotyl plants. Some fragments could not be assigned to any of these categories and remained ‘undetermined’. For monocotyl plant fragments, a more detailed determination on genus/species-level was intended. If they could not be determined any further, they were added to the ‘undetermined monocotyl’ group. The relative area of each considered fragment was estimated via the scale in the microscope ocular. The proportion of different grasses in the sample was estimated by measuring the area of the fragments. Counts of fragments are invalid as grasses may break into fragments differing in size (Stewart 1967). Thus, results are not based on the number of fragments but on the proportional fragment area of each plant in the samples.

3.2.5 Data analyses

Different calculations were performed to assess niche breadth and overlap in relation to diet. Depending on the amount of different plants in the diet, the diet breadth can be calculated via the Levin's index as presented by Colwell & Futuyma (1971). The diet breadth B was calculated from the proportion *P* of plant species *i* in the diet: $B = (\Sigma p_i^2)^{-1}$. The value of B increases with decreasing niche breadth (Colwell & Futuyma 1971). A standardised form gives $B_{standard}$ calculated from B where B_{max} is the total number of categories in the diet: $B_{standard} = (B – 1) / (B_{max} – 1)$. Values of $B_{standard}$ range between 0, minimum diet breadth, and 1, maximum diet breadth (Phillips et al. 2007). Differences in diet breadth were tested using one-way and two-way ANOVA. If the variables show significant results in the Levene test of homogeneity of variance, the KW-test was used instead.

In order to assess food preferences of the bovid species, the Jacobs Index (Jacobs 1974) was used: $D = (r-p) / (r+p-2pr)$. In the case of this study, r is the ratio of the plant in the diet, and p the fraction of the plant in the environment. Only plants with an availability of more than 5% were included in the analysis because otherwise they might not be well represented (Palomares et al. 2000). The Jacobs index results in values from -1, meaning avoidance, to 1, indicating maximum preference. As exact grass species composition could not be evaluated for Kafue Region, the preference analysis via the Jacobs index was carried out for Kasanka NP only. Results of the dung samples were checked for preferences with the results in the presence/absence data of grasses from the adjacent transect line. This was not possible for some puku-regional samples and the sitatunga samples from 2009. The mean values of the puku-regional samples and the buffalo samples were compared to the overall presence/absence of grasses.

Overlap of diets was calculated using the Pianka index (Pianka 1974), one of the most widely used indices: $O_{ij} = \Sigma (X_{ik} * X_{jk}) / ((\Sigma X_{ik}^2) * (\Sigma X_{jk}^2))^{1/2}$. The overlap O_{ij} between two bovids $_i$ and $_j$ was calculated from the proportion of plant species $_k$ in the diet (Prins et al. 2006, Hurlbert 1978). The mean values of the samples were the basis of the analyses. The Pianka index reaches values between 0, no overlap, and 1, total overlap of the compared diets. A Principal Component Analysis (PCA) was carried out to check for differences between bovids and between seasons. All samples were taken into consideration. It resulted in components that allowed an evaluation of the overlap between the diets. As the food composition of the bovids included fewer plants in the Kafue Region, two PCA were conducted: one for each study region.

For waterbuck in Kafue-Region (Kafue NP) in the cool dry season 2010, and male puku in Kafue-Region (PPKR) in the late rainy season 2011, only 3 and 2 dung samples were available. They did not enter the statistical evaluation of the data.

Statistics were carried out in SPSS 13.0. This program was used to create the graphs of the PCA. Other diagrams were created using Microsoft Excel 2010.

3.3 Results

3.3.1 Grass species in the study regions

The assessment of grasses in the study region resulted in 15 grass genera (including the group *Hyparrhenia/Andropogon*) that were found at the sample points along the transect lines in Kasanka NP. In Kafue Region, only 10 grass genera (including the group *Hyparrhenia/Andropogon*) were found. *Phragmites australis* and *Cyperus papyrus*, included in the reference collection of grass epidermis, were not found at the sample points.

Table 3-1: Occurrence of grass species in the study regions expressed by the number of sample points (absolute and relative) along the transect lines. * Grass not sampled at all in Kafue Region.

grass taxon	Kasanka NP		PPKR		Kafue NP	
	absolute	%	absolute	%	absolute	%
Brachiaria sp.	25	42.37	*		*	
Cynodon spp.	1	1.69	2	2.82	1	3.57
Digitaria sp.	15	25.42	27	38.03	3	10.71
Eragrostis spp.	33	55.93	19	26.76	5	17.86
Hemarthria altissima	7	11.86	*		*	
Hyparrhenia/Andropogon-Group	52	88.14	65	91.55	24	85.71
Loudetia sp.	14	23.73	*		*	
Melinis nerviglumis	7	11.86	*		*	
Oryza ssp.	1	1.69	0	0.00	1	3.57
Panicum spp.	35	59.32	6	8.45	0	0.00
Pennisetum sp.	4	6.78	1	1.41	0	0.00
Pogonarthria sp.	1	1.69	1	1.41	0	0.00
Setaria spp.	14	23.73	11	15.49	2	7.14
Sporobolus spp.	31	52.54	10	14.08	7	25.00
Tristachya sp.	3	5.08	*		*	
number of sample points	59		71		28	

In all study areas, grasses of the *Hyparrhenia/Andropogon*-Group were found at most of the points – only at a few sample points in all study areas these grasses were absent. Other genera that were found in high amounts in all study areas are *Eragrostis*, *Setaria* and *Sporobolus*. *Digitaria* was found at a higher number of points in PPKR than in Kasanka NP. *Panicum* was found much more often in Kasanka NP than in Kafue Region. Grasses of the genera *Brachiaria*, *Hemarthria*, *Loudetia*, *Melinis* and *Tristachya* were not found at all in

Kafue Region. On the contrary, no grass was found that was specific to the Kafue Region only. Generally, in Kafue Region, other grasses except *Hyparrhenia*/*Andropogon* were found in much smaller numbers than in Kasanka NP.

Distribution of grasses was assessed for Kasanka NP only. The results of the most abundant grasses are shown by the distribution maps given in the Appendix (Figure A. 12 to Figure A. 21).

3.3.2 Diet of puku and other bovid species

A total of 150 (sub) samples of dung were viewed under the microscope, which led to 15,000 observed fragments.

The diet of puku in Kasanka NP, when speaking of the **Kasanka River puku**, (Table 3-2) was marked by a very high amount of grasses. The amount of monocotyl plants was always above 99%. The diet comprised 15 grass species. Dung samples of puku could be collected during all seasons including after the onset of the rains in November 2010. Except for the late rainy season 2011, a differentiation between male and female puku was possible. Grasses with a generally high amount in the diets were *Brachiaria* sp., *Panicum* ssp. and *Sporobolus* ssp. with the males having a generally higher amount in *Brachiaria* sp. than females through all seasons. This grass was taken especially in the hot dry season, after the onset of the rains and above all in the late rainy season when contributing to 66% to the puku's diet. In the cool dry season, *Brachiaria* sp. had an amount of only 10% and 14% in females and in males, respectively. Except for the period after the onset of the rains, *Panicum* ssp. was taken in higher amounts by females than by males. The amount of this grass in the diets remained relatively high throughout all seasons and was highest in the cool dry season with 36% in females and 26% in males. *Sporobolus* ssp. was taken by male puku in the cool dry season with an amount of 33% in the diet, whereas it reached only 2% in females in the same season. It was the third-important grass for males, but not for females, in the hot dry season and after the onset of the rains as well as for puku in the late rainy season. In female puku, the *Hyparrhenia*/*Andropogon*-grasses were the third-important plants, but without reaching high values neither in the hot dry season nor after the onset of the rains. In the cool dry season, puku females showed a fairly high amount of *Phragmites australis* in their diets. The food spectrum of puku was generally broader in the cool dry season, as amounts of different grasses were relatively equal; diet breadth values and the number of food items per sample were relatively high. The puku's diet was narrow in the late rainy season, where *Brachiaria* sp. made up 2/3 of the diet while other grasses were poorly consumed. *Oryza* sp. and *Tristachya* sp were not found in the diets of puku. The grasses *Loudetia* sp., *Melinis nerviglumis*, *Pennisetum* sp. and *Cyperus papyrus* were taken in very small amounts only. *Cynodon* sp., *Digitaria* sp., *Hemarthria altissima* and *Setaria* spp. were taken in relatively small but more consistent amounts. *Eragrostis* spp. was found in small to sometimes medium amounts in the puku's diet.

The results of the **puku-regional** (Table 3-3) samples collected in the dry season showed a mean amount of 99% monocotyl plants. The amount of dicotyl plants in the diets of puku was highest at P-0 when they reached more than 6% of the diet. Puku diets from other sites showed no dicotyl plants at all. Indicated by the mean amount of fragment areas, *Panicum* spp. was the first food plant of the puku, followed by *Hyparrhenia*/*Andropogon*-grasses, *Sporobolus* spp. and *Brachiaria* sp. The amount of different grass species in the diets of puku from different sites in Kasanka NP varied. A total number of 13 different grasses were found in the diets, but not all grasses were found at all sites. *Panicum* spp. was represented in high amounts in all puku-regional diets, a fact that could not be stated for the other plants. The amount of *Sporobolus* spp. in the diet varied a lot: puku at P-0 did not consume it at all, whereas this grass was represented in high amounts at P-A, P-B and especially P-E with more than 30%. The amount of *Hyparrhenia*/*Andropogon* grasses was similar in variation. Remarkable were the small, but relatively higher amounts of *Eragrostis* spp. at P-0 and P-E, of *Hemarthria altissima* at P-G, *Melinis nerviglumis* at P-D, of *Pennisetum* sp. at P-0 and of *Setaria* spp. at P-G. *Orzya* sp. was found in the diet of puku in a small amount at P-D, as *Loudetia* sp. at P-F. The values for diet breadth showed high values for P-D and P-G, but small values for P-0, P-A and P-C.

Generally speaking for the analysis, a high amount of fragment areas of monocotyl plant could not be determined up to genus level. This concerned especially the females in the cool dry season, in the hot dry season it was valuable for both sexes. After the onset of the rains undetermined monocotyl plants reached 1/3 to almost 50% of the fragment area. Concerning puku-regional samples, high amounts of undetermined monocotyl plants were noted for P-A, P-B, P-E and P-G.

Table 3-2: Diet composition and diet characteristics of the puku (*Kobus vardonii*) (Kasanka river puku) in Kasanka NP differentiating between sexes and between seasons. The amount of each plant species in the diet is given as % from the total fragment area of all observed fragments. SE: Standard error.

	2009				2010								2011	
	cool dry season				hot dry season				onset rains				late rainy season	
	females		males		females		males		females		males		unknown sex	
	%	SE	%	SE	%	SE	%	SE	%	SE	%	SE	%	SE
plant taxon														
dicotyledons	0		0.37	0.29	0.08	0.08	0.09	0.09	0		0.13	0.13	0.08	0.08
total monocotyledons	99.71	0.19	99.09	0.46	99.74	0.26	99.91	0.09	99.93	0.07	99.84	0.13	99.76	0.24
Brachiaria sp.	9.74	4.14	13.81	4.32	27.48	3.96	29.45	8.12	33.30	4.52	45.10	9.00	66.02	3.34
Cynodon sp.	1.10	0.43	0.77	0.51	0		1.64	0.66	0.19	0.19	0.13	0.13	0	
Digitaria sp.	0.64	0.40	1.40	0.81	0.48	0.31	0		0.20	0.13	0.32	0.25	0	
Eragrostis spp.	2.39	2.09	1.75	1.18	0.90	0.83	1.06	0.74	0.19	0.12	0.35	0.27	0.76	0.27
Hemarthria altissima	0.29	0.21	1.57	1.00	0.38	0.24	1.57	0.90	0.52	0.44	0.51	0.39	0.19	0.19
Hyparrhenia/Anthropogon spp.	4.50	1.71	0.53	0.22	1.38	0.45	2.50	1.10	1.40	0.46	1.55	0.28	2.80	1.08
Loudetia sp.	0		0		0		0.31	0.31	0		0		0	
Melinis nerviglumis	0		0		0.19	0.19	0		0		0		0	
Oryza sp.	0		0		0		0		0		0		0	
Panicum spp.	36.04	6.05	25.68	6.16	21.43	3.80	19.44	4.55	22.32	6.37	26.27	4.74	14.40	2.97
Pennisetum sp.	0		0.18	0.18	0		0.07	0.07	0.17	0.17	0		0	
Phragmites australis	5.25	3.52	0		0.73	0.73	0.04	0.04	0.39	0.32	1.39	1.39	0	
Pogonarthria sp.	0.15	0.15	1.52	1.08	0		0		0.26	0.26	0		0.42	0.42
Setaria spp.	2.90	1.34	1.05	0.49	0.48	0.40	0.93	0.26	0.63	0.30	0.61	0.47	0.07	0.07
Sporobolus spp.	1.97	0.65	33.42	7.56	1.30	0.53	4.37	1.83	1.35	0.47	1.57	0.62	5.63	2.23
Tristachya sp.	0		0		0		0		0		0		0	
Cyperus papyrus	0.41	0.41	0		0		0		0.14	0.14	0.50	0.34	0	
undetermined monocotyl	34.33	5.85	17.42	2.97	44.99	6.72	38.53	9.09	38.85	4.15	21.54	7.90	9.46	1.77
undetermined plant-fragment	0.29	0.19	0.55	0.25	0.18	0.18	0		0.07	0.07	0.03	0.03	0.16	0.16
		SE		SE		SE		SE		SE		SE		SE
number of food items per sample	7.00	0.97	6.50	0.56	5.33	0.61	7.00	0.63	6.00	0.68	5.83	0.48	5.33	0.42
diet breadth (Levin's index)	2.58	0.40	2.71	0.29	2.42	0.12	2.58	0.32	1.94	0.10	2.13	0.18	1.78	0.15
diet breadth ($B_{standard}$)	0.09	0.02	0.10	0.02	0.08	0.01	0.09	0.02	0.06	0.01	0.07	0.01	0.05	0.01
number of dung samples	6		6		6		6		6		6		6	
number of fragments	600		600		600		600		600		600		600	

Table 3-3: Diet composition and diet characteristics of puku (*Kobus vardonii*) at different locations within Kasanka NP (puku-regional) in the cool dry season 2009. The amount of each plant species in the diet is given as % from the total fragment area of all observed fragments. SE: Standard error.

	P-0	P-A	P-B	P-C	P-D	P-E	P-F	P-G	Puku-regional-mean	
					%				%	SE
plant taxon										
dicotyledons	6.59	0.26	0	0	0	0	0	0	0.86	0.82
total monocotyledons	93.41	99.74	99.66	100.00	100.00	99.63	100.00	100.00	99.06	0.81
Brachiaria sp.	5.16	9.25	14.55	17.00	22.02	6.06	5.64	22.67	12.79	2.57
Cynodon sp.	0	1.43	0.47	0	0	2.97	0	0	0.61	0.38
Digitaria sp.	0	0	0	0	0	0	0	0	0.00	0.00
Eragrostis spp.	5.36	2.05	2.20	0	2.88	4.90	0	2.00	2.42	0.70
Hemarthria altissima	0	1.54	0	1.54	0.57	0	0	5.06	1.09	0.61
Hyparrhenia/Anthropogon spp.	37.85	0	1.46	36.81	18.99	0.74	33.75	1.07	16.33	6.21
Loudetia sp.	0	0	0	0	0	0	1.24	0	0.15	0.15
Melinis nerviglumis	2.86	0	0	0.84	5.12	0	0.60	0	1.18	0.66
Oryza sp.	0	0	0	0	1.90	0	0	1.09	0.37	0.26
Panicum spp.	13.83	31.13	14.33	17.75	25.57	19.73	18.20	13.84	19.30	2.19
Pennisetum sp.	7.64	0.77	0	0	1.83	0	0	5.39	1.95	1.04
Phragmites australis	0	0	0	0	0	1.35	0	2.69	0.50	0.35
Pogonarthria sp.	0	0	0	0	0	0	0	0	0.00	0.00
Setaria spp.	0	0.85	1.59	0.84	0.75	1.62	0	3.80	1.18	0.43
Sporobolus spp.	0	25.32	23.02	2.32	4.23	30.08	16.21	2.77	12.99	4.27
Tristachya sp.	0	0	0	0	0	0	0	0	0.00	0.00
Cyperus papyrus	0	0	0	0	0	0	0	0	0.00	0.00
undetermined monocotyl	20.71	27.41	42.04	22.92	16.15	32.19	24.37	39.63	28.18	3.23
undetermined plant-fragment	0	0	0.34	0	0	0.37	0	0	0.09	0.06
					value				value	SE
number of food items per subsample	7	9	7	7	10	8	6	10	8.00	0.53
diet breadth (Levin's index)	3.03	3.09	3.47	3.02	4.51	3.32	3.24	4.58	3.53	0.23
diet breadth ($B_{standard}$)	0.12	0.12	0.15	0.12	0.21	0.14	0.13	0.21	0.15	0.01
number of dung samples in subsample	4	6	6	6	6	6	6	6	46	
number of fragments	100	100	100	100	100	100	100	100	800	

While dung could be collected in both cool dry and hot dry season for sitatunga, reedbuck and sable, samples of buffalo and hartebeest could only be collected during the hot dry season (Table 3-4).

The diet of **sitatunga** (Table 3-4) was marked by a high amount of monocotyl plants reaching values over 93%. A total number of 11 grasses were found in the diets. The grasses *Phragmites australis* and *Cyperus papyrus* were taken in high amounts, 12% and over 32% respectively, in the cool dry season. In the hot dry season, these grasses were consumed in smaller quantities but the grasses *Cynodon* sp., *Eragrostris* spp., *Hyparrhenia/Andropogon*-grasses and *Panicum* spp. contributed about 45% to the diet. Grasses of low amounts in the diets were *Hemarthria altissima*, *Setaria* spp. and *Sporobolus* spp. The analyses of the sitatunga samples resulted in very high amounts of undetermined monocotyl plants, exceeding 36% in the cool dry season and 45% in the hot dry season.

Reedbuck (Table 3-4) generally had very high amounts of monocotyl plants in the diet, reaching 99%. A total number of 11 grasses were found in the diets. Half of the diets in the two survey periods consisted of *Hyparrhenia/Andropogon*-grasses. The second grass was

Panicum spp. with an amount of about 17% in the two seasons, followed by *Eragrostis* sp. with almost 17% in the cool dry season and almost 11% in the hot dry season. *Loudetia* was the fourth-important grass, but reached amounts of 3.3% only. Other grasses, *Brachiaria* sp., *Cynodon* sp., *Melinis nerviglumis*, *Setaria* spp. and *Sporobolus* spp. only had low amounts in the diet of reedbuck. The grasses *Digitaria* sp., *Oryza* sp., *Phragmites australis*, *Pogonarthria* sp., *Tristachya* sp. and *Cyperus papyrus* were not found at all. The analysis of the diets of reedbuck resulted in 14% of undetermined monocotyl plants.

The diet of **sable** antelope (Table 3-4) was marked by a fairly high amount of dicotyl plants in the cool dry season, almost 20%. In the hot dry season, the amount of dicotyl plants was reduced to almost 7%. A number of 13 grasses were observed in the samples. The *Hyparrhenia*/*Andropogon*-grasses represented by far the highest amount in the diet in the two seasons reaching a fragment area of more than 41% in the hot dry season. *Panicum* spp. and *Eragrostis* spp. were other main food plants. In the hot dry season, these three grasses made up more than 70% of the sable's diet. *Brachiaria* sp. and *Melinis nerviglumis* were taken in slightly higher amounts (about 3%) in the hot dry season than in the cool dry season. Other grass species were represented in low amount only, e.g. *Sporobolus* ssp. or *Loudetia* sp.; or not at, all as, e.g. *Digitaria* sp.

In the hot dry season, **buffalo** showed an amount of almost 93% of monocotyl plants in their diets (Table 3-4). With high values of diet breadth, buffalo showed some grasses in similar amounts in their diets; 12 grasses contributed to the diet. The grass with the highest amount was *Panicum* spp. representing 25%. *Hyparrhenia*/*Andropogon*-grasses reached a fragment area of almost 19%. *Eragrostis* spp. and *Cynodon* sp. reached more than 12% and more than 13%, respectively. *Digitaria* sp. was not found to be part of the buffalo's diet; *Sporobolus* spp. was found in a small amount only. Undetermined monocotyl plants summed up to about 14% of the fragment area.

A total number of 10 grass species contributed to the diet of **Lichtenstein's hartebeest** in the dry season (Table 3-4). Monocotyl plants were the main component with an amount of almost 98%. *Hyparrhenia*/*Andropogon*-grasses had by far the highest amount in the diet, reaching almost 43%. *Eragrostis* spp. represented about 18% in the diet, *Panicum* spp. was the third grass reaching an amount of almost 16%. *Loudetia* sp. reached 3% in the diet. Other grasses only reach low amounts, e.g. *Brachiaria* sp., *Cynodon* sp., *Melinis nerviglumis* or *Sporobolus* spp., or were not observed as, e.g., *Digitaria* sp. Not even 12% of the fragment area belonged to undetermined monocotyl plants.

Table 3-4: Diet composition and diet characteristics of different other bovid species in Kasanka NP in different seasons. The amount of each plant species in the diet is given as % from the total fragment area of all observed fragments. SE: Standard error.

	Sitatunga				Reedbuck				Sable				African Buffalo		Lichtenstein's Hartebeest	
	(*Tragelaphus spekii*)				(*Redunca arundinum*)				(*Hippotragus niger*)				(*Syncerus caffer*)		(*Alcelaphus lichtensteinii*)	
	2009		2010		2009		2010		2009		2010		2010		2010	
	cool dry season		hot dry season		cool dry season		hot dry season		cool dry season		hot dry season		hot dry season		hot dry season	
	%	SE	%	SE	%	SE	%	SE	%	SE	%	SE	%	SE	%	SE
plant taxon																
dicotyledons	5.04	1.11	1.15	0.75	0.15	0.15	0.38	0.25	19.68	5.77	6.62	2.75	6.01	1.65	2.10	1.36
total monocotyledons	93.53	1.29	96.79	0.96	99.79	0.15	99.36	0.38	79.79	5.82	93.08	2.89	92.63	2.13	97.74	1.32
Brachiaria sp.	0.09	0.09	0		0	0.00	1.23	1.23	0.23	0.23	2.78	1.61	3.10	1.89	0.96	0.57
Cynodon sp.	0.59	0.23	8.02	1.92	0.36	0.18	0.69	0.33	0.15	0.10	0.56	0.10	13.17	6.38	1.61	1.45
Digitaria sp.	0		0		0		0		0		0		0		0	
Eragrostis spp.	0.69	0.19	10.34	2.28	15.37	3.95	10.77	1.45	12.81	3.06	7.38	2.74	12.58	3.08	17.81	2.68
Hemarthria altissima	1.09	0.87	0.12	0.12	0.21	0.14	0.95	0.87	0.53	0.53	0.06	0.06	0.23	0.23	0	
Hyparrhenia/Anthropogon spp.	5.05	3.62	11.50	4.19	47.77	4.92	48.52	5.30	35.69	6.47	41.35	4.45	18.63	2.38	42.58	3.69
Loudetia sp.	0		0		3.30	1.93	3.33	0.92	1.22	0.93	0.24	0.15	1.09	0.51	3.14	1.04
Melinis nerviglumis	0		0		0.23	0.16	1.47	0.92	2.34	0.70	3.27	2.11	1.97	1.17	1.60	0.60
Oryza sp.	0		0		0		0		0		0		0		0	
Panicum spp.	2.84	1.12	14.08	3.72	17.21	3.43	16.61	3.35	14.53	3.60	22.92	5.97	24.91	6.20	15.90	2.07
Pennisetum sp.	0		1.27	1.27	0.63	0.50	0.34	0.34	0.23	0.23	0.12	0.12	1.20	0.48	0	
Phragmites australis	32.52	5.50	3.09	1.43	0		0		0		0		0		0	
Pogonarthria sp.	0		0		0		0		0.08	0.08	0		0		0	
Setaria spp.	0.57	0.32	0.60	0.47	0.26	0.16	0.46	0.29	0.13	0.13	0.13	0.08	0.81	0.36	0.36	0.24
Sporobolus spp.	1.58	0.51	0.52	0.34	0.91	0.32	1.08	0.74	0.09	0.09	0.22	0.12	0.71	0.19	1.74	1.50
Tristachya sp.	0		0		0		0		0		0.52	0.36	0.13	0.13	0.07	0.07
Cyperus papyrus	12.18	4.24	1.86	1.64	0		0		0		0		0		0	
undetermined monocotyl	36.23	7.71	45.40	4.87	13.55	1.14	13.92	3.25	11.77	2.24	13.54	1.85	14.11	3.03	11.99	2.20
undetermined plant-fragment	1.43	0.55	2.06	0.45	0.06	0.06	0.26	0.17	0.52	0.38	0.30	0.17	1.36	0.60	0.15	0.10
		SE		SE		SE		SE		SE		SE		SE		SE
number of food items per sample	8.00	0.45	6.83	0.60	6.33	0.61	6.83	0.60	6.67	0.49	8.17	0.40	9.50	0.62	6.67	0.71
diet breadth (Levin's index)	3.14	0.54	3.92	0.35	2.52	0.24	2.66	0.23	3.29	0.34	2.73	0.09	4.09	0.43	3.14	0.27
diet breadth (B_{standard})	0.13	0.03	0.17	0.02	0.09	0.01	0.10	0.01	0.13	0.02	0.10	0.01	0.18	0.03	0.13	0.02
number of dung samples	6		6		6		6		6		6		6		6	
number of fragments	600		600		600		600		600		600		600		600	

The grasses *Oryza* sp., *Pogonarthria* sp., *Pennisetum* sp. and *Tristachya* sp. were not found at all or only in very low amounts in the diets of all bovids in Kasanka NP. Reedbuck, sable and hartebeest were similar concerning the amount of their main food plants especially in the hot dry season. Buffalo was the only bovid species with a relatively high amount of *Cynodon* sp. Sitatunga consumed *Phragmites australis* and *Cyperus papyrus*, mainly in the cool dry season. None of the bovid species showed medium or high amounts of *Brachiaria* sp. or *Sporobolus* spp. in their diets as found in the diet of puku.

In Kafue Region, the diet of **puku** could be evaluated separately for both sexes in all survey periods, although only 2 samples of males were found in the late rainy season. One sample of puku female in Kafue NP turned out 100% dicotyl plants. It is mentioned here only, but not included in tables or statistics. The amount of monocotyl plants was very high, never below 97% of the observed fragment area. This high amount remained rather stable throughout sexes, regions and seasons. A number of 11 grass species were found in the diet of puku in Kafue Region (Table 3-5). While some grasses were noted in high amounts, others were only observed at a few occasions. *Panicum* spp., *Hyparrhenia*/*Andropogon*-grasses, *Sporobolus* spp. and *Brachiaria* sp. were represented in the diets at relatively high amounts. *Panicum* spp. was the first grass in the diets, having a share between 21% and 45%. For females in Kafue NP, *Panicum* spp. was second-important, but with not even 15% in the diet. The *Hyparrhenia*/*Andropogon*-grasses ranged mostly secondly – only for males in the late rainy season they reached a very low amount, not even 2%. In PPKR, *Sporobolus* spp. reached amounts of 8.3% in the diets in both seasons; in Kafue NP, though, it reached an amount of 17% in males and even 28% in females. In Kafue NP, *Brachiaria* sp. was detected in higher amounts in males than in females, 6.5% were opposed to 1%. In PPKR, this grass had higher amounts in both sexes in the late rainy season, when it reached 8% in females and 13% in males. *Eragrostis* spp. was the fifth grass reaching generally higher amounts in the cool dry season in the two study areas. *Digitaria* sp. had relatively low percentages in the diet, but reached slightly higher values in the late rainy season. Other grasses in the diets were *Cynodon* sp. and *Pogonarthria* sp. On a few occasions, the grasses *Loudetia* sp., *Phragmites australis* and *Setaria* spp. were found. *Hemarthria altissima*, *Melinis nerviglumis*, *Oryza* sp., *Pennisetum* sp., *Tristachya* sp. and *Cyperus papyrus* were not observed at all.

In all seasons, in all study areas and for both males and females, the amount of monocotyledons was generally very high and never less than 97% in the diet. The amount of

undetermined monocotyl fragments was generally high, too. The males in the late rainy season and the females in Kafue NP exceed 38% or more than 35%, respectively. Only in females in the late rainy season and in males in Kafue NP, the amount was at 22% or 24%.

In the cool dry season, the diet of **impala** had a high amount of dicotyledons (Table 3-6) in the two study areas, making up 2/3 or more of the diet. In the cool dry season *Panicum* spp. was the first grass in the diet, but did not reach amounts over 10%. *Hyparrhenia*/*Andropogon*-grasses and *Sporobolus* spp. were of importance in the two study regions, whereas *Eragrostis* spp. and *Brachiaria* sp. had low amounts in the cool dry season. In the late rainy season the amount of dicotyledons was 17%. *Hyparrhenia*/*Andropogon*-grasses reached almost 30% of the fragment area in the diet. *Panicum* was second reaching 20%. *Sporobolus* spp., *Digitaria* sp. and *Brachiaria* sp. reached medium values. Generally, eight grasses were noted in the diet of impala. The amount of undetermined monocotyls covered less than 10%, almost half of all fragment areas of monocotyl plants in the cool dry season and less than 20% in the late rainy season.

Dung of **defassa waterbuck** was only found on three occasions in the cool dry season and only in Kafue NP. The diet split up almost equally in monocotyl and dicotyl plants (Table 3-6). A number of 6 grasses were recorded. *Panicum* spp. had the highest amount, representing almost 18% of the diet. *Hyparrhenia*/*Andropogon*-grasses were second-common in the diet with an amount of 9%. *Melinis nerviglumis* and *Eragrostis* spp. reached relatively low values. Other grasses in the diet were *Cynodon* sp. and *Sporobolus* spp. Undetermined monocotyl plants reached an amount of 17%.

Especially in the cool dry season, the diets of impala differed from those of the puku by a high amount of dicotyl plants. In the late rainy season, impala changed their diets towards a higher amount of grasses. Waterbuck had a high amount of dicotyls in their diet, too. Concerning grasses, all antelopes studied in Kafue Region had a high or the highest amount of *Panicum* spp. in their diets. *Hyparrhenia*/*Andropogon*-grasses were taken by all antelopes, but to a different extent in all seasons and study areas. In Kafue Region, puku was the only antelopes that took *Sporobolus* spp. in considerable amounts.

Table 3-5: Diet composition and diet characteristics of puku (*Kobus vardonii*) in Kafue Region: at different locations and at different seasons. The amount of each plant species in the diet is given as % from the total fragment area of all observed fragments. SE: Standard error.

	PPKR								NP			
	2010				2011				2010			
	cool dry season				late rainy season				cool dry season			
	females		males		females		males		females		males	
	%	SE	%	SE	%	SE	%	SE	%	SE	%	SE
plant taxon												
dicotyledons	2.49	0.73	2.35	0.87	0.86	0.43	-		1.57	0.67	2.11	1.00
total monocotyledons	97.27	0.68	97.17	1.11	98.99	0.56	100.00	0.00	98.10	0.61	97.65	1.03
Brachiaria sp.	5.44	1.80	3.55	1.69	8.03	2.89	13.12	0.94	0.93	0.50	6.48	2.07
Cynodon sp.	0.46	0.36	0		0		0.82	0.82	0.53	0.37	1.19	0.84
Digitaria sp.	0.53	0.34	1.03	0.65	2.12	1.25	2.81	2.81	1.02	0.48	1.73	0.95
Eragrostis spp.	4.30	2.39	7.39	3.31	3.65	1.57	1.68	0.88	6.28	2.34	4.35	1.19
Hemarthria altissima	0		0		0		0		0		0	
Hyparrhenia/Anthropogon spp.	17.10	2.21	20.85	1.14	11.70	2.40	1.70	0.78	9.83	2.82	21.30	3.43
Loudetia sp.	0.23	0.23	0		0		0		0		0	
Melinis nerviglumis	0		0		0		0		0		0	
Oryza sp.	0		0		0		0		0		0	
Panicum spp.	32.36	2.59	29.05	6.06	45.22	3.76	40.35	25.55	14.67	3.19	21.54	6.12
Pennisetum sp.	0		0		0		0		0		0	
Phragmites australis	0		0		0		0		0.28	0.28	0	
Pogonarthria sp.	0.57	0.57	0		0		0		1.22	0.79	0	
Setaria spp.	0		0		0		0.57	0.57	0		0	
Sporobolus spp.	5.53	2.70	8.33	5.43	6.09	2.22	0.76	0.76	28.11	9.12	17.15	3.22
Tristachya sp.	0		0		0		0		0		0	
Cyperus papyrus	0		0		0		0		0		0	
undetermined monocotyl	30.75	3.61	26.97	1.90	22.19	2.41	38.18	19.88	35.22	3.25	23.91	1.73
undetermined plant-fragment	0.25	0.16	0.48	0.48	0.14	0.14	0		0.33	0.33	0.24	0.17
		SE		SE		SE		SE		SE		SE
number of food items per sample	6.50	0.56	5.80	0.37	0.21	0.52	6.00	2.00	7.00	0.32	6.50	0.56
diet breadth (Levin's index)	3.19	0.28	3.09	0.27	2.55	0.21	2.84	1.37	3.20	0.59	3.78	0.39
diet breadth ($B_{standard}$)	0.13	0.02	0.12	0.02	0.09	0.01	0.11	0.08	0.13	0.03	0.16	0.02
number of dung samples	6		5		6		2		5		6	
number of fragments	600		500		600		200		500		600	

Table 3-6: Diet composition and diet characteristics of other antelopes in Kafue Region at different locations and at different seasons. The amount of each plant species in the diet is given as % from the total fragment area of all observed fragments. SE: Standard error.

	PPKR				NP			
	Impala (*Aepyceros melampus*)				Impala (*Aepyceros melampus*)		Waterbuck (*Kobus ellipsiprymnus*)	
	2010 cool dry season		2011 late rainy season		2010 cool dry season			
	%	SE	%	SE	%	SE	%	SE
plant taxon								
dicotyledons	76.04	4.55	17.07	1.66	67.60	4.22	51.09	6.86
total monocotyledons	23.57	4.72	82.44	1.78	32.24	4.25	48.91	6.86
Brachiaria sp.	0.20	0.20	3.38	1.26	0.98	0.98	0	
Cynodon sp.	0		0.97	0.68	0		0.43	0.24
Digitaria sp.	0		3.66	1.73	0.19	0.12	0	
Eragrostis spp.	1.03	0.49	1.23	0.79	0.27	0.27	1.58	1.04
Hemarthria altissima	0		0		0		0	
Hyparrhenia/Anthropogon spp.	3.33	1.71	28.57	4.58	6.79	2.87	8.68	3.56
Loudetia sp.	0		0		0		0	
Melinis nerviglumis	0		0		0		2.82	2.82
Oryza sp.	0		0		0		0	
Panicum spp.	7.48	2.80	20.73	5.06	9.56	2.19	17.74	3.89
Pennisetum sp.	0		0		0		0	
Phragmites australis	0		0		0		0	
Pogonarthria sp.	0.85	0.85	0		0		0	
Setaria spp.	0		0		0		0	
Sporobolus spp.	1.52	0.61	4.05	2.32	6.84	2.96	0.89	0.60
Tristachya sp.	0		0		0		0	
Cyperus papyrus	0		0		0		0	
undetermined monocotyl	9.15	1.84	19.84	4.35	7.62	2.01	16.77	2.92
undetermined plant-fragment	0.39	0.25	0.50	0.17	0.15	0.10	0	
		SE		SE		SE		SE
number of food items per sample	4.50	0.22	6.17	0.48	4.17	0.40	5.33	0.33
diet breadth (Levin's index)	1.43	0.13	3.66	0.40	1.79	0.13	2.32	0.34
diet breadth ($B_{standard}$)	0.03	0.01	0.16	0.02	0.05	0.01	0.08	0.02
number of dung samples	6		6		6		3	
number of fragments	600		600		600		300	

3.3.3 Food preferences in Kasanka NP

The results of the Jacobs index for puku at Kasanka River did not show a strong preference for a specific grass in any of the surveyed periods surveyed (Figure 3-8 – Figure 3-11). The only grass for which puku showed a slight preference for through all seasons was *Panicum* spp. Puku showed a very small preference for *Brachiaria* in the hot dry season, after the first rains and in the late rainy season (Figure 3-9 to Figure 3-11). Other grasses showed values of partially high avoidance: *Eragrostis* spp., *Hemarthria altissima*, *Hyparrhenia*/*Andropogon*-grasses, *Setaria* spp. and *Sporobolus* spp. In the cool dry season 2009, differences between females and males were most distinct: females exhibited a stronger avoidance of *Hemarthria altissima* and *Sporobolus* spp. whereas males avoided *Hyparrhenia*/*Andropogon* and *Setaria* spp. to a higher extent (Figure 3-8). After the first rains, values of Jacobs index were almost equal (Figure 3-10).

The results of the Jacobs index for some of the puku-regional samples (Figure 3-12) did not show a strong preference for a specific grass at any of the sites through Kasanka NP. Again *Panicum* spp. was slightly preferred through the NP. In difference to the Kasanka River puku, *Brachiaria* sp. was not preferentially consumed at all places (P-O and P-E). For *Hyparrhenia*/*Andropogon* grasses avoidance could be strong (P-A) but also reached values of 0 (P-F). Similar for *Sporobolus* spp.: its values ranged from strong avoidance (P-0) to slight preference (P-A and P-E). *Digitaria* sp. and *Hemarthria altissima* were always strongly avoided. A medium avoidance was given at all places for *Eragrostris* spp. and *Setaria* spp.

In comparison to other bovid species (Figure 3-13 and Figure 3-14), it strikes that in the two survey periods, no bovid species except puku showed a preference for *Brachiaria* sp. They even avoided it to a sometimes high extent. Vice versa for *Eragrostris* spp. and *Hyparrhenia/Andropogon* grasses: only puku showed a stronger avoidance whereas other bovid species showed values near or slightly above zero. *Panicum* spp. was slightly more preferred by puku than by other bovids. All antelopes showed values of strong avoidance for *Digitaria* sp. *Loudetia* sp. was avoided to different extent by all bovid species. *Sporobolus* spp. reached only values of slight preferences for puku males and the puku-regional samples in the cool dry season 2009 as well.

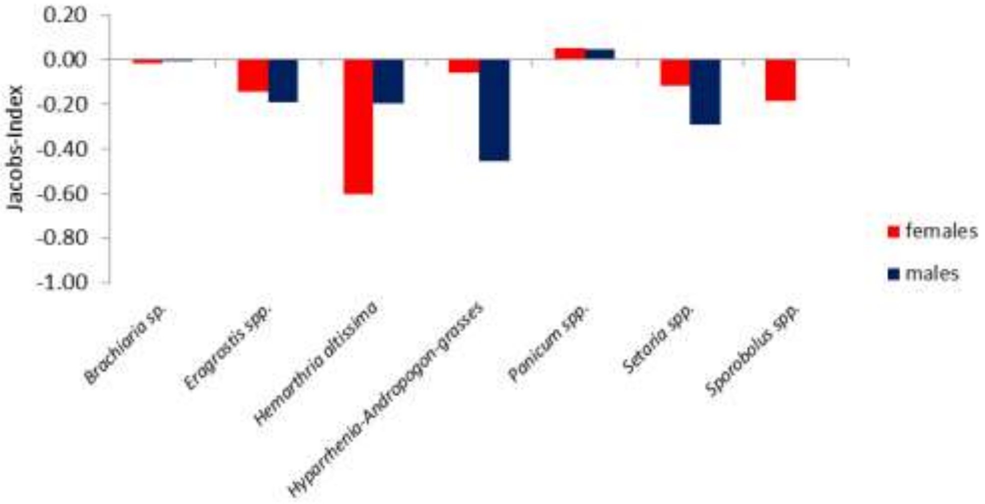


Figure 3-8: Results of the Jacobs index showing the preference/avoidance of puku (*Kobus vardonii*) for grasses at Kasanka River collected in the cool rainy season 2009. The analyses were based on the proportions of grasses at Puku-Loop.

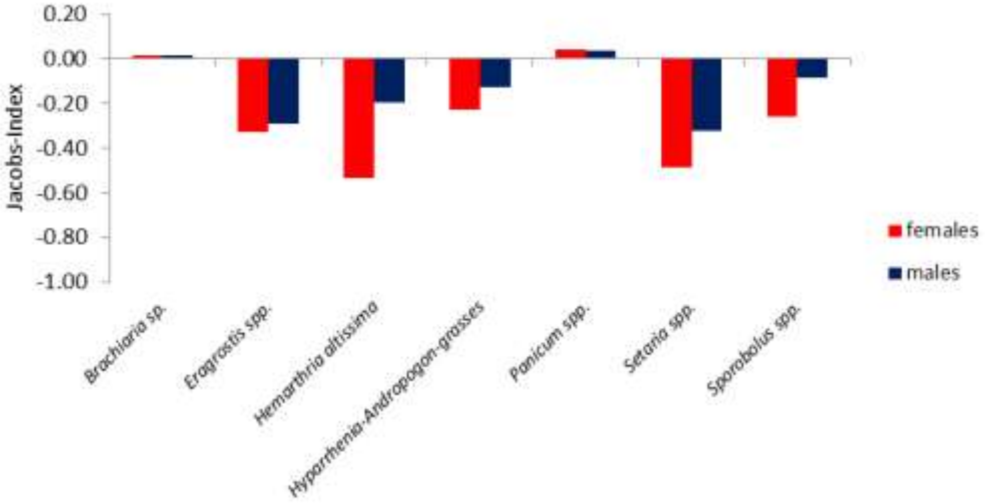


Figure 3-9: Results of the Jacobs index showing the preference/avoidance of puku (*Kobus vardonii*) for grasses at Kasanka River collected in the hot rainy season 2010. The analyses were based on the proportions of grasses at Puku-Loop.

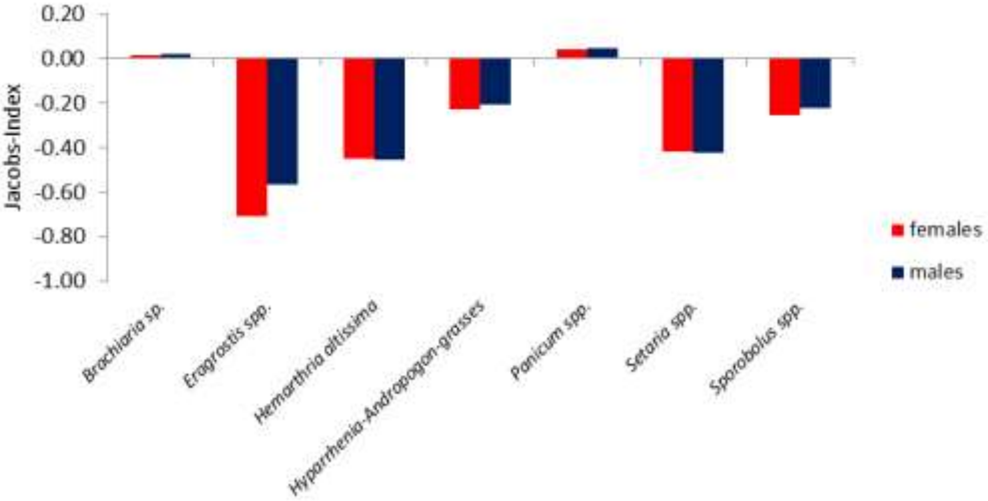


Figure 3-10: Results of the JACOBS index showing the preference/avoidance of puku (*Kobus vardonii*) for grasses at Kasanka River collected after the first rains in 2010. The analyses were based on the proportions of grasses at Puku-Loop.

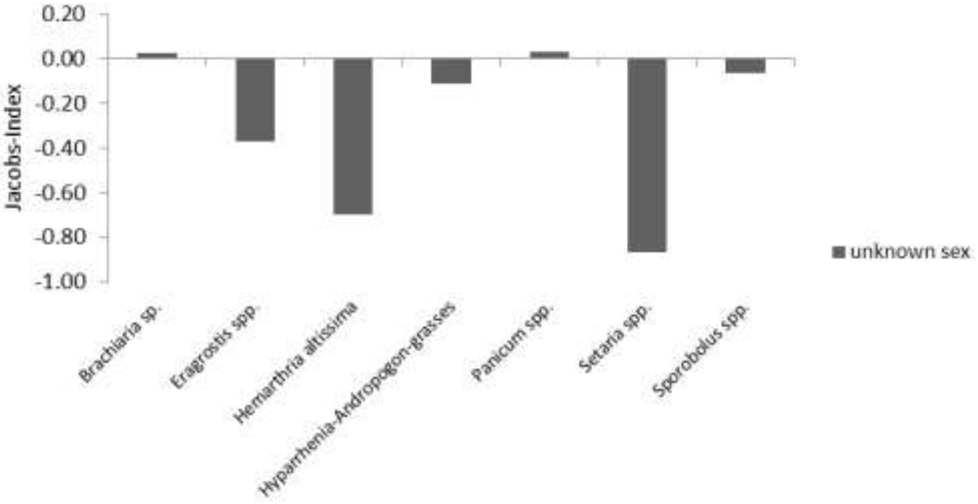


Figure 3-11: Results of the JACOBS index showing the preference/avoidance of puku (*Kobus vardonii*) for grasses at Kasanka River collected in the late rainy season 2011. The analyses were based on the proportions of grasses at Puku-Loop.

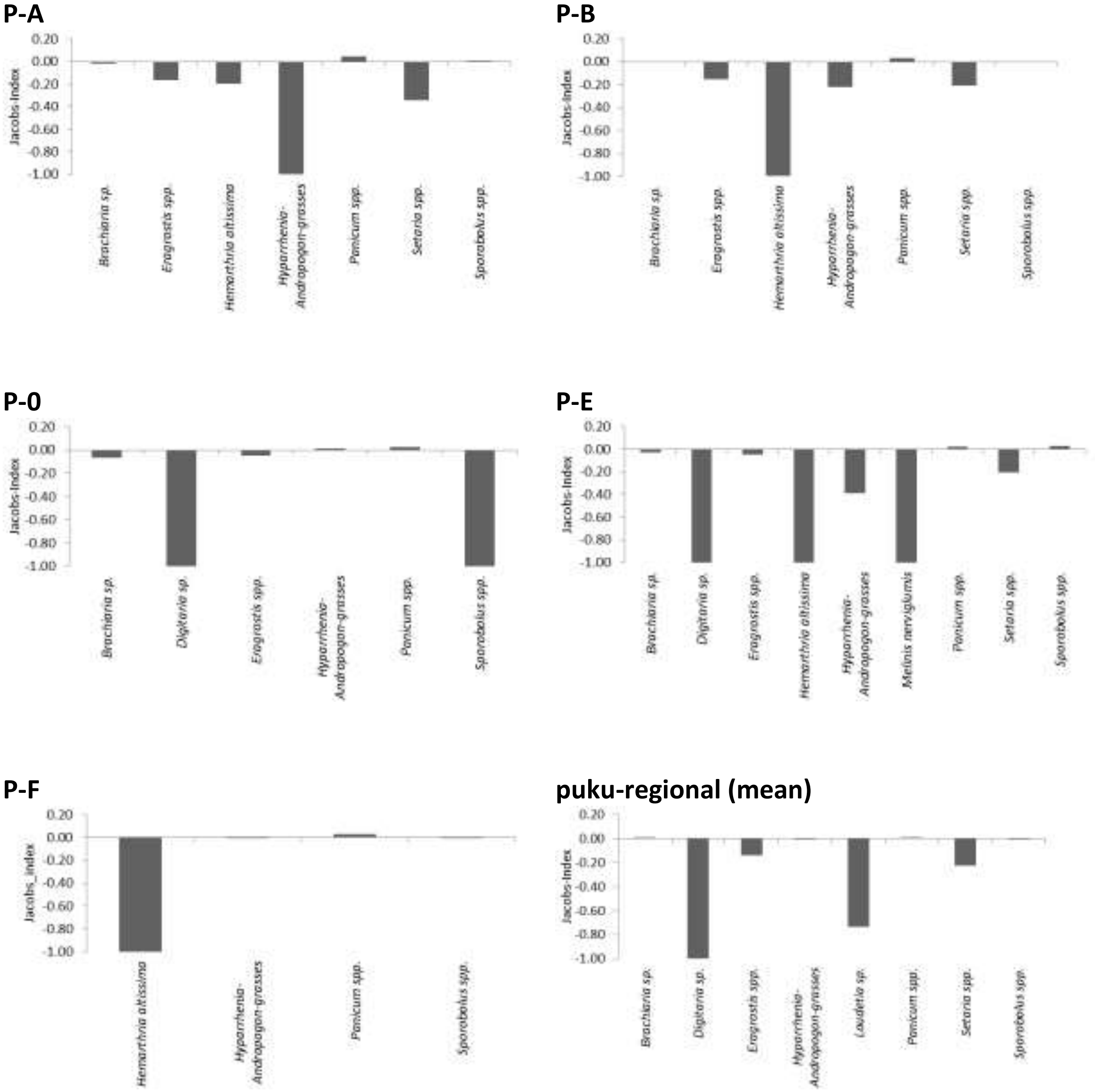


Figure 3-12: Results of the JACOBS index showing the preference/avoidance of puku (*Kobus vardonii*) for grasses at different locations in Kasanka NP in the cool dry season 2009. P-A and P-B at Kasanka River, P-0 in Luwombwa area, P-E at Fibwe Plain, P-F at Wasa and the mean for all puku-regional samples.
The analyses were based on the proportions of grasses at the specific locations and at all transect lines for puku-regional (mean).

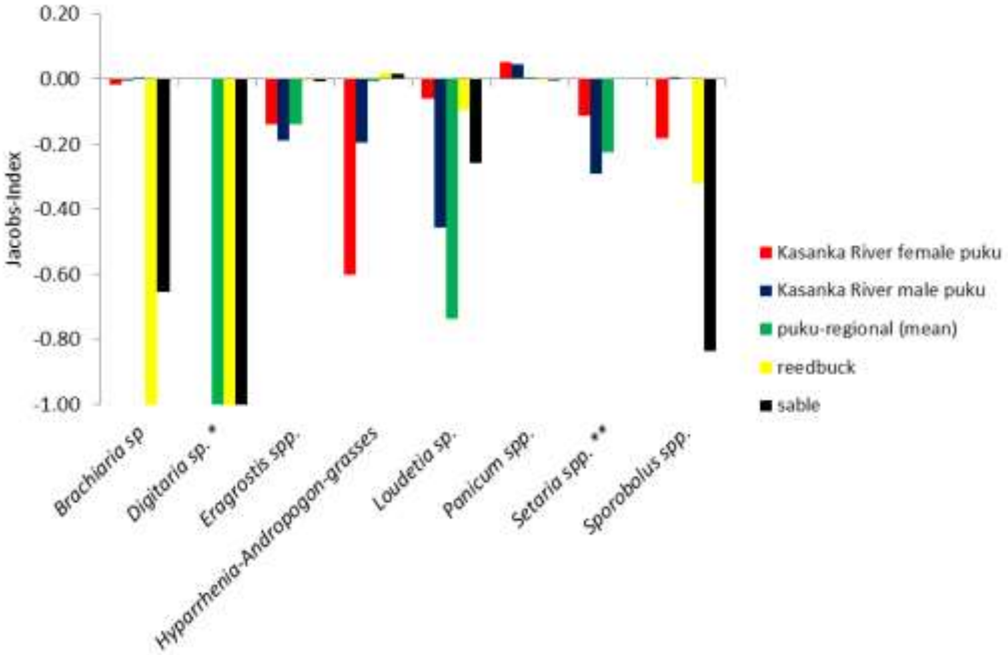


Figure 3-13: Results of the Jacobs index showing the preference/avoidance of bovids for grasses in the cool dry season 2009 in Kasanka NP. The analyses were based on the proportions of grasses at Puku-Loop for the Kasanka River puku, at Chikufwe for reedbuck and sable and at all transect lines for puku-regional (mean). * - preference not evaluated for Kasanka River puku, ** - preference not evaluated for Chikufwe.

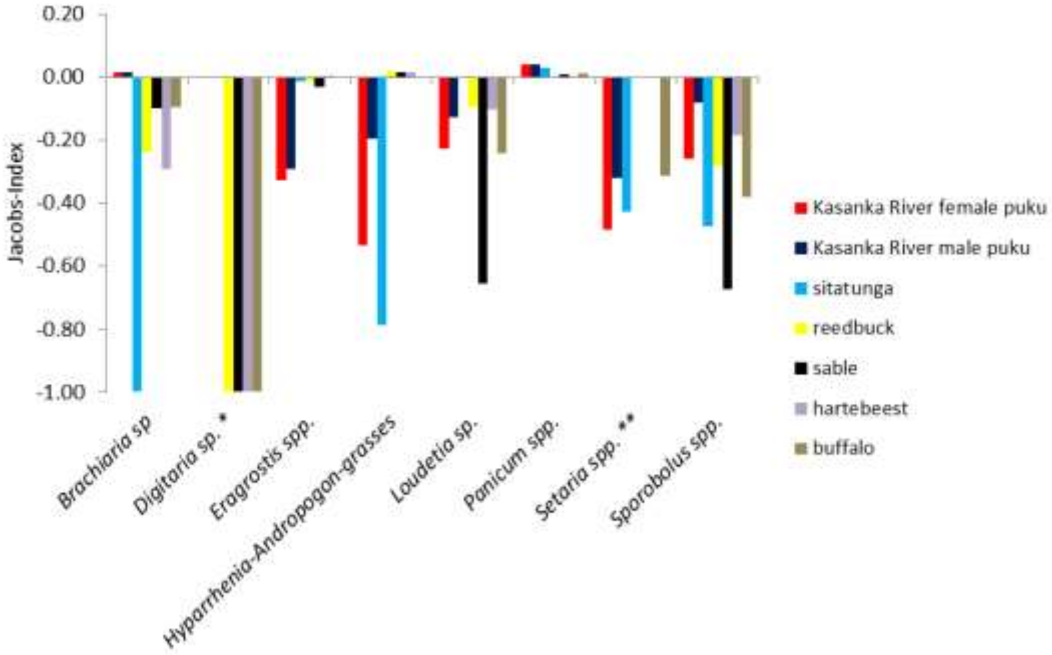


Figure 3-14: Results of the Jacobs index showing preference/avoidance of bovids for grasses in the hot dry season 2010 in Kasanka NP. The analyses were based on the proportions of grasses at Puku-Loop for the Kasanka River puku and sitatunga, at Chikufwe for reedbuck, sable and hartebeest and at all transect lines for buffalo. * - preference not evaluated for Kasanka River puku, ** - preference not evaluated for Chikufwe.

3.3.4 Measurements of diet breadth

The values of $B_{standard}$ and Levin's index showed a very high correlation (Pearson Correlation: 1.000, $p<0.001$, $N=136$). The standardised diet breadth ($B_{standard}$) was used for comparison and for further presentations in order to facilitate comparison with other studies.

Generally, the diet breadths of the bovid species were narrow, as values of $B_{standard}$ rarely reached 0.30. Impala in Kafue NP showed the most scattered values of diet breadth, the least scattered values of diet breadth were shown by the puku in the late rainy season in Kasanka NP.

In **Kasanka NP**, the diet breadth in the cool dry season lay between 0.20 and 0.05 for all bovid species (Figure 3-15 A). Sable antelopes had a wider diet breadth, whereas reedbuck and puku had a narrow diet breadth with their medians below 0.10. These differences were not significant (one-way ANOVA: df=4, F-value=0.862, p=0.5, N=30; 6 per bovid species). Ranging between a $B_{standard}$ value of 0.12 and 0.21, the puku-regional samples showed a much broader diet breadth (Table 3-3) than the diet of puku from Kasanka River and of other bovid species.

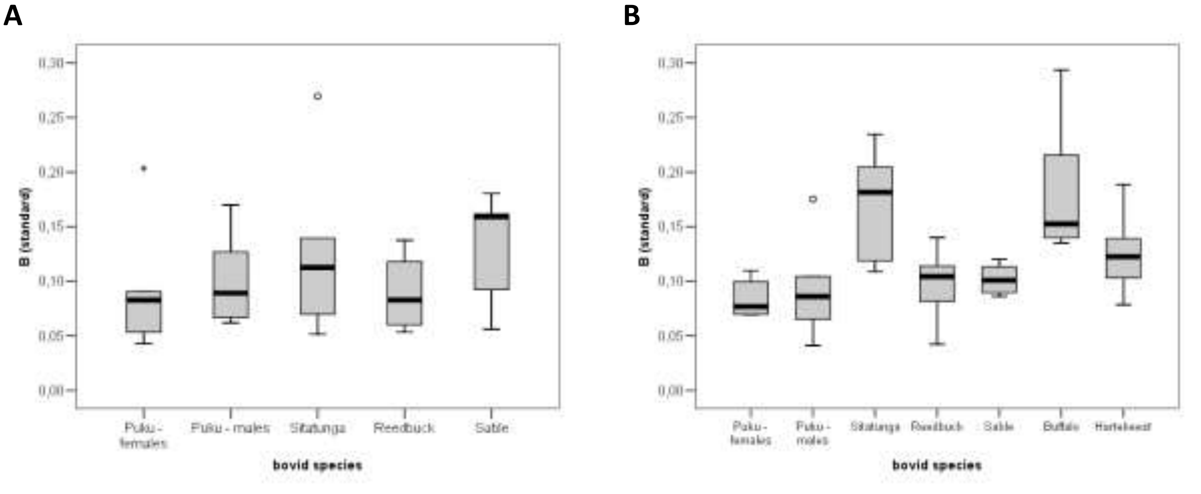


Figure 3-15: Boxplots showing the diet breadth ($B_{standard}$) of bovid species in Kasanka NP in the cool dry season 2009 (A) and in the hot dry season 2010 (B). Differences between species were not significant (see text).

In the hot dry season, the diet breadths remained generally narrow for puku and reedbuck (Figure 3-15 B). Sable antelopes had a narrower diet breath in the hot dry season than in the cool dry season, contrasting to the sitatunga whose diet breadths were broader in the hot dry season. Buffalo showed the highest diet breadth among all bovid species in Kasanka NP. The differences in the diet breadth were significant in the hot dry season (KW-test: df=6, p=0.002, N= 42; 6 per bovid species).

The two-way ANOVA showed no significant differences between bovid species and season (two-way ANOVA: bovid species*season: df=4, F-value=1.157, p=0.339, N=72).

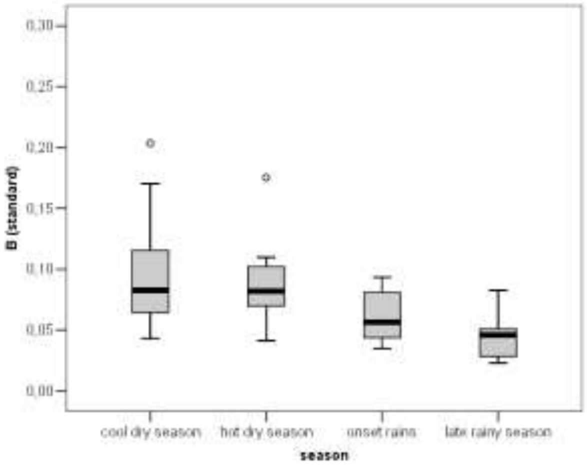


Figure 3-16: Boxplots showing the diet breadth ($B_{standard}$) of puku (*Kobus vardonii*) in Kasanka NP in different seasons, sexes were pooled.

The differences between sexes in the diet breadth were not significant (one-way ANOVA: df=6, F-value=2.1, p=0.078, N=42). The two-way ANOVA revealed no significant differences in diet between sexes and season in puku (two-way ANOVA: season*sex df=2, F-value=0.005, p=0.995, N=42). Differences between diet breadths in puku were significant for seasons when sexes are pooled (one-way ANOVA: df=3, F-value=4.252, p=0.011, N=42). Diet breadth were broadest in the cool dry season, narrower in the hot dry season and after the onset of the rains, but narrowest in the late rainy season (Figure 3-16).

In **Kafue Region**, the median puku's diet breadths ranged between about 0.08 and 0.14 and never exceeded 0.18. The differences in diet breadths in the cool dry season in puku in both PPKR and in Kafue NP were not significant (one-way ANOVA: df=1, F-value=0.949, p=0.342, N=22) but in contrast they were similar (Figure 3-17 A and C) with impala having a smaller diet breadth than puku. Differences between species in the dry season were significant for both PPKR (one-way ANOVA: df=2, F-value=18.544, p<0.001, N=17) and for Kafue NP (KW-test: df=2, p=0.031, N=17). In the late rainy season, the diet breadths of puku females were narrower, but those of impala were broader than in the dry season (Figure 3-17B). These differences between species were significant (one-way ANOVA: df=1, F-value=5.967, p=0.035, N=12).

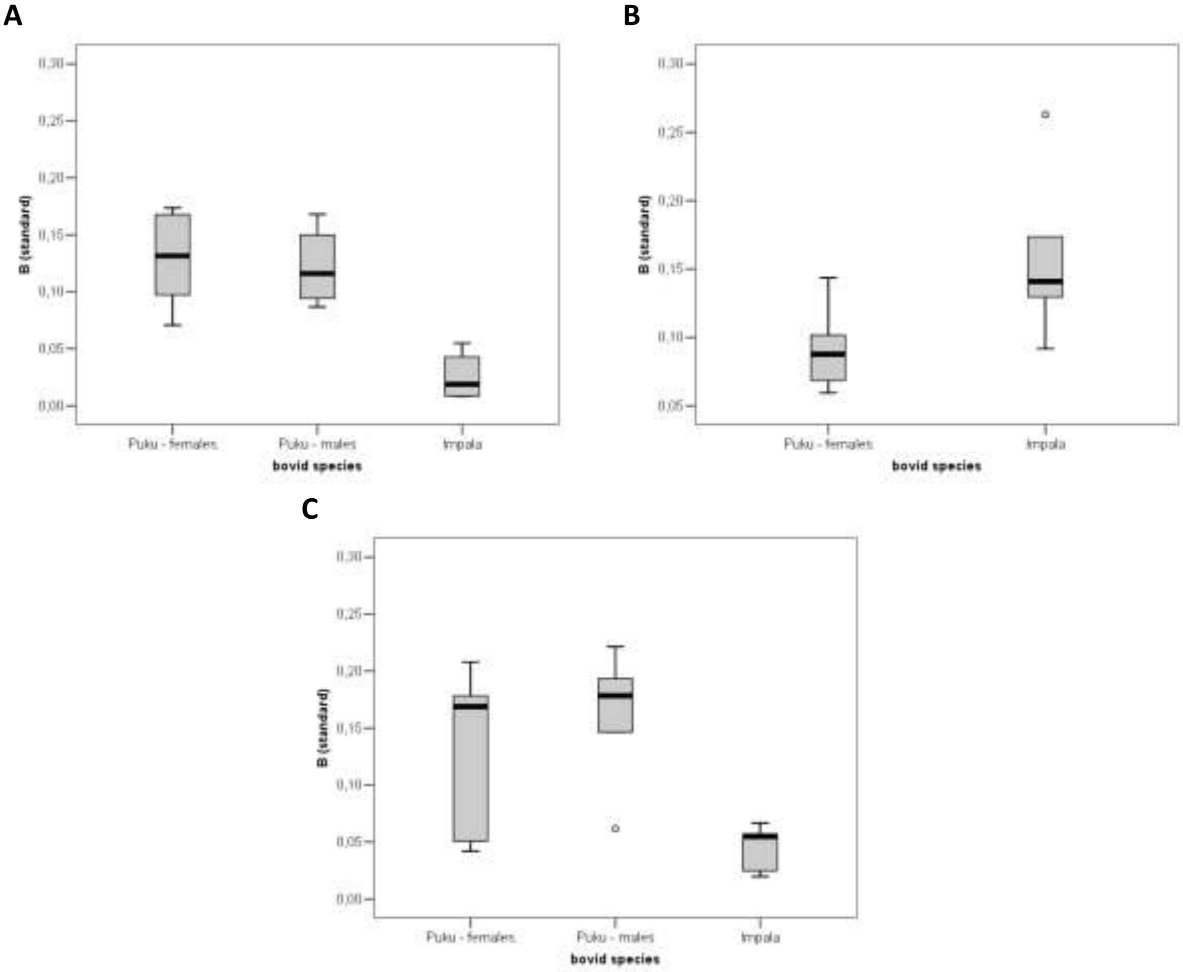


Figure 3-17: Boxplots showing the diet breadth ($B_{standard}$) of bovid species in Kafue Region. In PPKR in the cool dry season 2010 (A) and in the late season 2011 (B); and in Kafue NP in the cool dry season 2010 (C).

3.3.5 Evaluation of dietary overlap

The evaluation of dietary overlap via the **Pianka index** for the bovids in **Kasanka NP** in the cool dry season 2009 revealed the highest overlap between sable and reedbuck reaching a value of 0.90 (Table 3-7). Overlap between puku and other bovid species reached a maximum value between puku females, sable and reedbuck of 0.43 and 0.42. Sitatunga generally reached low values of overlap. In the hot dry season 2010 puku overlapped mostly with sitatunga and buffalo, but reach only values up to 0.51. Puku reached lowest values compared with reedbuck and hartebeest. Generally, there were higher values within all other bovid species than between other bovids and puku. Values were especially high between sitatunga and buffalo, and between reedbuck, sable and hartebeest. Diets of puku males and females overlapped less in the cool dry season. In the hot dry season, they overlapped almost completely. Comparing the diets of the bovids between survey periods, the Pianka indices of sable and especially reedbuck indicated very few to zero changes in the diet.

The Pianka index reached very different values when comparing the diets of puku at different sites in Kasanka NP (Table 3-8). There was a high overlap between P-A, P-B, and P-E, between P-0 and P-C and between P-C and P-F. Very low values were to be found between P-0 and P-A, P-B and P-E. The puku-regional compared to the other bovid species showed different Pianka index values than the Kasanka River puku: The Pianka index between puku-regional and sitatunga was lower or similar. Regarding the overlap of puku with reedbuck and sable, the Pianka index reached by far higher values between P-0, P-C, P-D and P-F. Diets of puku-regional were sometimes closer to other bovid species than to other puku (Table 3-8).

The Pianka index was used to compare the diets of puku between sexes and between seasons (Table 3-9). Males and females overlapped least in the cool dry season where the Pianka index reaches 0.67 only. They overlapped most in the hot dry season and after the first rains with values of 0.99 and 1.00. The highest differences between seasons were found comparing the cool dry season and the late rainy season where Pianka index values were below 0.50. On the contrary, diets of puku in the hot dry season and after the onset of the rains were very similar. A medium overlap occurred between the diet in the cool dry season and in the hot dry season.

Regarding the dry season in **Kafue Region,** there was a higher overlap between puku females and males in PPKR than in Kafue NP (Table 3-10). The diets of impala were very similar in PPKR and in Kafue NP, as the Pianka index reached 0.99. Overlap between puku and impala was generally low in the two study regions, reaching its highest values of 0.25 when comparing impala with puku males in Kafue NP. Overlap between puku and impala increased in the late rainy season: Between puku females and impala overlap was 0.71. When comparing the diets of puku between sexes and between seasons only high values of the Pianka index were resulting (Table 3-11).

Table 3-7: Pianka Index showing the dietary overlap between bovid species in Kasanka NP. Above the diagonal: values for the cool dry season 2009, below the diagonal: values for the hot dry season 2010, the diagonal: comparison within the same species between the cool dry season 2009 and the hot dry season 2010.

	Puku (*Kobus vardonii*) females	Puku (*Kobus vardonii*) males	Sitatunga (*Tragelaphus spekii*)	Reedbuck (*Redunca arundinum*)	Sable (*Hippotragus niger*)	African Buffalo (*Syncerus caffer*)	Lichtenstein's Hartebeest (*Alcelaphus lichtensteinii*)
Puku (*Kobus vardonii*) females	0.79	0.67	0.23	0.43	0.42	-	-
Puku (*Kobus vardonii*) males	0.99	0.67	0.09	0.23	0.22	-	-
Sitatunga (*Tragelaphus spekii*)	0.42	0.41	0.31	0.16	0.21	-	-
Reedbuck (*Redunca arundinum*)	0.26	0.27	0.76	1.00	0.90	-	-
Sable (*Hippotragus niger*)	0.37	0.34	0.80	0.97	0.93	-	-
African Buffalo (*Syncerus caffer*)	0.51	0.50	0.97	0.76	0.84	-	-
Lichtenstein's Hartebeest (*Alcelaphus lichtensteinii*)	0.26	0.27	0.82	0.98	0.96	0.81	-

Table 3-8: Pianka Index showing the overlap within the puku-regional samples and the overlap of the puku-regional with the Kasanka River puku and other bovid species in Kasanka NP for the cool dry season 2009.

		puku-regional samples								
		P-0	P-A	P-B	P-C	P-D	P-E	P-F	P-G	Puku-regional-mean
puku-regional samples	P-0		0.28	0.26	0.92	0.74	0.23	0.88	0.34	0.70
	P-A			0.92	0.42	0.68	0.95	0.59	0.63	0.74
	P-B				0.44	0.67	0.94	0.59	0.69	0.64
	P-C					0.88	0.34	0.91	0.55	0.71
	P-D						0.54	0.78	0.82	0.72
	P-E							0.58	0.49	0.72
	P-F								0.39	0.85
	P-G									0.41
Kasanka River	Puku (*Kobus vardonii*) females	0.45	0.81	0.61	0.58	0.82	0.61	0.56	0.70	0.78
	Puku (*Kobus vardonii*) males	0.25	0.97	0.98	0.40	0.64	0.98	0.59	0.62	0.81
Sitatunga (*Tragelaphus spekii*)		0.18	0.09	0.08	0.15	0.13	0.12	0.17	0.14	0.17
Reedbuck (*Redunca arundinum*)		0.95	0.27	0.23	0.88	0.67	0.24	0.87	0.22	0.70
Sable (*Hippotragus niger*)		0.92	0.26	0.21	0.79	0.62	0.23	0.89	0.21	0.65

Table 3-9: PIANKA Index showing the differences in the diet of puku (*Kobus vardonii*) between sexes and seasons in Kasanka NP.

			2009		2010				2011
			cool dry season		hot dry season		onset rains		late rainy season
			females	males	females	males	females	males	unknown sex
2009	cool dry season	females		0.67	0.79	0.75	0.75	0.70	0.46
		males			0.63	0.67	0.61	0.58	0.49
2010	hot dry season	females				0.99	1.00	0.99	0.90
		males					0.99	0.99	0.93
	onset rains	females						1.00	0.93
		males							0.95

Table 3-10: PIANKA Index showing the dietary overlap between bovid species and between the study regions in Kafue Region. Above the diagonal: values for the cool dry season 2010, below the diagonal: values for the late rainy season 2011, the diagonal: comparison within the same species between the cool dry season 2010 and the late rainy season 2011. Overlap between waterbuck or male puku in the late rainy season and other groups was not assessed due to the low number of samples.

	Puku (*Kobus vardonii*) females - PPKR	Puku (*Kobus vardonii*) males - PPKR	Puku (*Kobus vardonii*) females - NP	Puku (*Kobus vardonii*) males - NP	Impala (*Aepyceros melampus*) PPKR	Impala (*Aepyceros melampus*) NP
Puku (*Kobus vardonii*) females - PPKR	0.97	0.98	0.65	0.90	0.17	0.25
Puku (*Kobus vardonii*) males - PPKR	-	-	0.72	0.94	0.17	0.25
Puku (*Kobus vardonii*) females - NP	-	-	-	0.82	0.12	0.22
Puku (*Kobus vardonii*) males - NP	-	-	-	-	0.15	0.25
Impala (*Aepyceros melampus*) PPKR	0.71	0.56	-	-	0.51	0.99
Impala (*Aepyceros melampus*) NP	-	-	-	-	-	-

Table 3-11: PIANKA Index showing the differences in the diet of puku (*Kobus vardonii*) between sexes and seasons in PPKR. Overlap between male puku in the rainy season and other groups was not assessed due to the low number of samples.

			2010		2011
			cool dry season		late rainy season
			females	males	females
2010	cool dry season	females		0.98	0.97
		males			0.92

For Kasanka NP, the number of components for the **PCA** was reduced to 3 in order to assure a good legibility of the graphs and to make the components more concrete. For the same reasons and due to their low amount in the diet of all bovid species, the grasses *Oryza*, *Pogonarthria*, *Pennisetum* and *Tristachya* were excluded from the PCA. The rotated component matrix (Table 3-12) allowed reading the components. Component 1 could be interpreted by the “degree of miombo” with *Brachiaria*, *Cynodon* and *Sporobolus* on one end and *Eragrostris* and *Hyparrhenia/Andropogon* on the other end. Component 2 comprised the wetland plants with *Phragmites* and *Cyperus*. Component 3 was marked by *Panicum* and *Setaria* on one end, plants of open areas, and the dicotyl plants at the other end. All components explained 46.92% of the variance.

Based on the components, scatterplots showed the dietary overlap within the bovid species (Figure 3-18). Compared to the hot dry season the dietary overlap was less in the cool dry season. During the cool dry season, the degree of overlap was different between species. The sitatunga was distinguishable from all the other antelopes by a high value in relation to component 2 (Figure 3-18 A). Diets of reedbuck and sable overlapped in a fairly high amount (Figure 3-18 A and B). The puku males were the only group that separates from the others by low values in component 1. The puku females rather split from the other groups by low values in component 3. An overlap existed between puku males and females. There was no overlap between puku males and the other antelopes; puku females overlapped slightly with reedbuck and sable (Figure 3-18 A). The puku-regional and puku females overlapped with the diets of sable and of reedbuck (Figure 3-18 A and B). In the hot dry season, the diets of the bovid species resembled more to each other than in the cool dry season (Figure 3-18 C and D). The diets of puku males and puku females overlapped to a high degree, but there was only little overlap with sitatunga (Figure 3-18 A) and no overlap at all with the diet of other bovid species (Figure 3-18 B). Sitatunga showed the lowest overlap within the other bovid species. During the hot dry season, overlap in the diet was highest especially between reedbuck, sable and hartebeest.

There were little differences in the diet both between sexes of puku and between seasons (Figure 3-19). The points representing the diet of puku were narrowest in the late rainy season, but they were widespread in the cool dry season. In the cool dry season, there was the highest gap between the diet of males and females. The points representing puku-regional were most widespread (Figure 3-19 B).

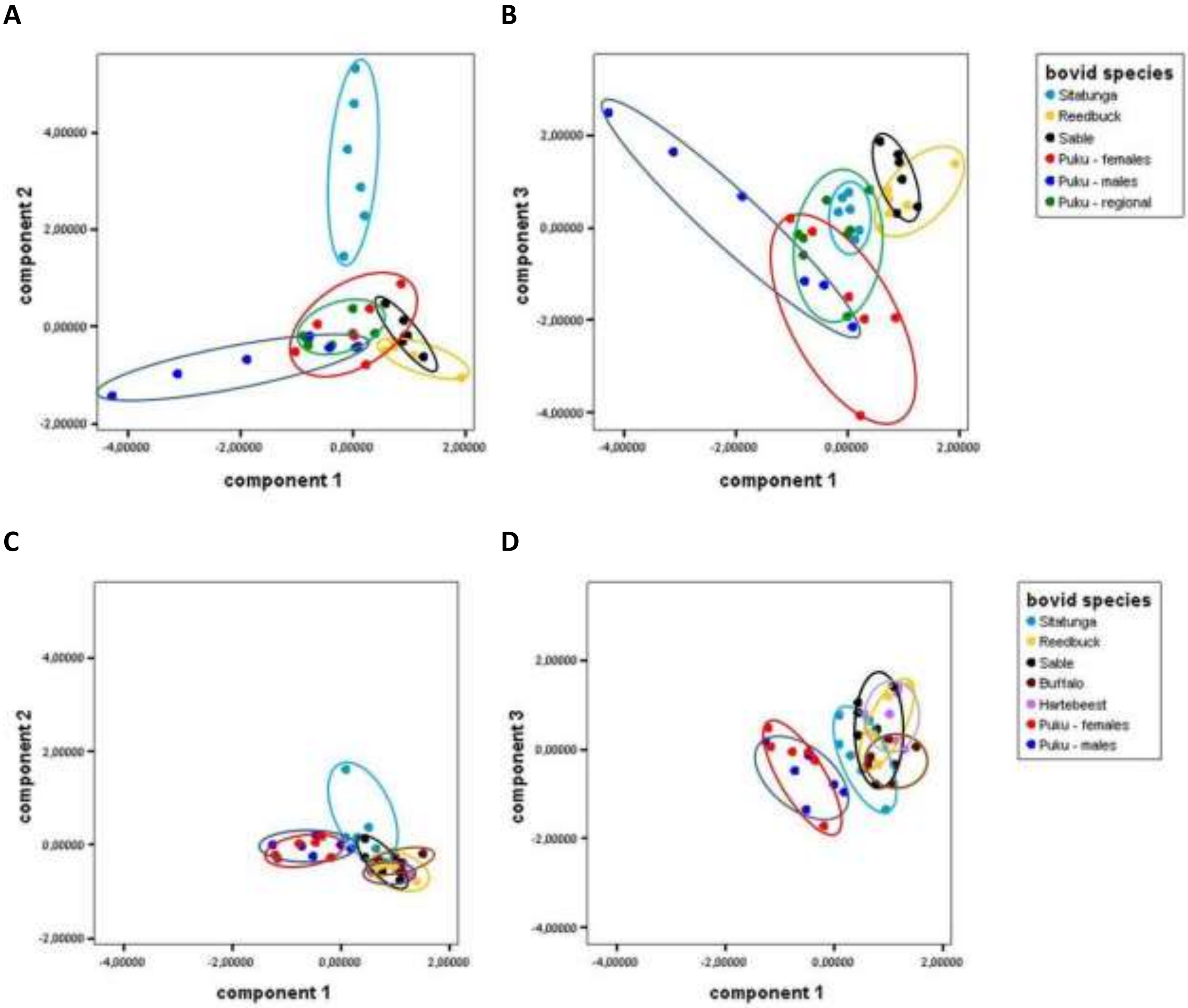


Figure 3-18: Scatterplots based on the results of the PCA showing the dietary overlap between bovid species in Kasanka NP. A 3D graph including all 3 components would be confusing; two graphs are shown different from each other by the component on the y-axis. Points belonging to the same species are encircled. Due to projection not all sample points might be visible. A and B show the situation in the cool dry season 2009, C and D show the situation in the hot dry season 2010.

Table 3-12: Rotated component matrix as given in SPSS 13.0. for Kasanka NP and total variance explained by the component. Highest absolute values are bold.

	component		
amount of plant group in %	**1**	**2**	**3**
dicotyl	0.276	0.140	**0.353**
Brachiaria sp.	**-0.631**		-0.165
Cynodon sp.	**0.285**		
Digitaria sp.	**-0.614**	-0.217	0.170
Eragrostis ssp.	**0.693**	-0.255	0.299
Hemarthria altissima			**-0.288**
Hyparrhenia/Andropogon grasses	**0.642**	-0.268	0.473
Loudetia sp.	**0.472**	-0.252	0.270
Melinis nerviglumis	**0.349**	-0.174	0.314
Panicum ssp.		-0.378	**-0.718**
Phragmites australis		**0.896**	
Setaria ssp.			**-0.775**
Sporobolus ssp.	**-0.647**	-0.203	0.142
Cyperus papyrus		**0.877**	
% of variance explained (rotation sum of squared loadings)	21.345	14.707	10.857

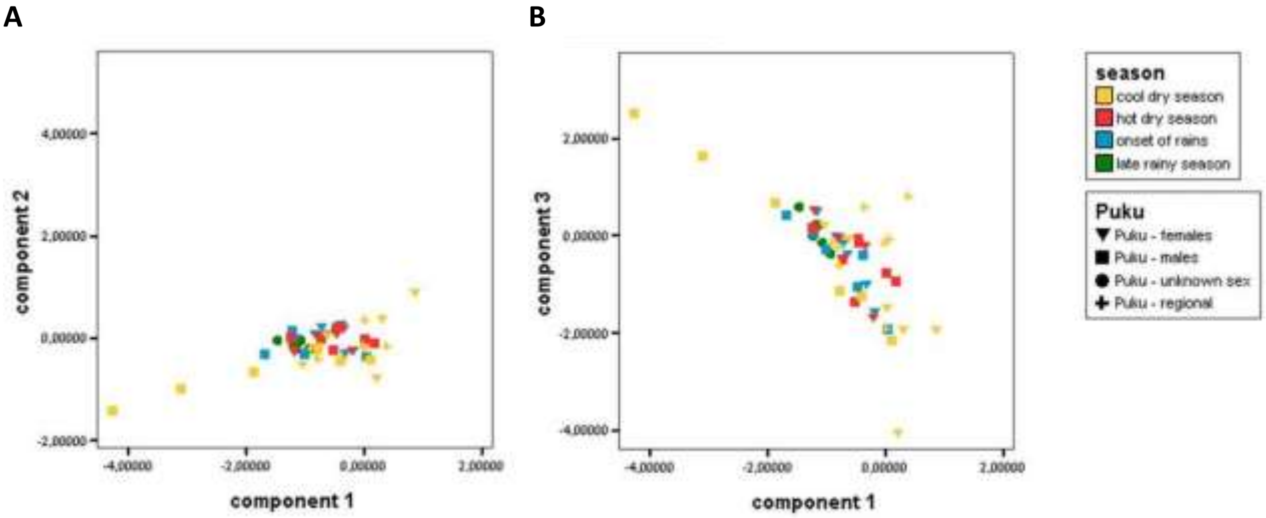


Figure 3-19: Scatterplots based on the results of the PCA showing the diet of puku (*Kobus vardonii*) in Kasanka NP – discriminating sexes, season and the puku-regional samples. A 3D graph including all 3 components would be confusing; two graphs are shown different from each other by the component on the y-axis. Points belonging to the same species are encircled. Due to projection not all samples might be visible.

For Kafue Region the number of components for the **PCA** was reduced to 2 to make the components more definite. For the same reasons only plants were considered for the analysis that occurred in sufficient amount in the diets. Thus, the grass species *Cyperus*, *Hemarthria*, *Loudetia*, *Melinis*, *Oryza*, *Phragmites*, *Pogonarthria*, *Pennisetum*, *Setaria* and *Tristachya* were excluded from PCA. The rotated component matrix (Table 3-13) showed the affinity of the plants to the components: The dicotyl plants influence component 1 negatively. Otherwise component 1 was influenced by Miombo grasses *Eragrostis* and *Hyparrhenia/Andropogon* and by grasses of more open areas like *Bracharia* and *Panicum*. Component 2 included *Cynodon*, *Digitaria* and *Sporobolus*. The components explained 52.14% of the variance.

Regarding first the situation in the cool dry season, the plots are similar for PPKR and in Kafue NP (Figure 3-20 A and C): in relation to component 1 and component 2, both puku and impala showed similar values. Diets of impala were different from those of the puku due to low values of component 1 resulting from the amount of dicotyl plants. The diets of puku males and females overlapped in the two regions. In the late rainy season, the situation changed. Particularly impala shifted their diet overlapping slightly with the puku females. Compared to the situation in the cool dry season, the puku females changed their diet to narrower values for components 1.

Table 3-13: Rotated component matrix as given in SPSS 13.0. for Kafue Region and total variance explained by the component. Highest absolute values of the components are bold

	component	
amount of plant group in %	**1**	**2**
dicotyl	**-0.834**	-0.359
Brachiaria sp.	**0.683**	
Cynodon sp.		**0.825**
Digitaria sp.	0.229	**0.656**
Eragrostis ssp.	**0.559**	-0.218
Hyparrhenia/Andropogon grasses	**0.506**	0.364
Panicum ssp.	**0.746**	-0.296
Sporobolus ssp.	-0.173	**0.538**
% of variance explained (rotation sum of squared loadings)	29.667	22.473

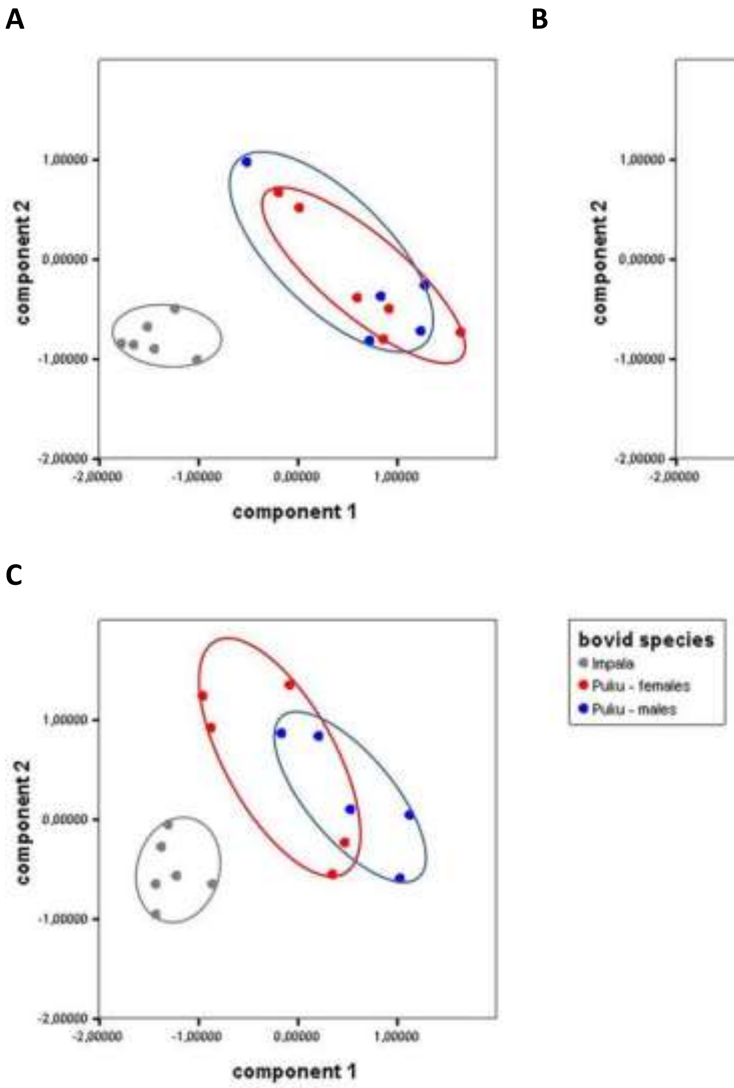


Figure 3-20: Scatterplots based on the results of the PCA showing the dietary overlap between bovid species in Kafue Region. Points belonging to the same species are encircled. Due to projection not all samples might be visible. A and B show the situation in the PPKR in the cool dry season 2010 (A) and in the late rainy season 2010 (B). C shows the situation in Kafue NP in the cool dry season 2010.

3.4 Discussion

3.4.1 General remarks about the methods

The doubtless origin of the dung samples is of major importance for this analysis. Dung of buffalo is unique and thus easy to recognise. Impala defecate on latrines (STUART & STUART 2000), called middens. The dung of waterbuck was easy to recognise as bigger pellets were clumped together as presented by STUART & STUART (2000). For the other antelopes I definitely relied on the experience of scouts. On very few occasions, sable antelope and reedbuck were seen defecating and the morphology of his dung of doubtless origin could be compared to the other ones. Although an absolute guarantee cannot be given, I trust in the determination of dung samples. For puku, except puku-regional and the late rainy season in Kasanka NP, the species and sex of the dung's origin was certain. During collection of dung from puku, I noticed that it can have very different morphologies: pellets can have different sizes, sometimes round or bean shapes, sometimes having a dent at one end, sometimes be clumped together. These different morphologies were more remarkable in puku than in other bovids (own obs.).

Generally, identification of epidermal fragments of plants was the easier the more pictures from the reference collection could be taken into consideration. Some epidermal layers could not be prepared properly – only a few pictures could be taken which lead to a certain lack of information regarding the evaluation of epidermal characteristics as well as possible variation within the epidermis. Due to these reasons, a determination of the genera *Oryza* and *Tristachya* in dung samples of antelopes might be somehow biased.

It was found that some characteristics of epidermal layer were lost during digestion. Long hairs, although quite characteristic for some grasses, were seldom found on epidermal fragments in the samples, so that this feature did not contribute much to determination. Micro hairs were helpful; more in the meaning of presence/absence than by their shape. Pickle hairs in the costal and especially hook hairs were considered very helpful. The same applied to the shape of the silica bodies of the short cells, the form and distribution of the stomata and the general cell patterns. Papillae were sometimes difficult to see, but then, they were very helpful for determination.

The collection of grasses was performed only along the transect lines. The line transects covered the main habitat types, so the main grasses of these habitats, miombo and grasslands, should have been collected. But as roads rarely go into the wetland or into the floodplains grasses from these areas are not well represented in the reference collection. Considering this, the high amounts of undetermined fragments of monocotyl plants in puku and sitatunga dung are not surprising. Nonetheless, this reference collection – to my knowledge the first reference collection of epidermal cell patterns of grasses in Zambia – comprises the main grasses of the study areas.

Generally, this method is budgetary friendly and does not need high end technology or equipment. A good microscope is essential, equipped with a good camera. The analyses of the dung samples under the microscope were time consuming and required concentration, as well as the compilation of the reference collection. In the field the collection of dung samples was accomplished rather quickly. The dung represents an average of the plants consumed a time span before defecation. Direct observations in contrast would have needed time to cover enough observation periods and individuals. Furthermore, direct observations of rare, or flighty shy bovids, as reedbuck or impala, would have been impossible. The same applies for bovids that occur in habitats where they are difficult to perceive, like sable or sitatunga. Microhistological analyses, although biased in some way, but non-invasive, were considered a good tool to assess the diets of wild bovids in protected areas.

3.4.2 General classification of the puku's diet

The diet of puku was characterised by 93 to 100% of monocotyl plants. The data of the puku's diet in Zambia thus support statements of other researchers from other areas about a high amount of grass (Skinner & Chimimba 2005, Rodgers 1984, Child & von Richter 1969). Stable isotope analyses reveal an amount of 96% of C4 grasses in the puku's diet which corresponds to the findings of this study (Sponheimer et al. 2003a). According to the definitions of Cerling et al. (2003), the puku in Zambia can be classified as hypergrazers. The slightly lower content of monocotyl plants in favour of dicotyl plants in the puku's diet from Kafue Region might be related to the environment that is influenced by the Kafue River and a relatively high number of elephants in Kafue Region. As reported from Chobe NP, the elephants create shrublands (DIPOTSO & SKARPE 2006). In these shrublands, puku graze in the open areas, but they also are reported to browse shrubs (DIPOTSO & SKARPE 2006). In contrast to other statements (ROSSER 1987), regarding the sexes, no differences could be found in the amount of mono- and dicotyl plants – both reach equal amounts.

Comparisons with the simple number of plants consumed by the puku are hardly applicable. ROSSER (1987) reported 16 monocotyl plants and another 16 plants of dicotyledons to be consumed by the puku in South Luangwa NP. A number of 18 perennial grasses were listed by Child & von Richter (1969) and 21 grasses were given by O'SHAUGHNESSY (2010) for the puku in Chobe NP. At least the two last ones go down to species level of grasses. In Kasanka NP, the puku were found to feed, to different amounts though, on all grasses of the reference collection except *Tristachya* sp., i.e. 16 different grass genera. Excluded are those grasses that were not included in the reference collection, even if they most probably were food plants of puku (see Chapter 3.4.3). Thus, 16 was the minimum number of grass genera that belonged to the puku's diet in Kasanka NP. In Kafue Region, the number of different grass species was smaller: only 11 genera contributed to the puku's diet.

3.4.3 Grasses in the puku's diet

Brachiaria reached high amounts in the puku's diet in Kasanka NP. High amounts for *Brachiaria* in the late rainy season are reported from Chobe NP: CHILD & VON RICHTER (1969) report an amount of 92.4% for all *Brachiaria* spp. in March, which is even much higher than. However, O'SHAUGHNESSY (2010) found amounts of *Brachiaria* of 30% by faecal and 18% by direct observation in Chobe NP. In the cool dry season, *Brachiaria* had lesser amounts but was still important for the puku in Kasanka NP. However, *Brachiaria* was not of highest importance for all puku. Differences in sexes occurred. Further, the puku-regional dung samples revealed some places within Kasanka NP, where the amount of *Brachiaria* in the diet was low (P-0, P-E, and P-F). Along the transect lines Fibwe and Wasa, *Brachiaria* sp. were rarely observed, what might explain the relatively low amounts in the diet. In Kafue Region, *Brachiaria* sp. generally made up lower amounts of the fragment area. This grass appears not important in the puku's diet in the late rainy season in Kafue Region.

Panicum was comprised the puku's diet in the two study regions in considerable amounts. It was the only grass that resulted in positive Jacobs index values, in other words in a slight preference in Kasanka NP for all places and all seasons. In Kasanka NP, *Panicum* spp. was mostly ranked second, behind *Brachiaria* sp., in the amount of fragment areas. During the cool dry season, *Panicum* spp. was the primary grass in the diet of female puku. *P. maximum* maintains its nutritive value throughout the dry season even when it is dried up (Junguis 1971) which might explain its consumption in the cool dry season. When comparing the puku-regional samples in the cool dry season in Kasanka NP, *Panicum* was always ranked at least at third position. However, in areas with a lot of puku, i.e. along Puku-Loop or Fibwe and also along Wasa, it was not observed at a lot of sample points because it was indeed absent or already eaten. Both cases emphasise the preference of puku for this grass. In Kafue Region, *Panicum* was mostly the grass with the highest proportion, but it was not often determined at the sample points; probably because there was only one survey. In the late rainy season, when *Panicum* spp. was consumed most in PPKR, the females had an amount of *Panicum* of 45% – higher than any value in Kasanka NP. *Panicum* was not considered by Child & von Richter (1969) as a part of the puku's diet in Chobe NP. O'Shaughnessy (2010) gave only low values for *P. repens*. Rosser (1992) did not report a use of communities with *Panicum* either. Only Kingdon 1982 reported a study by Vesey-FitzGerald (1965) mentioning *Panicum* as a food plant of puku. This might differentiate puku in the study regions in Zambia from other sites in Africa.

Puku sometimes consumed ***Sporobolus*** at high amounts. But at other places, this grass was not consumed or in low to medium amounts, as it was especially visible in the puku-regional samples. In the cool dry season, the males at Kasanka River had an amount of 33% of *Sporobolus* in the diet, whereas females had 2% only. Along Puku-Loop, *Sporobolus* spp. were observed on all sample points and this was one of the sites where puku-regional samples with high content of *Sporobolus* spp. were collected. In Kafue NP, the amounts of *Sporobolus* were medium but rather low in PPKR. In Chobe NP, Child & von Richter (1969) did not observe *Sporobolus* being eaten by puku. By direct observations only, O'Shaughnessy (2010) recorded a dietary proportion of 0.1% of *S. pyramidalis*. Vesey-FitzGerald (1965) as well Jenkins (2013) noted puku to feed on *Sporobolus* (Kingdon 1982) – but they gave no information about the amount in the diet. Thus, consumption of this grass appears known and maybe common for Tanzania. Concerning the results of this study, consumption of *Sporobolus* appears to be variable depending on the sites: if *Sporobolus* is available, it is likely to be eaten by puku.

The ***Hyparrhenia/Andropogon***-grasses could not be separated in the two genera. Thus, no statements about the consumed amounts of each species are possible. *Hyparrhenia* were encountered to much a higher degree in the study regions, hence most of the plant fragments in the dung samples might belong to *Hyparrhenia*. The presence of these two grasses in the puku's diet was not known before. Probably this is related to the situation of the study regions as both, Kasanka NP and Kafue Region lie within the miombo ecoregion: *Hyparrhenia* and *Andropogon* are typical grasses of miombo woodlands (Frost 1996). Moreover, *Hyparrhenia* grasses represent the fire climax in the miombo (Kingdon 1982); their growth is enhanced by frequent fires which occurred in both Kasanka NP and Kafue Region (own obs.). This grass was observed on nearly every sample point during the assessment of grasses in the two study regions. The puku along Kasanka River in Kasanka NP fed on *Hyparrhenia/Andropogon* in small amounts. At sites with more by woody vegetation, like Luwombwa, the New Airstrip or the Wasa region, the amounts of *Hyparrhenia/Andropogon*-grasses in the puku's diet were higher. Amounts of *Hyparrhenia/Andropogon*-grasses in Kafue Region in the cool dry season were rather similar in PPKR and Kafue NP. These grasses were commonly the third-most important plant in the puku's diet. Amounts were lower in the late rainy season. It appears likely that the presence of *Hyparrhenia/Andropogon* at the whereabouts of the puku influences their amount in the puku's diet. These grasses were generally avoided as revealed by the Jacobs index. But they were consumed in or near miombo woodland areas where other grasses, which were slightly preferred by puku like *Panicum* spp., were scarce to absent.

Eragrostis spp. are considered as good food plants (Jungius 1971). In Chobe NP, different species of *Eragrostis* made up high amounts of the puku's diet: 59% in December and 35% in July/August (Child & von Richter 1969). O'Shaughnessy (2010) recorded lower amounts of 11% and 3% in the high water season (March to August) and 9% and 4% in the low water season (September to February) as a result of direct observations and faecal analyses, respectively. This study found small to medium amounts of *Eragrostis* spp. in most of the puku's diet in the two study regions – but the Jacobs index revealed a clear avoidance of these grasses for Kasanka NP. For the puku at Kasanka River, *Eragrostis* spp. reached relatively low amounts although this grass was found at that place. This grass was not observed at the sample points along Wasa (Figure A. 14) which might explain low to zero amounts in the puku's diet in the western part of Kasanka NP. In Kafue Region, *Eragrostis* was found in generally higher amounts in the diet of puku than in Kasanka NP. Comparing PPKR and Kafue NP, the amounts of *Eragrostis* were similar within these subregions: 5 to 7%. This was about the same as for some places in Kasanka NP, but far less than amounts reported by Child & von Richter (1969). Additionally, the high differences in seasonal amounts of *Eragrostis* in the puku's diet as in Chobe NP (Child & von Richter 1969) could not be observed in Zambia.

Many authors highlighted the importance of ***Cynodon*** spp. in the puku's diet (Vesey-FitzGerald 1965, Rosser 1992, Dipotso & Skarpe 2006, O'Shaughnessy 2010, Jenkins 2013). *Cynodon* are palatable grasses and relatively high in protein content (Jungius 1971). But *Cynodon* sp. is not among the most important food plants of puku in Zambia. In Kasanka NP its amount in the diet never exceeds 3%, in Kafue Region highest amount is 1% in Kafue NP. This is far less than year-round amounts of around 20% and 25% resulting from faecal analysis and direct observation in Chobe NP (O'Shaughnessy 2010). For Chobe NP, Child & von Richter (1969) noted the consumption of *Cynodon dactylon* only in July/August, and to 3% only, which is very similar to the findings of Zambia. It is noteworthy to mention that *Cynodon* was observed only once in Kasanka NP and in Kafue NP and only twice in PPKR. This scarcity in the distribution of that grass might be the reason for the absence or the very low amounts of *Cynodon* in the puku's diet in the study regions.

The case was similar for ***Digitaria***: Vesey-FitzGerald (1965) reported it as a food plant of puku in Tanzania, and it is in the puku's diet in Chobe NP as well (O'Shaughnessy 2010, Child & von Richter 1969). There are differences in the amounts reported by O'Shaughnessy (2010): direct observations lead to amounts of 11% and 9% of *Digitaria eriantha* in March to August and in September to February, respectively. But faecal analyses reveal amounts of 19% and 6% in the same seasons (O'Shaughnessy 2010). Still, there is a relatively high consumption of *Digitaria* during the whole year. This contrasts to the findings of Child & von Richter (1969) who found puku to feed to 23% on *Digitaria* ssp. in January only. The results of the investigations on the puku's diet in Zambia revealed a very different aspect for *Digitaria*. Here, puku fed on this plant to a comparable low amount and the Jacobs index showed a strong avoidance. The amount did not exceed 3% in Kafue Region, where this grass was consumed at all sites, at all seasons and by all sexes. For the puku in Kasanka NP, *Digitaria* made up a maximum value of 1.4% only, and sometimes, e.g. in the late rainy season or at all the sites included in the puku-regional analysis, it was not found to be part of the diet. Some species of *Digitaria* have a poisonous HCN content (Jungius 1971). Ignoring which species exactly occurred, this might be an explanation for the observations. For this reason, reedbuck in Krueger NP, South Africa, feed on only one species of *Digitaria*, *D. eriantha* (Jungius 1971). *Digitaria* sp. was not a grass of high importance in the puku's diet in the study regions in Zambia.

Setaria is not an important grass for puku in the Kafue Region. It was found only in the diet of males in the late rainy season in PPKR. In Kasanka NP, it was sometimes consumed in medium amounts only. Considering that this grass occurred at nearly every site where puku could be found (Figure A. 20) these results are surprising. Further, the Jacobs index revealed a clear avoidance of this grass. Additionally, the findings contrast with the results of Child & von Richter (1969) who reported the highest amounts of this grass in December and January with 7.4% and 5.8%, respectively, when this grass was practically not consumed in Kasanka NP.

Grasses of the wetlands included in the reference collection were ***Hemarthria altissima***, ***Phragmites australis*** and ***Cyperus papyrus***. In Kafue Region *Phragmites* was found once, the other grasses not at all. In Kasanka NP, they were found in the diet but at low amounts, especially *Cyperus papyrus*. Two exceptions were detected: *Phragmites australis* was found at 5% in the diet of female puku in the cool dry season and *Hemarthra altissima* was found at 5% in the diet of puku at P-G, the eastern border of Kasanka River. On the one hand, Child & von Richter (1969) found low to zero amounts of *Phragmites mauritianus* in Chobe NP, on the other hand, O'Shaughnessy (2010) found about 4% to 9% of this grass in the diet depending on method and season. The findings of Kasanka NP lay in between. *Hemarthria altissima* was not included in the findings of O'Shaughnessy (2010), but Child & von Richter (1969) found amounts of 1.1% and 3.5% in December and January, respectively, which is in the scale of the findings from Kasanka NP. The only discrepancy is the season: they did not find *Hemarthria altissima* to be part of the puku's diet in the dry season. The findings of this study and those of Rosser (1992) as well, indicate a use of *Hemarthria altissima* throughout the year, especially in the drier months. In contrast to my findings, Rosser (1992) also highlighted a use of *Cyperus*, but *C. esculentus* communities, in different extents year-round. Other grasses of wetland areas were probably not well represented in the reference collection (see below).

From Tanzania, puku are reported to go into rice farmland in the wet season (Jenkins et al. 2002). Rosser (1992) reported the use of ***Oryza*** communities from May to October in South Luangwa NP, thus in the dry season. This grass was only found in the puku's diet at two sites in Kasanka NP. Thus, this rarely observed grass was not of importance for the puku's diet in both study regions during this study. The same can be stated for the other grasses that were found only occasionally in the puku's diet: ***Pennisetum***, ***Pogonarthria, Loudetia*** and ***Melinis nerviglumis*** in the two study regions. While the latter one reached an amount of 5% at the site P-D, at Chisamba Waponde, *Loudetia*, reached only one higher amount at P-F, around Wasa. *Loudetia* is a typical grass of miombo woodlands (Frost 1996); it is surprising that it was not consumed more often. In Kasanka NP, it was frequently found at Chikufwe Plain, and also along Kafubashi and Nafulwe (Figure A. 17), hence along transect lines where puku were observed only occasionally.

Some grasses which according to other studies form part of the puku's diet were not found in the study regions, thus not integrated in the reference collection and as a consequence not stated in the diet of puku. They still could play a minor role in the diet. One example is ***Vossia*** that is consumed by puku in Chobe NP (Child & von Richter 1969, O'Shaughnessay 2010). Another grass of this kind is ***Chloris***, a very palatable grass (Jungius 1971), that is reported in low amounts in the puku's diet from Chobe NP (O'Shaughnassey 2010) and from Tanzania (Vesey-FitzGerald 1965).

Unfortunately, the evaluation of the puku's diet very often resulted in high amounts of **undetermined monocotyl plants**. Regularly, one third or more of the monocotyl plants in the puku's diet could not be determined up to genus level. It appears that some grasses of the wetland areas that were not included in the reference collection occurred to a high degree in the diet of puku, and it was also the case with sitatunga. According to the presence and shape of silica bodies and the general cell patterns, some of these fragments might belong especially to ***Enteropogon*** and ***Leersia*** but also to ***Echinochloa*** – compared and identified with the reference collections and pictures provided by Barthlott & Martens (1979) Gutbrodt (2006) and Watson & Dallwitz (1992 onwards). These plants appear to make up especially high amounts of the diet in the ongoing dry season in Kasanka NP, when puku move into the floodplains. Meanwhile, these plants were not present to a high amount in the diet of puku during the late rainy season (9%), when the floodplain was inundated. Thus for Kasanka NP and PPKR, it is unlikely that puku occur in *Echinochloa* communities in April, in the late rainy season, as it was reported for female puku in Luangwa Valley by Rosser (1992).

The same principal food plants of puku were observed in both Kasanka NP and Kafue Region. *Panicum* spp., *Brachiaria* sp., *Sporobolus* spp., *Hyparrhenia*/*Andropogon* grasses and *Eragrostris* spp. were important food grasses – different to greater or lesser extent from diets revealed by other studies in Luangwa Valley (Rosser 1992) or in Chobe NP (O'Shaughnessy 2010, Child & von Richter 1969). This similar general food might be explained by both the study areas belonging to the miombo ecoregion.

3.4.4 Variation in the puku's diet

Niche breadth measurements indicated no significant difference between sexes. But focussing on food plants, females and males consumed different plants as shown by the amount of different grasses in the diet and underlined by the results of the PIANKA index and the PCA. In the cool dry season, compared to female puku, male puku were found to feed on *Sporobolus* spp. to much higher extent and less on *Panicum* spp. This was supported by results of the JACOBS index that indicated avoidance of *Sporobolus* ssp. in females. Additionally, the PIANKA index gave a value of 0.67, the lowest value between sexes in one season for puku, indicating the greatest dietary differences between sexes to happen in the cool dry season. This was also visible in the results of the PCA. In the drier seasons of the year, dietary differences between sexes were small. Still, after the first rains, males fed up to 12% more on *Brachiaria* sp. than females. These slight differences were neither reflected for the hot dry season by the values of the PIANKA index of 0.99 and 1.00 nor after the onset of the rains, respectively.

In the course of a year, according to the results of the PIANKA index, and also apparent in the scatterplots of the PCA, especially male puku showed a change in their diets more than females did. Some male puku hold territories to attract females for mating purpose (BALMFORD et al. 1992). The territories occupy areas with good habitat quality or reduced predation risk (BALMFORD et al. 1992, ROSSER 1992). Other males remain in bachelor herds (see chapter 2). Both territorial males and bachelor males occurred along the Puku-Loop, sometimes very close to each other (own obs.). In contrast to Luangwa Valley, where the territorial males showed a clear neckpatch (ROSSER 1990, own obs.), this feature was less prominent or not visible in Kasanka NP. This made it difficult to distinguish the males and thus, the origin of dung samples. It cannot be excluded that these marked differences between sexes were a result of differences between males. As territorial males occurred along with females, it could be assumed that differences between these males and females are less prominent but still existed, as males were observed alone (see chapter 2).

The niche breadths differed significantly between the seasons. The niche breadths (males and females pooled together) got narrower with the progression of the dry season. They were broadest in the cool dry season, with a mean $B_{standard}$ of 0.09 and 0.10 for females and males; after the onset of the rains it was $B_{standard}$ of 0.06 and 0.07 for females and males, respectively. In the late rainy season, the niche breadth was smallest with $B_{standard}$ 0.05 only. This was supported by the PCA showing less scattered dots from the hot dry season towards the late rainy season. It should be mentioned that general patterns of food plants and the preferences for food plants remain the same throughout the seasons. The exception is the late rainy season where *Brachiaria* sp. was consumed to much higher extents, to 66%, but not strongly preferred as shown by the Jacobs index. This pattern is interesting: according to general opinion, the range of food is smallest in the dry season, especially in the late dry season when food is scarce and species use their 'food refuges', but largest in the wet season as enough food is available (Sinclair 1983). Do the puku concentrate on fewer food plants in the late rainy season as their 'normal' food plants are less available due to the inundated floodplain? Here again it would be interesting to get information about puku at other sites. During the dry season, especially in the hot dry season, the diet of puku at Kasanka River might represent the diet of most of puku in Kasanka NP; this is not the case in the late rainy season when puku are widespread over Kasanka NP. Thus, the pooled diet breadth of puku of more than one site might reveal a broader niche breadth, a diet not based on *Brachiaria* sp. but perhaps on more or on other grasses.

Generally, the diets of puku in Kasanka NP and Kafue Region consisted of the same food plants. Interestingly, the diets of puku in PPKR and in Kafue NP were more alike than were diets from puku at different sites within Kasanka NP. This was underlined by the results of the PCA: the dots of puku showed similar patterns in the sub-regions in Kafue Region. The assessment of grasses was conducted in one cool dry season only and therefore was considered incomplete. The results of this assessment showed that, except *Hyparrhenia*/*Andropogon*-grasses*,* other grasses were observed less frequently in Kafue NP than in PPKR. Maybe they had already been eaten by antelopes and thus could not be determined during the assessment. Generally, vegetation in the sub-regions appeared alike (own obs.), both are situated at the border of Kafue River, which might result in similar grass communities and thus to similar diets.

Although differences between sites in Kasanka NP reached a Pianka index of up to 0.26, differences between puku females in PPKR and Kafue NP resulted in a Pianka index of up to 0.65 only. Dots of different sexes overlapped most in PPKR, which was supported by a higher Pianka index for this region. Similar to the situation in Kasanka NP, the slight changes in overlap might have been be due to the origin of the collected dung of puku bachelor males or territorial males. Additionally, females in both sub-regions exhibited a slightly different diet that partly caused the overlap between sexes as well.

Diet breadth measurements revealed a broader niche for puku in Kafue Region than in Kasanka NP. Similar to the observations in Kasanka NP, the niche breadth was smaller in the late rainy season. Although dots were scattered in a somewhat different alignment for the late rainy season, the Pianka index gave a high similarity for the female puku's diet during the cool dry and the late rainy season. Puku in PPKR, especially in the late rainy season, were sampled with a focus on puku at the waterhole at PukuPan-Lodge. During the dry season, this waterhole was regularly refilled with water regularly to attract animals for the tourists. Additionally, the grass around the waterhole was artificially clipped from time to time to force new sprouting. This indeed attracted puku (own obs.) that came especially at daytime to feed and rest, whereas they left the area during the night (see chapter 5). This artificial maintenance of sprouting grass might influence the puku's food.

According to measurements, puku had a small diet breadth. This might be true when considering specific small-scale sites as the Kasanka-river puku. But considered as a whole, puku appear flexible concerning their diet. This was underlined by the Pianka index analyses for the puku-regional samples. Further, the Jacobs index revealed that grasses preferred at one site could be avoided at another site which was visible for *Sporobolus* spp. However, in Kasanka NP, puku showed a preference for *Panicum* grasses. Then, puku showed differences between sexes and even more pronounced ones between the seasons, if one has a look at the quantity of food plants. Comparisons with the results from other protected areas show that there appears to be no real 'common-theme' in the diet of puku except that they feed on grasses. This leads to the conclusion that puku might be able to adapt to local differences in grass community and availability of grasses at small-scale and large-scale.

The small-scale differences in diet between sites in Kasanka NP were remarkable. For red deer (*Cervus elaphus*) in the Alps, it has been shown that only little variability exists between diets at different sites. The sites were situated in a way that excluded red deer roaming in between (Suter et al. 2004). It was concluded that they exhibit selective feeding which results in this similar dietary composition even in areas with different grassland vegetation (Suter et al. 2004). In contrast, the puku in Kasanka NP showed a relatively high variability at landscape scale between sites that they can easily reach. Illius & Gordon (1992) present a formula that allows calculating mean retention time (MRT) for ruminants. According to this formula ($\text{MRT} = 15.3\ W^{0.251}$; *W* is the weight of the animal), the puku's food needs 40.23 hours to 47.47 hours from being eaten to excretion. This is enough time for puku to travel some distance between sites in Kasanka NP, separated by a few kilometres only. Does this indicate that puku are faithful to one site at least during the dry season? Otherwise the differences in the puku's diet at different sites would not be that distinctive.

The opportunistic food choice of puku might enable them to live at various places in Kasanka NP and elsewhere: the minimum requirement appears to be that the vegetation is characterised by grasses. The grass community might be of less concern. Generally, some antelope species like freshly sprouting grass after bushfires, like impala or kob antelopes (*Kobus kob*) (Wronski 2003). The puku's flexible food enables them to cope with short-term and to long-term changes in the vegetation community that result from bushfires or other events. The response of puku following new food sources is reported by Jenkins (2013). Additionally, this flexibility might be one factor that leads to their high numbers of individuals, although the areas can be different as Kasanka NP, Kafue NP (this study, chapter 2) and Luangwa Valley (Rduch 2008). On the other hand it has to be mentioned that in Kasanka NP, there are places like Chikufwe, Nafulwe and the southern end of Kafubashi, where food plants of puku occur, but where puku were absent during the sampling for this study.

Puku are reported to live and to feed along water (de Vos & Dowsett 1964), sometimes feeding in water that is up to 15 cm deep (Huffman 2011). Observations of puku and their diet in the drier seasons of the year were concentrated along rivers and near to water where puku occurred (see chapter 2). This dependence on water, also highlighted by Skinner & Chimimba (2005), is more or less cancelled in the wet season, when water is everywhere. Jenkins et al. (2002) report small scale movements of puku within the course of a year: in the wet season, puku leave protected areas and go into rice farms. Where do the Kasanka puku go during the rainy season and what do they feed there? This question could not be answered during this study (see chapter 2). But information on the puku's occurrence might tell us if, for example, puku use the Nafulwe area of Kafubashi area more extensively in the wet season.

This opportunistic food choice of puku that depends on the available food plants available has implications for the research as well. The results of analyses of the puku's diet do not only depend on the general vegetation in the study area as a whole, but also on the exact site where observations were conducted or samples were taken. The results of the puku's diet in the course of a year would certainly be different if I had chosen another focal site than e.g. Kasanka River for the collection of the puku dung.

3.4.5 Dietary competition between bovid species

All observed bovid species showed relatively narrow dietary niches: they feed on few species of grasses only. Puku fed mainly on *Panicum* spp., *Brachiaria* sp., *Sporobolus* spp., *Hyparrhenia*/*Andropogon*-grasses and *Eragrostris* ssp. – but also on other grasses that remained not determined. Except for *Sporobolus* ssp. and *Brachiaria* sp., these grasses were main components in the diet of reedbuck, sable, hartebeest and buffalo in Kasanka NP: The same applied to impala and waterbuck in Kafue Region. Impala, waterbuck and sable showed a considerable amount of browse in their diet. This group of plants was considered as a whole during data analyses, not split up into genera or even species. This might affect the interpretation of competition between the considered species. Nevertheless, as puku consumed very low to zero amounts of browse, this fact does not concern the competition with puku and hence does not touch this study.

The amounts of these grasses differed in the diet of the bovid species. Above all, reedbuck, sable and hartebeest in Kasanka NP showed a very similar diet. According to the results of the JACOBS Index, these three species showed also similar preferences/avoidance patterns for of grass species. The same applied for the results of the PIANKA index: values between these bovid species indicated a high degree of overlap. This competition happened during the cool season (only for reedbuck and sable) and especially during hot dry season and was supported by the results of the PCA as well. It probably resulted from the food shortage in the dry season. Lack of food and mortality are highest as reported for grazers of the Serengeti (SINCLAIR 1979b). This matches with the observation in the dietary overlap between bovid species at Chikufwe in Kasanka NP.

Food plants of sitatunga in the cool dry season differed from those of other bovid species. Consequently the PIANKA index resulted in low values of overlap for the cool dry season, supported by the results of the PCA. In the hot dry season, overlap between sitatunga and other bovid species was slightly higher. Puku and sitatunga showed the lowest degree of overlap according to the PIANKA index and to PCA. The consumed food plants were more similar to those of other bovids and also puku. In the hot dry season, the samples of sitatunga came from Kasanka River and not from Fibwe plain in the hot dry season. But in contrast to puku at the same site, sitatunga showed a strong avoidance of *Brachiaria* sp.

In the cool dry season, the PIANKA index for puku-regional samples and other bovids was higher than this was the case for Kasanka River puku. This was especially true for sites near or in more wooded areas as Luwombwa, New Airstrip or Wasa (P-0, P-C and P-F). Here, the diets of the puku were more similar to reedbuck and hartebeest indicating a possibly higher degree of competition.

The Jacobs index revealed inversed patterns of avoidance and preference comparing puku and the other bovids: Puku slightly preferred *Brachiaria* sp. and preferred *Panicum* ssp. more than the others. Reedbuck, sable, hartebeest and, to a certain degree, buffalo preferred *Hyparrhenia*/*Andropogon* grasses and avoided *Eragrostis* ssp. to a much lesser extent than puku. Nevertheless, all bovids showed a slight preference for *Panicum* ssp. that probably maintains its good nutritive values throughout the dry season (Jungius 1971). The status of competition for food between the Kasanka River puku and the other bovid species was relatively low through the two surveyed seasons. This low overlap was even decreasing with the progression of the dry season, when comparing the competition between puku and reedbuck and between puku and sable. This light degree of competition between the Kasanka River puku and the other bovid species in Kasanka NP was emphasised or even amplified by the results of the PCA. It has been reported from other protected areas that other antelopes come into the range of reedbuck especially after fires (Jungius 1971). To avoid competition with other ungulate species, reedbuck feed on relatively unpalatable grasses (Huffman 2011). While sable showed strong avoidance for *Loudetia* sp., this grass was less avoided by reedbuck but also hartebeest. Is it possible that especially sable are attracted by the freshly sprouting other grasses? *Hyparrhenia* is the characteristic grass of the fire climax vegetation in the miombo ecoregion (Kingdon 1982). It was less avoided or even slightly preferred by reedbuck, sable, hartebeest and buffalo in contrast to the puku, and sitatunga, which avoided it. Irregardless of the moving power, puku mainly occurred at different sites than reedbuck, hartebeest, sable (see chapter 2) and buffalo. This separation on a spatial scale is another step to avoid competition.

In Kafue Region, dietary overlap between puku and impala was assessed. Although other bovid species occurred in the study regions, no dung samples could be gathered. The results from the line transect sampling revealed a high spatial overlap between puku and impala in the cool dry season, during which the Pianka index values were low between those two in both PPKR and Kafue NP. The scatterplots for the sub-regions showed impala and puku well separated from each other. This was different in the late rainy season where Pianka index values increase between puku and impala. This degree of higher potential overlap was reflected by the results of the PCA as well. To evaluate the dietary overlap and potential competition between puku and impala, dung was taken from the middens that are used mainly by territorial males (Stuart & Stuart 2000). These territorial males are reported to have fewer amounts of dicotyledons in their diet than females or bachelor males (van Rooyen & Skinner 1989, Sponheimer et al. 2003b). If this is true for Kafue Region the actual dietary overlap between puku and impala might be even less marked. This could be one factor that explains the high numbers of these two antelope species in Kafue Region and their sympatric occurrence. Although waterbuck was not included in the statistical evaluation, the results of its diet suggest a medium overlap in the cool dry season based on the fact that waterbuck include considerable browse in its diet.

Bovid species are characterised by anatomical differences. They are assumed to reflect the proportions of C3 browse and C4 grass in the diet, but are proven to correlate with the degree of feeding selectivity also in regard to short-, medium- and tall grass grazing (Codron et al. 2008). It is the part of the plant or the specific growth stage of the plants that might be consumed by each bovid species (Murray & Brown 1993) that leads to resource partitioning. The coexistence of sables with zebra and buffalo in Kruger NP is enabled by their precise selection for green parts of the plants. Buffalo tolerate grass that is mostly brown (Macandza et al. 2012). The methods used for this study did not allow a differentiation of the growth stage or the parts of the plants taken neither would they allowed a statement on the nutritional value of the food plants actually taken which all probably affect the choice of food plants.

The bovids influence the vegetation by their grazing activity. Murray & Illus (2000) reported on wildebeest (*Connochaetes taurinus*) and topi (*Damaliscus lunatus*), going for bite quantity and bite quality, respectively. They can modify the vegetation in such a way that it is less profitable for the competing species. Thus herbivores can preclude the utilisation of resources by other species (Murray & Illus 2000).

It has to be mentioned that although bovid species compete with each other, the ecosystem has further species of whom they might be influenced in regard to their feeding. Sinclair (1979a) reports of invertebrates having a much higher impact on the grasslands than large mammals. By consequence, mammals could be affected by the fluctuations of phytophagous insects (Sinclair 1979a). From the small to the big member of the ecosystem: The feeding activity of megaherbivores, especially of elephants (*Loxodonta Africana*), affects mediums sized mixed feeders (Fritz et al. 2002). Populations of these mesomixed feeders, e.g. impala, can decline when megaherbivores are abundant (Fritz et al. 2002). Mesograzers, thus also puku, are supposed to be rather unaffected by the presence of megaherbivores

(Fritz et al. 2002). In Chobe NP, increasing number of elephants lead to increasing numbers of puku: elephants opened the woodland; more grassland was available (Dipotso & Skarpe 2006). Thus here puku were positively affected by the elephants.

Two bovid species may be competitive if they exhibit an important degree of similarity in resource use at least during periods of forage scarcity (Bagchi et al. 2003). This was the case for the bovid species in Kasanka NP: reedbuck, sable, hartebeest and, to a lesser extent, buffalo. The Kasanka River puku showed little dietary overlap with the species mentioned above as well as with sitatunga especially in the dry season, which is the time of suggested food scarcity. The dietary overlap between puku and impala, which showed the same population densities in Kafue Region, was low in the cool dry season, where each species appears to occupy a segregated food niche. In the late rainy season, the time of food abundance, especially impala changed their diets in a way that these two antelopes showed an increased dietary overlap. Unfortunately apart from puku, dung collection was not possible for the rainy season Kasanka NP.

The bovid species and their status of competition depend on the availability of food (Sinclair 1979a, White 1978). In return, plant growth is limited by soil moisture (Jarman & Sinclair 1979) which is mostly influenced by rainfall. But this rainfall, as stated by McNaughton (1979) for the Serengeti ecosystem, is extremely variable over space and time. In consequence, competition varies throughout a year and also between years. Thus the results of this thesis give only a small insight into the dietary competition between bovid species in Zambia.

3.4.6 Conclusions

Microhistological analyses of dung, thought time-consuming and depending on a good reference, but non-invasive and budgetary-friendly, provided a good tool to understand the ecology and coexistence of both rare and abundant (grazing) antelope species in the study regions.

Puku, confirmed as hypergrazer, fed mainly on *Panicum* spp., *Brachiaria* sp., *Sporobolus* spp., *Hyparrhenia*/*Andropogon* grasses and *Eragrostris* spp. Other grasses were found to low amounts in their diet. However, some other grasses might have contributed to the puku's diet but were not included in the reference collection. Puku in Kasanka NP were found to have a spatial variability concerning the proportion of different grass species in their diet which leads to the assumption of an opportunistic food choice. Differences between sexes were observed, especially during the cool dry season in Kasanka NP. These results might be explained by the possibility that the samples came from bachelor males. Territorial males are thought to have diets more similar to female puku supported by the results from PPKR where no great differences could be detected in the diets of male and female puku. Puku consumed the same grasses in all surveyed seasons, but with changing amounts. The puku's dietary niche was broadest in the cool dry season and narrowest in the late rainy season. In Kasanka NP, reedbuck, sable, hartebeest and buffalo fed mainly on the same grasses as puku, but took only low amounts of *Sporobolus* spp. and *Brachiaria* sp. The same applied for impala and probably also waterbuck in Kafue Region. Further sable, impala and waterbuck were found to browse to considerable amounts during the dry season. Hence, the diets of puku differed from those of reedbuck, sable and hartebeest in Kasanka NP. These differences were highest when taking into account the diets of puku along Kasanka River and less important for puku from other sites. Consequently, in Kasanka NP, dietary overlap between reedbuck, sable, hartebeest, buffalo and, to a few extent, sitatunga was indeed high in the cool dry season and highest in the hot dry season, but low in overlap between these and puku. In Kafue Region, puku and impala, that overlap spatially, overlap to a lesser extent in their diets during the cool dry season and to higher extent in the late rainy season. Thus, the highest competition between puku and impala takes place in the period of food abundance. Thus, in the dry season where lack of food is most severe (SINCLAIR 1979b), the puku generally experiences low dietary competition.

Further research is needed to assess the dietary niches of bovid species in the study regions. For none of the study regions, a complete year-round dietary survey of all bovid species possibly competing with puku was carried out. For Kasanka NP, data of roan, waterbuck or orebi that are reported in this region (FRANK WILLEMS, pers. comm., KASANKA 2013, Chapter 2) were missing completely. Data of reedbuck, sable, hartebeest, buffalo and sitatunga did not cover the whole year. It should be attempted to collect data of these bovid species from other sites as well to evaluate a possible variance at spatial scale, too. In Kafue Region, the dung of a lot of potential competitors was not sampled: reedbuck, sable, hartebeest or orebi, although all observed in Kafue Region (Chapter 2). Furthermore, the data of waterbuck were not enough.

Feeding on the same plants does not immediately stand for high level of competition. It can be reduced among others by the choice of the vegetation community and by the choice of the part of the food plants (JARMAN & SINCLAIR 1979). Although whereabouts of puku at daytimes where assessed, the question may be asked where they occur at different times during the night. Underlined by the observations on activity patterns that puku do feed at night-time (see Chapter 5) it should be interesting to find out from which places they get their food during the night.

The data for this study were not collected in the consecutive progression from cool to hot dry season. They did not cover the same cool dry season for the different study regions. Data collection in the course of one year could reveal additional information on the competition throughout a year. Furthermore, more attention has to be paid to the state of puku males since this could affect their diets: are they territorial or non-territorial males? This requires a more detailed observation of the males concerned (e.g. belonging to a bachelor group), as the neckpatch is less visible as reported for puku from Luangwa Valley (Rosser 1990, own obs.). Additionally, in the rainy season, if most of the puku are not assembled along Kasanka River, beside the question where they do occur, it should be interesting to know what their food is. Furthermore, in the season in question no data about the status of dietary competition within the bovid community could be gathered. It should be interesting to find out if puku exhibit variation at spatial scale at different places in Kafue Region as they were observed in Kasanka NP. Data collection in other regions within Kafue NP and adjacent GMA could reveal the answer. Additionally, the course of a year was not entirely covered for the study sites in Kafue Region, but this might reveal interesting information.

The reference collection on epidermal patterns in grasses did not comprise all the grasses of the study regions. Possibly important food plants of puku were missing: *Echinochloa*, *Leersia* and *Enteropogon*. To evaluate the diets of other regions in Zambia, this reference collection provides a good basis, but it has to be extended. Dung from puku of other areas might reveal interesting new details that support the status as opportunistic grazer. Furthermore, the dietary niches of puku in combination with other antelopes, or with the same antelopes in other environments might vary (or not) between the protected areas in Zambia. Awareness of food plants can explain antelope abundance and their distribution and thus points out potential threats. Hence, knowledge of the food plants provides the background for purposeful conservation measures.

4 Predation on the puku antelope

Abstract

In order to assess a possible top-down regulation of the puku's (*Kobus vardonii*) population, the large carnivores of the two study regions were brought into focus. The aim was to find out where carnivores occur and if and how much they prey upon puku.

Scats of predators that might prey upon puku were searched. Data collection was carried out in the cool dry season both in 2009 Kasanka NP and 2010 in Kafue Region as well as in the hot dry season 2010 in Kasanka NP. Focussing on hair characteristics, the remains were attributed to prey species and scats were reliably assigned to predators. Further camera-traps were set.

It turned out that most of the scats found in Kasanka NP did not belong to large predators. With a few exceptions they could be assigned to the white-tailed mongoose (*Ichneumia albicauda*), the African civet (*Civettictis civetta*), the serval (*Leptailurus serval*) and the caracal (*Caracal caracal*). However, probably by scavenging white-tailed mongooses and civets consumed puku, but caracals, although preying upon bovids, did not. Servals did not include any bovid in its diet. Hair of puku and sitatunga (*Tragelaphus spekii*) was found to almost equal amounts in the scats of Nile crocodiles (*Crocodylus niloticus*). It is assumed to be the most important predator of puku in Kasanka NP. With respect to localities of the scats, the crocodiles were restricted almost exclusively on Kasanka River, where puku occur at high density. The scats of terrestrial predators were found above all in the centre of Kasanka NP, probably not interrelated but still similar to puku. This is also the area where the camera-traps revealed the presence of servals and African civets.

Scats of lions (*Panthera leo*) and especially of spotted hyenas (*Crocuta crocuta*) were found along roads in Kafue Region. Puku occurred to about 54-55% in their scats, but compared to the puku's relative amount in their diets and in the antelope society, none of them preferred to prey upon puku; rather puku was consumed in accordance to its availability. Nevertheless, these large carnivores were suggested to be important predators on puku. Only the spotted hyena was detected by the camera-traps in PPKR.

Additionally to the results of the found scats, leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*) and wild dogs (*Lycaon pictus*) might be important predators of the puku. However, information about the diet of most predators is rather lacking for the miombo ecoregion, so that further research is needed to assess properly the relation between predators and their prey in Zambia.

Connecting the characteristics of the puku population in the study regions to the findings of this analysis, predation pressure of terrestrial large predators appears rather low in Kasanka NP and thus not able to limit the population of puku. But in Kafue region though, it is assumed to be higher and maybe regulating the puku's population.

“The flesh of the puku is stated by Selous to be even more nauseous and unpalatable than that of the common waterbuck”

Sclater 1900

4.1 Introduction

There are many cases where animal populations are affected by predators (top-down) and resources (bottom-up) in terrestrial ecosystems (Sinclair et al. 2003). Proponents of the top-down view argue that the world is green because predators regulate the numbers of herbivores and thereby limit the damage herbivores do to vegetation (Terborgh et al. 2001). Further, the presence of top-predators can increase the diversity of prey species through intermediate disturbance effects (Sinclair & Byrom 2006).

This chapter will deal with the predation on the puku (*Kobus vardonii*). There is no focus on a specific predator but all predator species that might prey on bovids and thus exhibit a potential top-down effect on the puku’s populations in the study regions are considered. Presumably terrestrial predators of puku are the spotted hyena (*Crocuta crocuta*), the lion (*Panthera leo*), the leopard (*Panthera pardus*), the African wild dog (*Lycaon pictus*) and perhaps the cheetah (*Acinonyx jubatus*). However, with a body weight of 77 kg for males and 66 kg for females (Huffman 2011), the puku falls within the preferred prey weight range of the spotted hyena, only (Hayward & Kerley 2008), but young puku might be preyed. Although rather avoided, the kob antelope (*Kobus kob*) can make up 28% of the lion’s prey (Hayward & Kerley 2005) so that puku are assumed to be preyed by lions in Zambia. This chapter aims to find out more about the occurrence and diet of predator species in the study regions:

- Which carnivore species occur in the study region and what are the main predators of the puku? The puku is suggested to be prey for the spotted hyena, the lion, the leopard, the cheetah and the wild dog. Although not the preferred prey, the puku might be consumed in considerable amounts.

Faeces of predators are the main source of information to assess the predation on the puku. Faeces of animals are the most readily-available and easily collected source of information (Putman 1984). The amount of information that can be gathered is amazing

(Putman 1984); faeces bring out biological and ecological data as species presence, diet, behaviour, territory, parasitic fauna and home-range use (Chame 2003). The analysis of prey remains in faeces, particularly hair, is convenient to examine the prey spectrum of mammalian predators (Oli 1993). The microscopical examination of faecal is a technique widely used (Putman 1984), but the microscopical identification of hair can be difficult because hair features vary within and between species (Oli 1993). A convenient tool for routine identification of hair in faeces is a photographic reference of diagnostically important structures (Oli 1993). These structures are cross-sectional appearance, shape and arrangement of medulla, the ratio of cortex to medulla, and the form and distribution of pigment in medulla and cortex (Oli 1993). Based on these features, hair identification keys can be compiled as done by De Marinis & Asprea (2006) for ungulates from southern Europe or by Schneider & Buramuge (2005) for small mammals in southern Africa. In the context of the ZamBio Project, a reference hair catalogue was compiled by Rebecca Ray, containing hair of mammals occurring in Luambe NP in order to assess the leopard’s prey spectrum. Macroscopic features of hair as its length, thickness, coloration and colour patterns are important aids for the determination (R. Ray, pers. comm. and own obs.).

The most challenging task in the analysis of faeces of predators is to determine the respective predator. Diagnostics based on morphometric features permit a primary identification which is complicated by the great diversity of medium and large carnivores in Africa (Chame 2003). Often diameters are used to include or exclude faeces as a supplement to the identification by general characteristics (Ray 2011) or to exclude scats not identified by the analysis of guard hair (Thiel 2011).

Beside terrestrial predators, Nile crocodiles (*Crocodylus niloticus*) prey on puku (Mitchell et al. 1965) so that the study needs to encompass this reptilian and aquatic predator:

- Is it possible to apply the method of determining hair in faeces, used for terrestrial predators, in order to get information about the crocodile’s diet? As Nile crocodiles prey upon antelopes, it is suggested to prey also upon puku. Is it generally possible to find crocodile faeces?

The faecal samples of predators in Kasanka NP were analysed by Jennifer Michaelis for her bachelor thesis (Michaelis 2011) but reinvestigated for this thesis.

4.2 Methods

4.2.1 Searching for signs of carnivore species

The search for faeces of predators was conducted mainly at random but also systematically. Faeces were collected whenever they were detected during the data collection in field. Generally, faecal samples were taken if they could be attributed to a predator that might prey upon puku. Identification was based on shape, colour, characteristics and size as well as on the information of the escorting WPO. Some faeces were found in latrines, i.e. when more scats are situated close to each other. Nevertheless, later at the ZFMK, the determination of the faeces origin could change (see Chapter 4.2.2). The location was made out using a GPS device (Garmin eTrex Legend HCx). If possible, a picture with a scale (mostly a metre stick) was taken. The area around the faeces was scanned for tracks or other signs that might help to determine the predator. The sample's number, the date, the GPS position and the number of the picture were recorded and the faecal sample was labelled. Then faeces were transported and stored in plastic bags. If not dry yet, faeces were air dried later. Faeces were collected in Kasanka NP in the period from 2nd July to 4th September 2009 and from 2nd October to 29th November 2010. In Kafue Region, faeces were collected in PPKR from 10th July to 27th August 2010 and from 18th September to 25th September and in Kafue NP from 27th August to 6th September 2010.

Kasanka NP was systematically scanned for indications for predators. During foot surveys through grids, possible signs for predators or their activities were searched. In Kasanka NP, a number of five grids with an edge length of 1 km were placed in such a way that a link between the results of the transect line survey and the results of the search for predators was possible (Figure 4-1). A survey covering the entire NP was not possible due to constraints of this research project. However, the grids were placed in order to cover different habitats in different areas of Kasanka NP (see Appendix Figure A. 22). Grid 1 near Luwombwa and grid 5 near Wasa include entirely miombo, although different in their aspects. The other grids include miombo and other habitat types: grassland situated next to a waterhole and therefore partially wet for grid 2 at Chikufwe, floodplain and dambo habitat for grid 3 at Kabwe/Puku-Loop and grassland for grid 4 at Fibwe. They were walked diagonally in different orientation, though, to deal with accessibility or natural constraints (rivers, swamps). The grids were walked and thus examined twice; from 10th October to 17th October 2010 and from 3rd to 7th November 2010. Further, during walks, independently from the grid survey, crocodile faeces were searched in the Kasanka River floodplain. Also other research tasks for this study and other ad libitum walks were carried out in different areas of Kasanka NP. A WPO was needed for security reasons but he could also provide very useful information. For the survey of predators in Kasanka NP in 2010, I was assisted by Jennifer Michaelis.

Further, camera-traps were mounted in Kasanka NP and in PPKR in order to prove the presence of carnivore species (see Chapter 2.2.3 for more details).

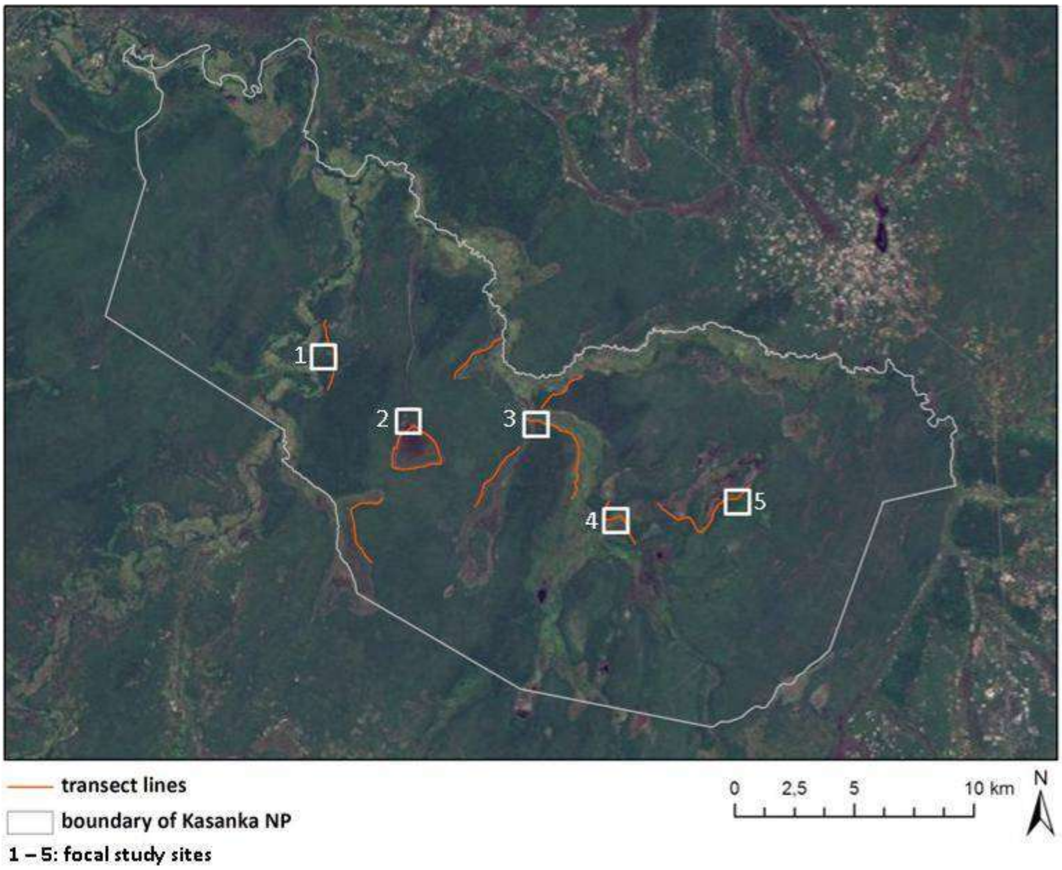


Figure 4-1: Situation of the focal study sites for the search for faeces and other signs for predators (grid survey) in Kasanka NP.

4.2.2 Analysis of the faeces of carnivores

Analyses took place at the ZFMK. All dry faeces were photographed with an adjacent scale. The diameter was measured at the thickest part of the faeces. Then, the faeces were put into 70% alcohol for softening and disinfection purpose. After at least one day, the faeces were broken up. All components that were not hair (bones, bone fragments, teeth, claws, hoofs, horns, soft parts like sinews, skin or cartilage, arthropods, endoparasites, feathers, scales, vegetable matter like grass, twigs, leafs or seeds, stones or stone-like material) were sorted out. The hair was washed under tap water. The sorted components of the faeces were then air-dried or put into 70% alcohol, each labelled with the number of the faeces, and stored for later analysis. During this task I was assisted by students.

In the dried hair we searched for different kinds of cover hair that might belong to different species of mammals. To facilitate handling and macroscopic comparison of the hair, some were separated from the bundle and put in a small zip bag, one for each kind of hair. A number of about 3 to 10 hairs of each hair type were fixed on microscope slides using nitrocellulose (i.e. transparent nail polish) and covered with cover slips.

The main component of the analysis was to assign the found hair to reference hair. For this purpose an already existing reference collection of hair from Zambian mammals could be used. It was initiated and elaborated by Rebecca Ray within her Leopard-Monitoring-Project situated in Luambe NP in Luangwa Valley, Zambia (Ray 2011). As some additional mammal species occur in the study regions of my research, some more reference hair was added. While most of the hairs remained in zip-bags for macroscopic investigation, some of the reference hair samples were fixed on microscope slides for reference pictures of the medulla and cortex. These hair added to the reference collection include hair from all the following: large grey mongoose (*Herpestes ichneumon*), dwarf mongoose (*Helogale pervula*), honey badger (*Mellivora capensis*), Cape Clawless otter (*Aonyx capensis*), striped weasel (*Poecilogale albinucha*), all carnivora; bush duiker (*Sylvicapra grimmia*), sitatunga (*Tragelaphus spekii*), sable (*Hippotragus niger*) and tsessebe (*Damaliscus lunatus*) all Artiodactyla; a primate, the mohol bushbaby (*Galago moholi*), and two hyraxes, the tree hyrax (*Dendrohyrax validus*) and the bush hyrax (*Heterohyrax brucei*). All reference hair added came from specimens in the mammal collection of the theriology section at the ZFMK. Furthermore, hair of a dead puku from Kasanka NP was added, although already available in the reference collection (Figure 4-2 A and B). By doing so, confusion about possible differences in both macroscopical and microscopical aspects on the western side of

Luangwa Valley due to an eventual different subspecies of puku (Ansell 1960a, 1978) should be prevented.

The samples were compared to the reference collection. Following criteria were useful for macroscopic investigation: shape, colour, colour patterns, thickness and contingently the length. During the microscopic investigation colour and texture of cortex and the characteristics of the medulla were taken into consideration (Figure 4-2).

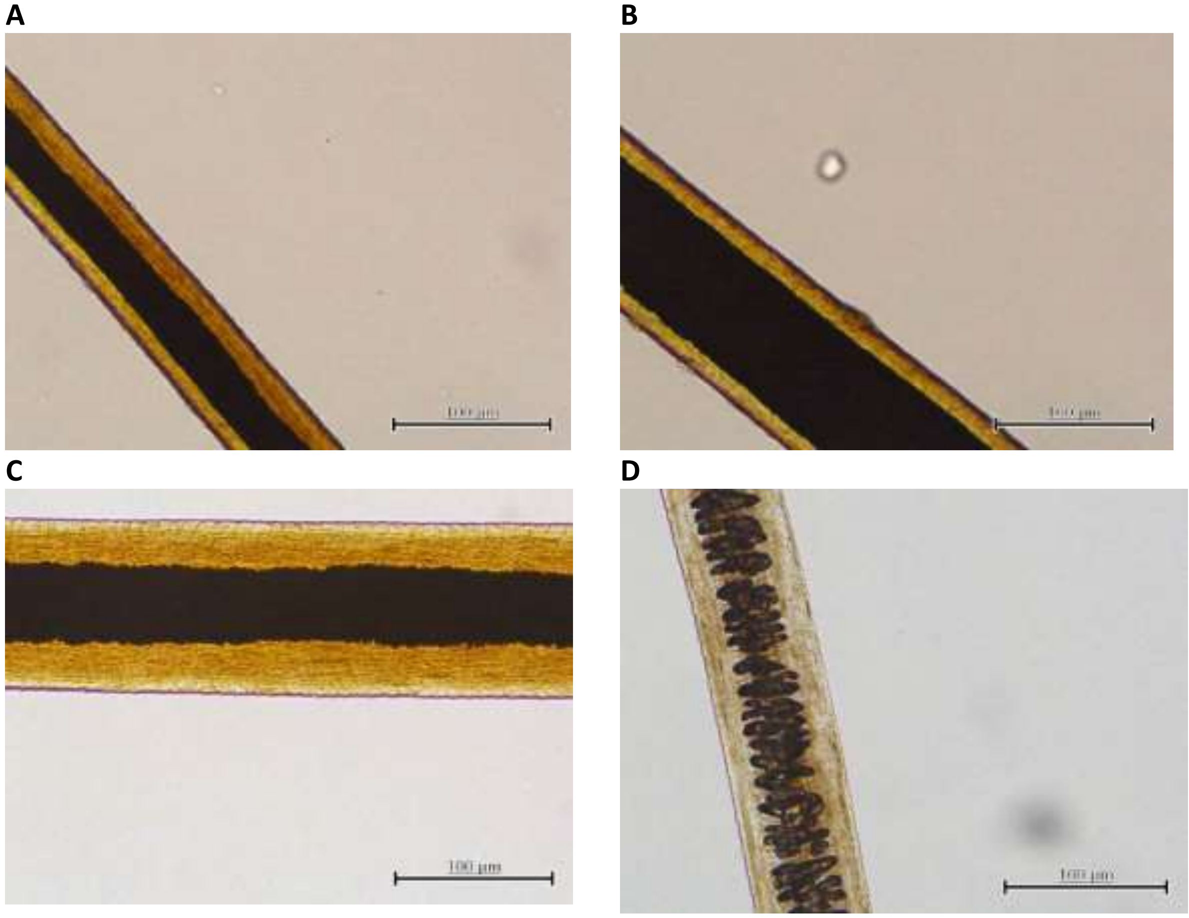


Figure 4-2: Microscopic aspects of hairs: A and B: Hair of puku (*Kobus vardonii*): a segment situated distal within the hair beneath the tip (A) and a basal segment (B) within the same hair collected from a dead puku in Kasanka NP; a basal hair segment from sitatunga (*Tragelaphus spekii*) (C) and from tree hyrax (*Dendrohyrax validus*) (D). The scale gives 100µm.

Thus, the analysis of the faeces followed mainly the methods used for other research projects within the ZamBio Project (confer Ray 2011, Thiel 2011, Stommel 2009). But unlike to the procedure in these research projects, the cuticula of the hair was not investigated. Scale patterns of the cuticula vary a great deal over the length of a hair and overlap between species, are often confusing and are considered at least useful (Oli 1993).

Hair from the samples might belong to both prey and predator species. As the faecal samples could not always be determined with certainty in the field, especially for terrestrial carnivores in Kasanka NP, a determination of the predator species via guard hair was the target. Usually, guard hair of predators is far less abundant in the samples than those of the prey. The samples whose origin was proven by guard hair served in the following to determine the origin of those samples without guard hair of the predator. The shape and posture of the faecal samples was compared using the pictures taken. In doing so a considerable amount of samples could be determined in retrospect.

Beside the hair other components of the faecal samples could provide information on the consumed prey, such as horns or claws. Further, feathers of birds and teeth of small mammals were determined by experts of the ZFMK, namely Dr. RENATE VAN DEN ELZEN and Dr. RAINER HUTTERER. The results of a more detailed view on the diet breadth of some predator species are not presented within this thesis.

4.2.3 Data analyses

Independent photographs of carnivores from the camera-traps were counted (JENKS et al. 2011) and the Relative Abundace Index (RAI) was calculated (see Chapter 2.2.4 for more details).

A cumulative curve showing the number of found prey items in relation to the number of analysed scats, allowed checking if the prey spectrum can be assumed complete.

Following LOCKIE (1959), the amount of items in the scats was given as ‘frequency of occurrence’ (FO) which is the percentage of scats in which a particular item was found and as ‘percentage occurrence’ (PO) which is the number of times a prey item was found, expressed as a percentage of all items recorded.

The consumed biomass was calculated by the formula provided by ACKERMAN et al. (1984): $Y = 1.98 + 0.035 X$, where Y is the weight of prey consumed and X the prey’s body weight. In this study this formula was applied to calculate the consumed bovid biomass by all types of carnivores, although it was derived from the digestion of cougar (*Felis concolor*) (ACKERMAN et al. 1984). In order to take account of calves and subadults, the weight of ¾ mean adult female body weight was used for the calculations, also to allow comparison with other studies (HAYWARD et al. 2006a). The body mass of bovids was taken from HAYWARD et al. (2006a). With the FO the biomass consumed by the predator species was derived. In order to compare the consumed biomass of each predator with each other, these results were set to 100%, which gave the respective relative amounts.

In order to assess food preferences of the predator species, the Jacobs Index (Jacobs 1974) was used: $D = (r-p) / (r+p-2pr)$. In the case of this study, r is the ratio of the prey in the diet, the PO is used, and p the proportional abundance of that prey. The proportional abundances of bovid species in Kafue Region are derived from the results of the DISTANCE estimations (chapter 2). If proportional abundance is less than 5%, the respective bovid species is excluded from the analysis (Palomares et al. 2000).

All maps were created using ESRI ArcMap 10.0. Diagrams were created using Microsoft Excel 2010.

4.3 Results

4.3.1 Faeces and other signs of predators

In Kasanka NP, a number of 33 faecal samples could be attributed to a predator via guard hair analysis which was about 31% of all samples and 40% of the samples of terrestrial predators. A considerable amount of samples could be assigned to the serval (*Leptailurus serval*), to the caracal (*Caracal caracal*) and to the white-tailed mongoose (*Ichneumia albicauda*). Found in latrines, so called civitries, a number of 5 samples were attributed to the African civet (*Civettictis civetta*). In the civitries and in these faecal samples, big seeds were found. Thus, the presence of this kind of seeds in the faeces was considered as a hint for their belonging to civets. In combination with shape and other characteristics of the faeces, a number of 21 scats were attributed to the civet. Collected mainly as scats of spotted hyenas, a considerable amount of scats found in Kafue Region turned out to belong to the lion. Although possibly white in colour, the faeces of lions were softer in consistence and contain bones or bone fragments. From most of the samples, the diameter could be measured (Table 4-1).The faeces of all terrestrial predators found in Kasanka NP were similar in their diameters; only the diameter of faeces of civets ranged to higher values. The faeces of lions and hyena were similar in diameter, but larger in diameter than the faeces from predators in Kasanka NP. In the following, the presentation of the observations made during the field trips refers to the final determination of the predator belonging to the scats.

Table 4-1: Diameters of the faecal samples. Not all samples could be measured.

predator species	mean [mm]	min [mm]	max [mm]	N
serval (*Leptailurus serval*)	23.7	17.4	29.6	18
caracal (*Caracal caracal*)	20.3	15.0	29.3	5
white-tailed mongoose (*Ichneumia albicauda*)	21.6	15.0	28.0	23
African civet (*Civettictis civetta*)	24.7	12.7	32.8	24
lion (*Panthera leo*)	37.7	22.4	45.0	22
spotted hyena (*Crocuta crocuta*)	37.4	14.6	52.8	65

In Kasanka NP, a number of 18 faecal samples of predators was found during the grid survey. The 18 samples were distributed unevenly over the five grids (Table 4-2). While no samples were found in grid 2 and 3, only 2 samples each were found, both in grid 1 and 4, belonging to different predators in these grids. The highest number of 15 samples was found in grid 4, at Fibwe Plain. Especially faeces of white-tailed mongooses, servals and caracals were found here. Some tracks of medium and small predators were found in grid 4 on the dirt road, but they could not be identified. Not only during the grid survey dead puku were found on the ground, dead for some time already. They could not be determined as kill of a specific predator.

Table 4-2: Number of faecal samples and their belonging to predator species in the grids surveyed in Kasanka NP.

predator species	grid					total number found during the grid survey
	1	2	3	4	5	
Nile crocodile (*Crocodylus niloticus*)	0	0	0	0	0	0
serval (*Leptailurus serval*)	0	0	0	3	1	4
caracal (*Caracal caracal*)	0	0	0	3	1	4
white-tailed mongoose (*Ichneumia albicauda*)	0	0	0	5	0	5
African civet (*Civettictis civetta*)	2	0	0	2	0	4
undetermined predator	0	0	0	1	0	1
total number found during the grid survey	2	0	0	14	2	18

Faeces of predators were mainly found at random. Another 89 faecal samples of predators were gathered. Thus, a sum of 107 faecal samples of predators was available for the analyses. Detached from the grids, they were found to different extents in different areas of Kasanka NP (Figure 4-3). Faeces of crocodile were found mainly along Kasanka River. Faeces of all terrestrial predators were found mainly in Fibwe Region. Scats of cats i.e. servals and caracals were found mainly in the eastern part of Kasanka NP. This pattern was less exhibited for the localities of faeces of the white-tailed mongooses which were found also near Kasanka River. Faeces of civets were found in many parts of Kasanka NP. Only one scat of spotted hyena was found along Kasanka River. A few faeces could not be clearly allocated to any predator.

In Kafue Region, faecal samples of predator species were found at random. They were found along and on roads (Figure 4-4, Figure 4-5). Most of the faeces could be related to the lion and the spotted hyena. Some few faecal samples could not be related beyond all doubt to a specific predator species. While scats of lions were mostly found individually, the scats of spotted hyenas were found in different numbers ranging from 1 to 22 at one locality. A total of 22 faecal samples of lions and 70 faecal samples of spotted hyenas were found. From these, a number of 14 scats of lions and 3 scats of spotted hyenas were found Kafue NP.

The camera-traps detected three carnivore species in Kasanka NP, the serval (RAI of 0.01), the African civet (RAI of 0.04) and the marsh mongoose (*Atilax paludinosus*) (RAI of 0.01). They reached low RAI values compared to the RAI of antelopes (see Chapter 2.3.4). These carnivores were detected at the focal region Fibwe-Area only. In this specific area, the African civet had the highest RAI, 0.61. Both servals and marsh mongooses reached lower

RAI of 0.23. In PPKR, the only larger carnivore detected by the camera-traps was the spotted hyena reaching a RAI of 0.19. Otherwise mongooses were captured: Meller's mongoose (*Rhynchogale melleri*) and the white-tailed mongoose reaching each a RAI of 0.19, too.

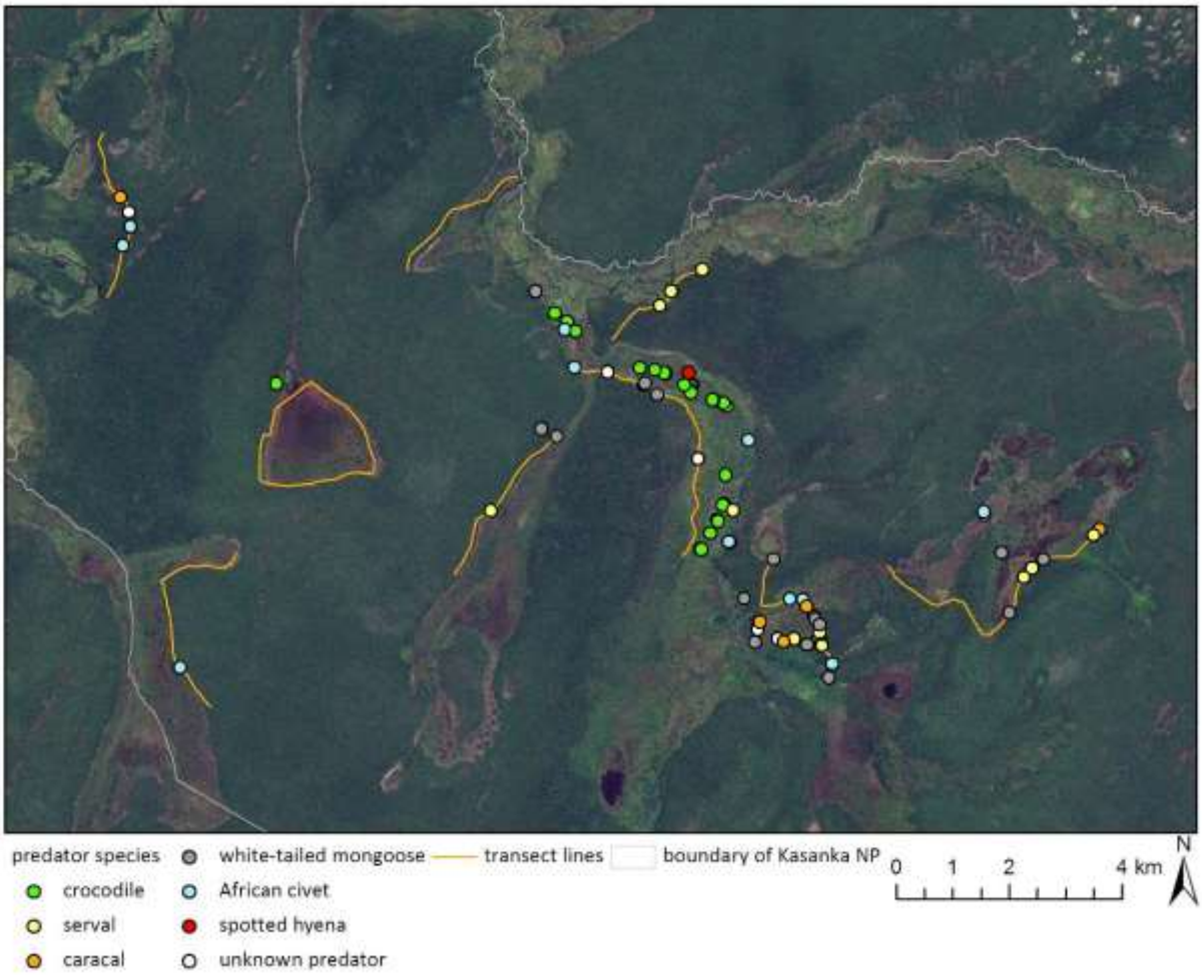


Figure 4-3: Localities of the faecal samples found by the grid survey and by random collection in Kasanka NP during all field trips. As some samples were found at the same locality the number of dots does not represent the number of samples.

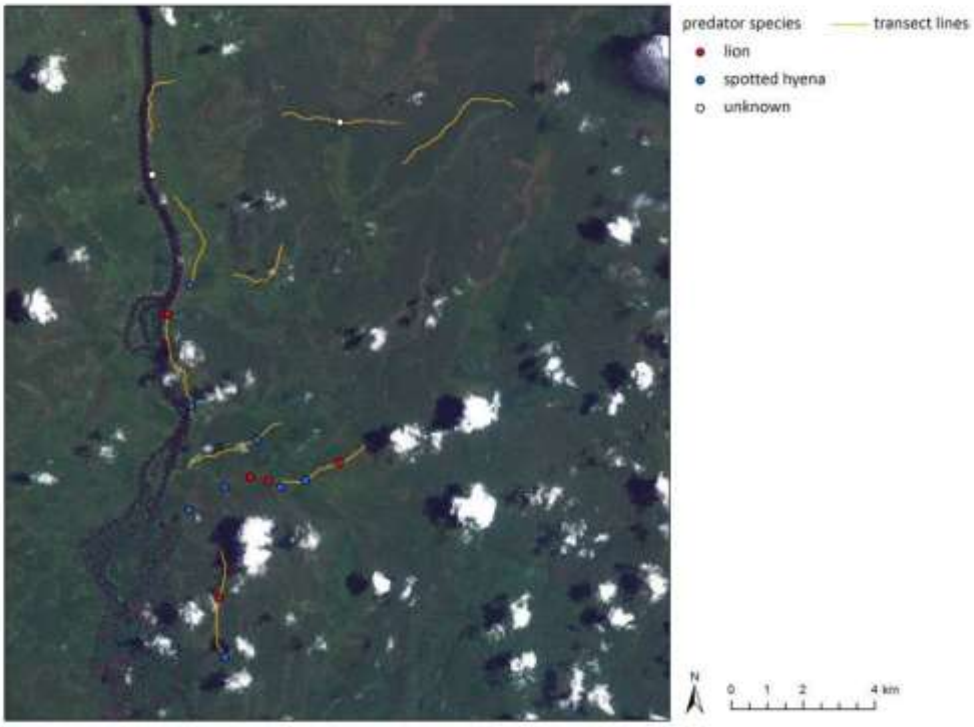


Figure 4-4: Localities of the faecal samples found in PPKR and the respective predator species. As some samples were found at the same locality the number of dots does not represent the number of samples.

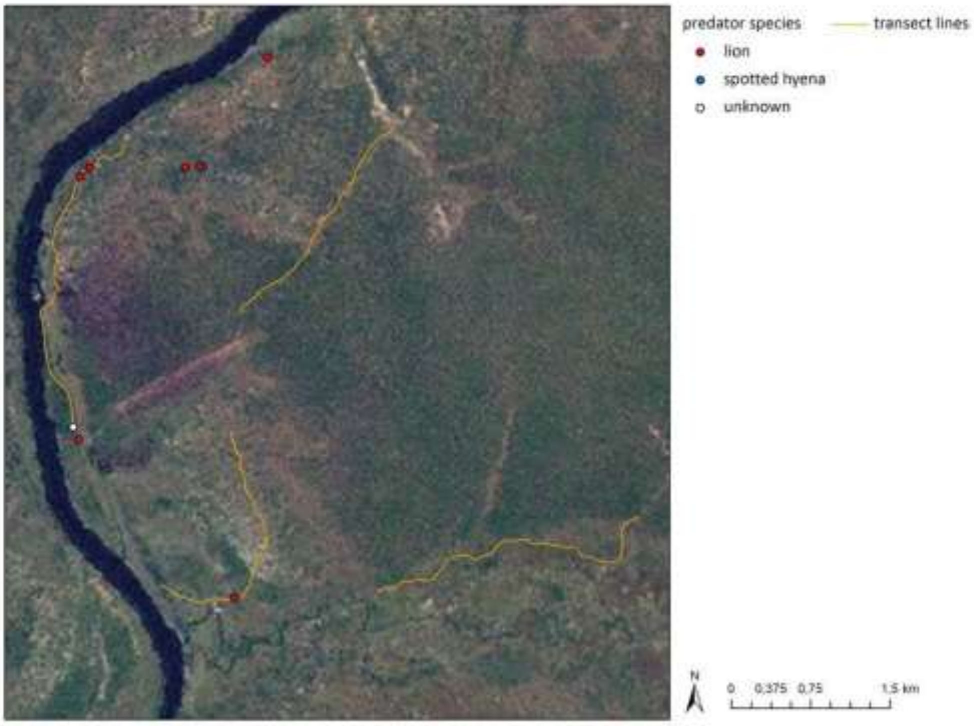


Figure 4-5: Localities of the faecal samples found in Kafue NP and the respective predator species. As some samples were found at the same locality the number of dots does not represent the number of samples.

4.3.2 Determination of prey in the faecal samples

The cumulative curves plotted the number of scats against the number of all prey items found in the scats (Figure 4-6). For Kasanka NP, none of the curves exhibited the shape of an asymptote. The number of prey items was 19 for civets and white tailed mongooses while only 5 prey items were found in the scats of caracals. For Kafue Region, the number of prey items found in the scats was much less, only 5 prey items for each species. Nevertheless, the curve of the hyena shows asymptotic features.

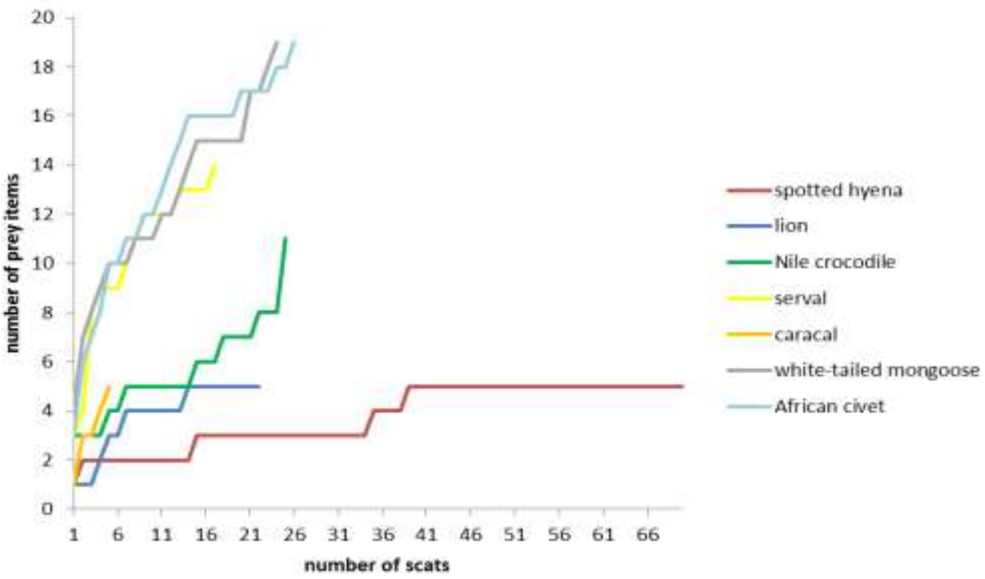


Figure 4-6: Cumulative curve showing the relation between the number of scats and the number of prey items found for all faecal samples found during this study.

In Kasanka NP, depending if considering FO or PO of prey (Table 4-3), crocodiles or civets had the highest amount of bovids in their diet. Servals, caracals and white-tailed mongooses rather consumed other mammals. Nevertheless, caracals and white-tailed mongooses preyed also on bovids while servals did not. All predators were found to feed on other prey items (e.g. birds, arthropods, fishes), but details on these results are not presented within this thesis. Concerning crocodile, the content of a high amount of faeces could not be determined. Beside the faeces from determined predators, faeces from unknown predators showed a high amount of bovid prey. One scat of spotted hyena was found; it included hair of bushbuck (*Tragelaphus scriptus*). Concerning bovid prey a number of 5 species was found in the scats in Kasanka NP (Table 4-4). Puku were consumed by crocodiles, white-tailed mongooses, and undetermined predators and to a considerable amount by civets. To about equal amounts puku and sitatunga (*Tragelaphus spekii*) were consumed by crocodiles. Also other predators consumed sitatunga. Bushbuck were eaten to an extensive amount by almost all predators consuming bovids. Otherwise, reedbuck (*Redunca arundinum*) and bush duiker (*Sylvicapra grimmia*) were found as prey in the faeces.

In Kafue NP, on three occasions, faeces could not be related to a predator; probably they belong to a larger cat species. All three samples contained puku hair (Table 4-3). Both spotted hyenas and lion showed a high amount of bovid prey species concerning FO and PO. While traces of only few other mammals were observed in the faeces of hyenas, lions consumed other mammals to about 30% in both FO and PO. In comparison to the analyses of the other scats, the amount of undetermined prey was rather high for the faecal samples of hyena. Both spotted hyenas and lions consumed puku to the highest amount of all bovids found (Table 4-4). For hyena the remaining amounts were shared rather equally by impala (*Aepyceros melampus*), bushbuck and waterbuck (*Kobus ellipsiprymnus*) with slightly higher amounts for the latter in FO and PO. Lions consumed reedbuck and, to a considerable amount, impala.

From all bovid species that were found in the faeces of predators in Kasanka NP, puku were consumed most (Figure 4-7). In terms of biomass it was eaten especially by civets, but also by crocodiles and to the least amount by white-tailed mongooses. Regarding bovid prey, only the mongoose fed above all on bushbuck, which is ranked second in the consumed biomass. Sitatunga ranked third was mainly eaten by crocodiles. The consumed biomass of bush duiker was the smallest amount. In Kafue Region, from all bovid species, the puku was by far consumed most in terms of biomass (Figure 4-8). Based on the relative amount of consumed biomass, the lion consumed more puku than hyena. In contrast to amounts based on FO and PO, the waterbuck made up a considerable part in the diet of hyena; it was the second prey behind the puku. Impala were not much consumed by any of two predators but rather by lions.

The analysis of preference via the Jacobs index resulted in values close to zero. Neither puku nor impala had high values of being avoided or preferred as prey by spotted hyenas (Jacobs index for puku: -0.004; Jacobs index for impala: 0.04) or lions (Jacobs index for puku: -0.005; Jacobs index for impala: 0.013). Other bovid species found in the diets of predators, waterbuck, bushbuck and reedbuck, have a proportional abundance of less than 5% and were thus excluded from the analysis.

Table 4-3: Prey categories found in the faeces of predators in the study regions, expressed as frequency of occurrence (FO) (based on all scats of each predator) and percentage of occurrence (PO) (based on all determined prey items of each predator).

		number of		**FO/PO**			
study region	**predator species**	**faeces**	**prey items**	**bovid**	**other mammals**	**other prey items**	**undefinite content**
Kasanka NP	Nile crocodile (*Crocodylus niloticus*)	25	23	64.00/73.91	8.00/8.70	16.00/17.39	28
	serval (*Leptailurus serval*)	18	42	0/0	83.33/69.05	66.67/30.95	0
	caracal (*Caracal caracal*)	5	8	40.00/12.50	80.00/87.50	20.00/12.50	0
	white-tailed mongoose (*Ichneumia albicauda*)	25	48	32.00/14.58	72.00/54.17	52.00/31.25	4
	African civet (*Civettictis civetta*)	27	54	92.59/44.44	25.93/14.81	81.48/40.47	0
	spotted hyena (*Crocuta crocuta*)	1	1	100.00/100.00	0	0	0
	undetermined predator	7	8	85.71/75.00	14.29/12.50	14.29/12.50	0
Kafue Region	spotted hyena (*Crocuta crocuta*)	70	64	82.86/95.31	4.29/4.69	0/0	17.14
	lion (*Panthera leo*)	22	24	77.27/70.83	31.82/29.17	0/0	4.55
	undetermined predator	3	3	100.00/100.00	0/0	0/0	0

Table 4-4: Bovid prey found in the faeces of predators in the study regions, expressed as frequency of occurrence (FO) (based on all scats of each predator) and percentage of occurrence (PO) (based on all prey items of each predator).

		FO/PO of bovid prey						
study region	**predator species**	**puku** **(*Kobus vardonii*)**	**impala** **(*Aepyceros melampus*)**	**waterbuck** **(*Kobus ellipsiprymnus*)**	**sitatunga** **(*Tragelaphus spekii*)**	**bushbuck** **(*Tragelaphus scriptus*)**	**reedbuck** **(*Redunca arundinum*)**	**bush duiker** **(*Sylvicapra grimmia*)**
Kasanka NP	Nile crocodile (*Crocodylus niloticus*)	24.00/26.09	0/0	0/0	28.00/30.43	8.00/8.70	0/	8.00/8.70
	serval (*Leptailurus serval*)	0/0	0/0	0/0	0/0	0/0	0/0	0/0
	caracal (*Caracal caracal*)	0/0	0/0	0/0	0/0	20.00/12.50	0	0
	white-tailed mongoose (*Ichneumia albicauda*)	4.00/2.08	0/0	0/0	4.00/2.08	16.00/8.33	0/0	4.00/2.08
	African civet (*Civettictis civetta*)	44.44/22.22	0/0	0/0	7.41/3.70	25.93/12.96	0/0	11.11/5.56
	spotted hyena (*Crocuta crocuta*)	0/0	0/0	0/0	0/0	100.00/100.00	0/0	0/0
	undetermined predator	14.29/12.50	0/0	0/0	14.29/12.50	42.86/37.50	14.29/12.50	0/0
Kafue Region	spotted hyena (*Crocuta crocuta*)	54.29/59.38	10.00/10.94	12.86/14.06	0/0	10.00/10.94	0/0	0/0
	lion (*Panthera leo*)	54.55/50.00	18.18/16.67	0/0	0/0	0/0	4.55/4.17	0/0
	undetermined predator	100.00/100.00	0/0	0/0	0/0	0/0	0/0	0/0

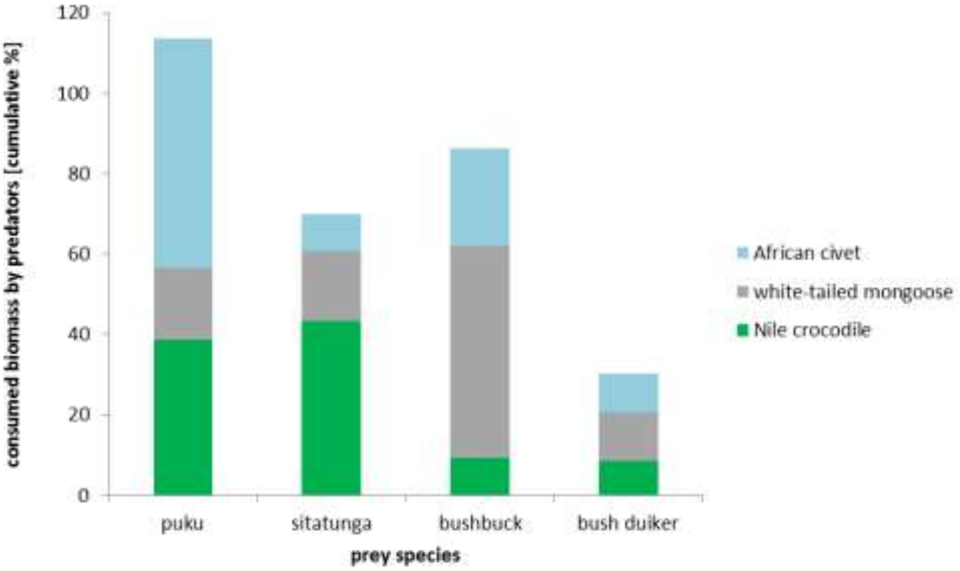


Figure 4-7: Biomass of different prey species consumed by predators in Kasanka NP; expressed as the cumulative percentage amount of the calculated consumed biomass of bovids in the diet of the predators. Nile crocodile (*Crocodylus niloticus*): N=25; white-tailed mongoose (*Ichneumia albicauda*): N=25; African civet (*Civettictis civetta*): N=27.

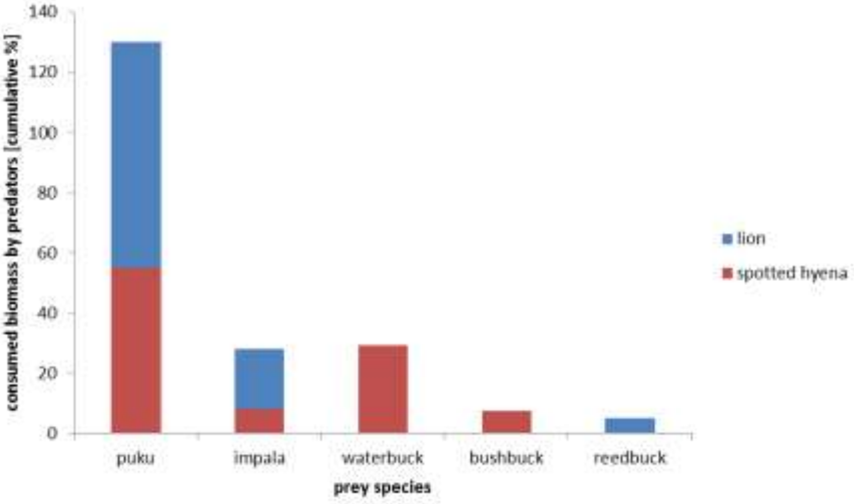


Figure 4-8: Biomass of different prey species consumed by predators in Kafue Region; expressed as the cumulative percentage amount of the calculated consumed biomass in the diet of the predators. Spotted hyena (*Crocuta crocuta*): N=70; lion (*Panthera leo*): N=22.

4.4 Discussion

4.4.1 Assigning the faecal samples to predators

Indeed, distinguishing faeces of medium to large(r) terrestrial predators in Africa was challenging because of sometimes similar appearance (see also Appendix Figure A. 23) but not impossible. A lot of samples, if not most of the samples of terrestrial predators collected in Kasanka NP, were collected as faeces of leopard; and both WPO and scientifics agreed on the predator. It was impossible to find tracks next to the scats because either the soil was hard due to the dry season, or, in the case of scats on sandy roads, passing vehicles had removed it. As predators groom themselves, the guard hair of predators can be involved in the analysis. In 40% of the scats of terrestrial predators in Kasanka NP a reliable assignment to a predator was possible. Above all, this applied to scats of servals and white-tailed mongooses, but to caracals, too. In consequence, pictures of those scats served as reference to identify most of the remaining scats via their apparent characteristics like shape, strangulations or disposal. The faecal samples of the African civet were recognized by their locality in civitries, then referenced and identified alike.

The attribution of scats to their respective carnivore species resulted in new information about their diameter which allows for comparison between carnivore species and data from other researchers/authors (Table 4-5). Although generally a smaller mean diameter is given for scats of white-tailed mongooses, the scats found in Kasanka NP had also diameters of up to 28 mm. By this, the range of diameter was similar for servals, caracals and white-tailed mongooses. Nevertheless, the diameter of serval scats was slightly larger. THIEL (2011) noted it with 21.72 mm and 19.94 mm for Luambe NP and other areas in Zambia, respectively. Scats of servals and caracals are said to be similar in every aspect (WALKER 1996); all scats of these cats except two samples of servals were assigned by guard hair, so that a wrong assignment could be excluded. However, scats of caracals can be very long (WALKER 1996). The diameters of scats of African civets were rather large. This was already stated by WALKER (1996). In matters of diameter measurements, confusion with leopard scats is possible especially if a lot of hair is in the faeces. Scats of leopard can have a diameter of 20-30 mm or larger (STUART & STUART 2000). Lions and spotted hyenas are characterised by scats that are very large in diameter, but the values from this study were below the range given by Walker (1996). Due to high calcium content of ingested bones, faeces of both lions and spotted hyenas can be totally white (Chame 2003). Nonetheless, resulting from digested blood and flesh (Stuart & Stuart 2000) dark coloured scats of lions, were found. However, the measured diameters of the assigned faeces fit with the known information. This underlines the validity of the results.

Table 4-5: Comparison of indications about diameter/width (all given in mm) of scats of different predator species. *diameter/width derived from picture and adjacent scale

predator species	Chame 2003	Walker 1996*	Stuart & Stuart 2000	Cillié 2009 *	this study	
					mean	**range**
serval (*Leptailurus serval*)	22	20	-	22	23.7	17.4-29.6
caracal (*Caracal caracal*)	17	15-17	20 rarely exceeding	20	20.3	15-29.3
white-tailed mongoose (*Ichneumia albicauda*)	13	15	-	-	21.6	15-28
African civet (*Civettictis civetta*)	-	large for such an animal	-	20	24.7	12.7-32.8
lion (*Panthera leo*)	44	50-60	usually more than 40mm	45	37.7	22.4-45
spotted hyena (*Crocuta crocuta*)	50	-	-	30	37.4	14.6-52.8

From the analysed scats only those of civets and spotted hyenas were found to different extent in latrines sites as also reported by Stuart & Stuart (2000) and Walker (1996), called civitry for African civets (Stuart & Stuart 2000). If roads go through the hyena's territory these latrines are often close to them (Stuart & Stuart 2000) as also supported by this study. However, not in every case, white scats close to each other represent a hyena latrine site. Lion scats can be encountered in loose accumulations at lying-up sites or near kills (Stuart & Stuart 2000) as observed in this study. On the basis of the scats from Kafue Region, the one and only scats of a spotted hyena in Kasanka NP could be reliably assigned. A number of 7 scats of terrestrial predators in Kasanka NP could not be assigned. Some of them might belong to cat species and thus also to the leopard.

On account of their location near the river and their form that differed from those of terrestrial predators, faecal samples of crocodiles could be found and assigned accordingly. Some of them were flattened, probably by the crocodile itself.

Generally, the assignment of faeces to the respective predators by the chosen methods was considered as reliable. Only few samples could not be associated to a predator and were therefore presented separately.

4.4.2 Occurrence of predators in the study regions

Generally, it is possible that scats were overlooked during the walks. BULINSKI & MCARTHUR (2000) reported that between 3% to 12% of scats were overlooked during standard counts when searching for faeces of two species of macropods. That means that 3 to 13 scats might have been overlooked in Kasanka NP. The probability of overlooking faecal samples is positively related to vegetation height and negatively related to vegetation cover (BULINSKI & MCARTHUR 2000). The grids in Kasanka NP covered different habitats: Fibwe Plain was covered with relatively high dry grass; other areas were miombo woodlands either providing dry vegetation or burned areas with less vegetation in terms of grass height and general vegetation cover. Thus, the conditions for the detection scats altered between and within the grids. All cats are reported to make frequently use of roads and trails to avoid “bush bashing” when moving around and droppings are easy to see (STUART & STUART 2000). Thus, the study was slightly biased toward the area along roads, but at the same time the collection success of scats of all kind of predators vindicated this kind of search.

Concerning the detection of scats during the grid survey, most of them were found in grid 4 at Fibwe Plain. Beside the high number this grid provided the highest biodiversity on predators i.e. according to the results of the scat analyses four different species occurred: serval, caracal, white-tailed mongoose and African civet. No scats were found in grid 2 and 3, at Chikufwe and at Kabwe. Two scats of civets were found at grid 1, near Luwombwa, and one scat of serval, one of caracal were found in grid 5 at Wasa. The grid survey’s results revealed that in means of number and species, the highest predator activity took place around Fibwe. This was also supported by the results of the camera-trap study, detecting servals, African civets and marsh mongooses only at Fibwe.

During walks along Kasanka River and through the floodplain, scats could be collected on both shores. The scats belonged mainly to the crocodile, but also scats of other predator species were found. The one and only scat of a large terrestrial predator, of the spotted hyena, was found at the northern shore of Kasanka River. Scats of different predators were found in some other areas of the park (along the transect line Luwombwa or Kafubashi). Nevertheless, the centre of terrestrial predator activity appeared to be Fibwe Area, expanding slightly to Wasa Area and the area along Kasanka River. This distribution of predators’ activity towards the centre of Kasanka NP was similar to the puku’s distribution (see Chapter 2): rather low densities were observed in the eastern parts of the park and towards the borders whereas highest densities were observed in the centre. As most of the predators are not assumed to prey upon puku, this distribution might not be interrelated. According to their amphibian-like mode of life (Trutnau 1994) the activity of crocodiles concentrates along Kasanka River where in addition encounters between crocodiles and puku are likely to happen (see Chapter 2). With one exception all scats of crocodiles were found here. Generally, all kind of animals might suffer less from poaching or other disturbance in the centre of Kasanka NP than towards the borders. Thus, all kind of predators and possible prey might assemble in this area.

The serval might be the cat species to that the environment in Kasanka NP fits best. It is associated to permanent water sources; it needs cover provided by tall grass or reed-beds (Hunter & Bowland 2013). Most common in savannah, grassland and dry forests, the serval is associated with wetlands, rivers and floodplains (Hunter & Bowland 2013) highly provided by the setting in Kasanka NP. This might explain why from all cat species the scats of servals were found most often. Further it was the only cat species on the camera-traps. The caracal can also be found in a wide range of habitats, but it prefers drier woodlands and savannah regions providing some cover (Stuart & Stuart 2013). Only the scats of white-tailed mongooses and African civets were found more often than scats of the serval. Based on scats, these two species were the most abundant and widespread mammalian carnivore species in Kasanka NP. These two species are widespread, flexible and occur in woodland and bush habitats (Ray 2013, Taylor 2013); the civets further lives also in aquatic environments (Ray 2013) and the mongoose in grasslands (Taylor 2013). Thus, both species find adequate habitats in Kasanka NP. Furthermore, they can cope with human presence and activity occurring in secondary forest (Ray 2013) and adapt to human influence on habitat (Taylor 2013).

Having a wide habitat tolerance, leopards are most successful in woodland, grassland savannah and forest (Hunter et al. 2013) which are provided in Kasanka NP. Also lions and spotted hyenas can be present in nearly all kind of habitats (West & Packer 2013, East & Hofer 2013). Thus, by their rather broad demands on habitat these three large predators should be able to occur in Kasanka NP. However, also cheetahs might be able to occur in miombo areas. Although depicted as a species frequenting open plains, much of their range is found in savannah woodlands and they do occur in miombo woodlands (Caro 2013).

In consequence, Kasanka NP provides habitat suitable for large as well as for medium-sized predators but with the latter having been more present during the data collection for this study. The scat of spotted hyena was the only proof of large predators that could be made during this study. However, this does not mean that large predators are absent. But the results of this study let suggest that they might occur at very low numbers. The choice of the spots for camera-traps in Kasanka NP was based among others on information of Frank Willems where captures of predators might be possible or more probable than in other areas. Hence, a considerable amount of camera traps was mounted at Fibwe. This area was further partly covered by grid 4. Photographs and scats of leopard should have been made or found. However, one undetermined scat from that area might be from leopard. Other areas where leopards were sighted, at Mulaushi, along Luwombwa River or the plains south west from the Pontoon (Frank Willems pers. comm.), were not covered by this study. Furthermore, other large predators were not detected by the camera-traps either. In this context it is important to distinguish non-detection sites where animals are absent and non-detection sites where animals are present but not recorded (Giman et al. 2007). The timeframe, the number of camera traps and camera trap stations operating at the same time might have been too small to detect rare species in Kasanka NP, e.g. the leopard (see Chapter 2.4.5).

The only large predator detected by the camera-traps was the spotted hyena in PPKR. In Kafue Region, a standardised collection of scats was not planned. They were found and collected at random while driving or while conducting other research task in the study regions which explains the allocation of faeces of spotted hyena and lion along roads. Is cannot be excluded that scats and thus probably also the animals occur at other sites more frequently. However, it was astonishing to see how many scats were found as ‘bycatch’. Further, the habitat requirements of leopards and cheetahs appeared fulfilled; sightings, signs and roaring did and do prove their occurrence in Kafue Region (Vivian and Tom Heinecken, Martin Manguwe, Charlotte & Chris McBrides all pers. comm.). The scats of undetermined predator might belong to one of these cats. No detections of other carnivores than hyena were made by the camera-traps, probably because they were set for a too short period of time (see Chapter 2.4.5). However, it appeared that biodiversity and probably also density of large carnivores was higher in Kafue Region than in Kasanka NP.

4.4.3 The puku as prey

With a number of 70, scats of spotted hyena were found most often of all carnivore species investigated. Researching diets of lions and spotted hyenas, Breuer (2005) recommended at least 70 samples, but admitted that even after more than 100 faeces, more prey species might be found. Analysing the diet of the leopard in India Mukherjee et al.

(1994) gave 80 as the minimum number of scats. However, based on data of lions and spotted hyenas, most of the prey would be detected after 30 samples (Breuer 2005). The cumulative curves showed asymptotic characteristics for the spotted hyena and potentially for the lion in Kafue Region. After about 40 scats, no new prey item completed the diet of spotted hyenas in Kafue Region. Thus, although only 5 prey items were found in the faeces, the hyena's diet might be assessed completely. Despite asymptotic features, the diet of the lion might not be well represented by 22 scats only. It might be probable that the curve would still go up if more scats were found. In Kasanka NP, a total number of 107 scats were found. However, subdivided according to each carnivore species, the numbers were a maximum of 27 and 25 for African civet and white-tailed mongoose, respectively, and 25 scats for crocodile. None of the cumulative curves showed asymptotic traits and thus for none of the predator species the diet could have been assessed completely. As this analysis was based on faeces and not on direct observations of the predator it is impossible to determine the way the predator got its diet, scavenging and active hunting may generally contribute both to the food acquisition of all carnivore species. During analysis the consumed biomass by each predator was calculated with the formula presented by Ackerman et al. (1984) that they derived from observations of cougar (*Felis concolor*). Up to my knowledge no other formulas are available to get information about the consumed biomass. The results should therefore be regarded as trends. However, compared terrestrial predator species are comparable in body size i.e. white-tailed mongoose vs. African civet and lion vs. hyena. The results might give an impression about their impact on bovid community. Altogether, the data give a general first approach on the carnivore guild.

All items within the scats were used to determine the prey. This means that not only hair of mammals, but also feathers, scales or (parts of) exoskeletons were used to determine the diet of the carnivore species. Nonetheless, a presentation of all results would take too far afield the aims of this study. However, as even medium-sized carnivores fed on antelopes the diets of all species are roughly presented with a focus on bovid prey.

The only carnivore species that did not feed on bovids at all in Kasanka NP was the serval. The serval is known as a specialist to catch small mammals and also birds, lizards, snakes, frogs and insects (Sunquist & Sunquist 2002). A previous study within the ZamBio Project found servals in Kasanka NP to feed especially on small mammals; the amount of FO was 85% for teeth and 75% for hairs (Thiel 2011). Furthermore birds, arthropods and reptiles are included in its diet with a FO of 35%, 30% and 5%, respectively (Thiel 2011). This picture of the serval in Kasanka NP was reflected by the findings of this study with high amount of other mammals than bovids and other prey items in the diet. Nevertheless, the amounts of different prey classes can change regionally within Zambia (THIEL 2011) and within Africa (GEERTSEMA 1985). Generally, more than 90% of the serval's prey species have less than 200 g (SUNQUIST & SUNQUIST 2002); but servals are also reported to take prey of up to 2 kg (THIEL 2011). A few notes exist reporting the serval to take larger prey such as the young of small antelopes (HUNTER & BOWLAND 2013), or duiker (SUNQUIST & SUNQUIST 2002) and also THIEL (2011) listed some bovid prey reported by other researchers. Thus, the question arises how often servals actively hunt probably young and/or small bovids and if it does so in Zambia. Scavenging was observed rarely only (GEERTSEMA 1985, HUNTER & BOWLAND 2013) and it appears that servals do not scavenge in Kasanka NP, either. Supported by the data of this study and of THIEL (2011) it is very unlikely that serval prey upon puku in Zambia.

This might be different for the caracal. However, the hair of puku and caracal look very much alike. Thus, assigning faeces with hair from puku by guard hair analysis to the caracal is really challenging if not impossible. Caracals are said to be generalist feeders concentrating on what is most abundant (AVENANT & NEL 2002). Generally, caracals take prey of less than 5 kg like rodents, hares, hyraxes and birds (SUNQUIST & SUNQUIST 2002). Although their most common prey are mammals (STUART & STUART 2013, AVENANT & NEL 2002) which were found their unique prey class in Kasanka NP, caracals also feed on birds, reptiles, invertebrates or fish (STUART & STUART 2013). But caracals prey as well upon antelopes, sheep and goats (SUNQUIST & SUNQUIST 2002) as also proven by the scats from Kasanka NP. In one of the five caracal scats hair bushbuck were found. The largest prey species recorded are bushbuck, as in this study, but also mountain reedbuck (*Redunca fulvorufula*), grey rhebok (*Pelea capreolus*), springbok (*Antidorcas marsupialis*) and young greater kudu (*Tragelaphus strepsiceros*) (STUART & STUART 2013). Thus, caracals might be able to prey at least upon young puku in Kasanka NP. As only five scats of caracals were found, a real estimation about the potential predation on puku was not possible, but it should be interesting to find out more about it.

White-tailed mongooses are predominantly insectivorous but feed also on small vertebrates (murids, reptiles, birds) or berries and fruits (TAYLOR 2013, GILCHRIST et al. 2009). African civets are omnivorous, feeding on fruit, arthropods and mammals as rodents or hare with variable amounts according to regions and seasons (RAY 2013). These characteristics in the diet of these species were reflected by the high amounts in other prey categories. Oil palm (*Elaeis guineensis*) nuts are a favoured food source of African civets (RAY 2013). In this context it might be important that scats of civets identified by civettery or by shape comprised seeds probably from palm nuts in 17 of 27 cases. Interestingly, African civets and white-tailed mongooses consumed the highest amount of bovid from all terrestrial carnivore species. Especially in the diet of civets, bovids made up a considerable amount. While civets consumed more puku, white-tailed mongooses fed to a higher percentage amount of biomass on bushbuck. Based on only 25 and 27 scats, this distribution might be related to the weak data basis. However, for these species, consumption of bovid prey might not be related to active hunting, but rather to feeding activities on carrion; the teeth of civets are not adapted to kill large prey (Ray 2013). White-tailed mongooses were recorded to eat carrion (Taylor 2013) which can represent a major food item for civets (Ray 2013).

After all, a number of 25 scats of Nile crocodile were found in Kasanka NP. According to Trutnau (1994) the only things that are not digested by crocodiles are teeth, hairs, feathers and nails. This means that parts of other prey items as scales from fish and reptiles or exoskeletons from crustacean or other arthropods are unlikely to be found in the scats. The method of looking into the crocodile’s scats to find out more about their diet might result in a picture biased towards animals characterised by teeth, hairs, feathers and/or nails. To get an answer to the question if puku are a prey of crocodile this method worked! Indeed a high amount of the remains found in the faeces of crocodile belonged to mammal species; a high number of items could not be identified or the scats revealed no items to be identified at all. The great advantage of this method towards stomach analyses is that it is non-invasive since the crocodiles do not need to be captured.

Feeding on birds or mammals might be regarded as an additional food source in Nile crocodiles because fishes compose up to 90% of their diet and are considered their main prey (Trutnau 1994). In the Okavango Delta, investigations on crocodiles up to the subadult stage revealed the following: yearlings consume primarily aquatic insects and arachnida, from the juvenile stage onwards the diet becomes more and more diverse and includes crustaceae, amphibian and fish, whereas subadults consume almost exclusively fish (Wallace & Leslie 2008). Thus, the non-adult crocodiles live almost entirely from the river itself, apart from some few small mammals that were probably taken while trying to cross the water (Wallace & Leslie 2008). This fits to the presentation of Trutnau (1994) that very young Nile crocodiles live mainly on insects and shift their diet from invertebrate prey to vertebrate prey while growing. Prey items other than mammals were recorded in the crocodile’s diet in Kasanka NP and made up about 20%. Due to the differences in methods and the assumed bias in scat analyses, a comparison of the figures might be rather unreliable. However, large Nile crocodiles of 4-5 m body length are reported to feed to about 25% on mammals, assessed by stomach content analyses (TRUTNAU 1994); only large crocodiles were detected along the water during walks through the floodplain of Kasanka River. Bovid prey was found most often i.e. in 64% of the scats and bovids made up more than 70% of the prey items. Hair of four different species of bovids was found in the scats: hair of puku, sitatunga, bushbuck and bush duiker. According to local conditions, crocodiles are known to prey upon large and small mammals that come to water to drink. They apply their particular ambushing hunting technique: they lie in the water, have only nose or eyes above the water surface and strike very quickly (TRUTNAU 1994). In terms of occurrence in the scats and prey items (FO and PO) and in terms of consumed biomass puku and sitatunga were similarly taken. These were the bovids most closely associated with floodplains, swamps and thus water (see Chapter 2), just like crocodiles (TRUTNAU 1994). Additionally, puku are said to go into water to escape from predators, where they risk to get killed by crocodiles (MITCHELL et al. 1965). However, it is not exactly clear how much kilograms of antelopes large, adult crocodile might consume during a specific period of time. Thus, the exact level of impact of crocodiles on puku is rather difficult to assess and probably not well represented by the biomass estimates. It is suggested that they might get enough food by eating antelope once a year (WOLFGANG BÖHME, pers. comm.). A 50 year old crocodile requires little energy; it regulates its body temperature by sunbathing (TRUTNAU 1994). If temperatures fall below 20°C, they stop their food intake; appetite and digestion are influenced by temperature (TRUTNAU 1994). In Kasanka NP, in the cool dry season, temperature especially at night can be rather low, which is enhanced by the high level of humidity (own. obs.). Nevertheless, as otherwise puku and sitatunga were consumed by scavenging civets and mongooses and since other large predators are virtually absent, the crocodile, although the exact impact is unknown, might be considered as their most important predator in Kasanka NP and generally as an important predator of puku in Zambia.

In contrast to most of the terrestrial carnivores whose scats were found in Kasanka NP, both lion and hyena hunt on large prey (EAST & HOFER 2013, WEST & PACKER 2013). Nevertheless, both are also reported to scavenge. Primarily lions hunt their food, but up to 53% of their food can result from scavenging which thus can represent a major source of food (WEST & PACKER 2013). For spotted hyenas, the amount of scavenging is related to the density of other carcass-producing predators (HAYWARD 2006). In Chobe NP, hyena feed mainly on carrion which makes up about half of their diet (COOPER 1990). From 24.9 to 36.5% of the diet were kills of spotted hyenas themselves while the remaining diet was kills from other predators, the amount changes throughout the seasons (Cooper 1990). In Kruger NP, South Africa, half of the mass consumed came from own kills (Henschel & Skinner 1990) and in Masai Mara, Kenya, the amount of carrion was only 5% and at the same time very little food was acquired by robbing kills from other predators (Cooper et all. 1999). Thus, spotted hyenas can kill 60 to 95% of their prey by themselves (Holekamp & Kolowski 2009). Nevertheless, the amount of own kills in the diet of spotted hyenas and also lions in Kafue Region remained unclear. Generally, the diets of these two species are rather well studied. However, except the report given by Mitchell et al. (1965), data from Zambia that would relate eastern and southern Africa are lacking.

The prey spectrum of the lion might not be represented in its whole extent by the data of this study. Nevertheless, the results may provide some tendencies about the lion's diet in Kafue Region which appears to be composed of mammalian prey only. Generally, lions feed on almost every imaginable land mammal, with ungulates being their principal prey (Sunquist & Sunquist 2002). However, it should be mentioned that lions also take a few aquatic species (Sunquist & Sunquist 2002). With regard to bovid prey species considering FO, PO and consumed biomass, lions took a considerable amount of puku which represented about half of their prey in Kafue Region. Data on puku are poorly available, but as puku are sometimes referred to as the southern savannah version of the kob (Estes 1991), I assume equal conditions for both species if regarded as potential prey species for large carnivores. In Faro NP, Cameroon, the lion's diet is composed to 35.5% of kob antelopes (*Kobus kob*) (Breuer 2005). Further, the kob is ranked at second position in the list of species that are commonly killed by lions (Hayward & Kerley 2005). However, kob antelopes are taken to proportionally less extent than available (Hayward & Kerley 2005). According to Chris McBrides (pers. comm.) lions prey upon puku in Kafue NP because they live at high numbers on the dambos. Thus, lions prey upon puku in Kafue Region, but they might not prefer it. This is underlined by the weight range of 190-550 kg for preferred prey (Hayward & Kerley 2005) which is far above the body mass of puku that weigh 77 kg for males and 66 kg for females (Huffman 2011). Preferred prey species of lions are gemsbok (*Oryx gazella*), buffalo (*Syncerus caffer*), wildebeest (*Connochaetes taurinus*), giraffe (*Giraffa camelopardalis*) and zebra (*Equus* sp.) (Hayward & Kerley 2005). Impala are lighter in body mass than puku, up to 60 kg for males (Jarman 2011) while reedbuck are slightly heavier reaching up to 95 kg for males (Huffman 2011). However, both of them are below the lion's preferred prey body weight and were observed at much lower amounts in the lion's diet. In Mana Pools NP, Zimbabwe, impala were principal food of lions as the numbers of buffalo decreased and those of impala increased (Dunham 1992). Thus, although preferring large ungulate species, lions adapt their diet to what is abundant. This again indicates in favour of predation of puku by lions. Nevertheless, by occurring among others on dambos and on floodplains (see Chapter 2) more or less swampy according to the season, puku choose a habitat where lions have great difficulties to hunt (SHORROCKS 2007). This local habitat can restrict predation (SHORROCKS 2007) possibly not only by lions but also by other terrestrial predators. This might also justify the low number of puku killed by lions as reported by MITCHELL et al. (1965). But behind all this, as indicated by the citation at the very beginning of this chapter, puku have an oily secretion due to the glands in the face and in inguinal pouches (DE VOS & DOWSETT 1964), similar to the related waterbuck. At least, this causes the lion prey upon waterbuck according to their abundance only (HAYWARD & KERLEY 2005); and this might apply for puku, too.

The spotted hyena was the only predator species investigated within this study whose diet might be completely represented by the analysis. It comprised only five species. This appears few, but reports from observations in Etosha NP, Namibia, list also 5 ungulate prey species only (TRINKEL 2010). However, one mentioned example of another study from Niokolo Koba NP, Senegal, list 22 prey items found in 117 scats (DI SILVESTRE et al. 2000). Except for one other determined mammal species, and respecting the undetermined prey, the hyena was found to feed almost exclusively on bovid species: puku, impala, waterbuck and bushbuck. Nothing except mammal prey was observed. This agrees with statements that spotted hyenas focus on medium and large ungulates (HOLEKAMP & KOLOWSKI 2009). Furthermore, spotted hyenas generally show no significant preference for a particular prey, but do avoid buffalo, zebra and giraffe (HAYWARD 2006). This was also the result of the analysis of preference carried out for this study. Generally, prey is taken in accordance to availability and it is suggested that very few species are free from threat of spotted hyenas (HAYWARD 2006). Nevertheless, hyena prefer to prey on species within a body mass range of 56-182 kg (HAYWARD 2006) which includes male and female adult puku weighing 77 kg and 66 kg, respectively (HUFFMAN 2011). The potential predation of hyena upon puku is supported by data from areas where kob antelopes exist: they were preyed upon according to their abundance but were found in 15.5% of the scats (n=117) (DI SILVESTRE et al. 2000). In Faro NP, Cameroon, hyenas take kob to considerable amounts of 59.2% (BREUER 2005). Other frequent prey species are buffalo and hartebeest (*Alcelaphus buselaphus*) that are further eaten more than expected in contrast to kob (DI SILVESTRE et al. 2000). Though not frequently found in the scats but according to estimated ingested biomass, waterbuck were an important prey species for hyena in Kafue Region as well. However, by their weight of 161-262 kg with the females being lighter than males (HUFFMAN 2011), waterbuck are rather at the upper bounds of the hyena's preferred prey weight. Impala are second ranked within the most frequently killed species by spotted hyenas (Hayward 2006); interestingly impala were not found often in the hyena's diet in Kafue Region. According to their weight, 57-60 kg for southern males and 43-47 kg for females (Jarman 2011), especially females are situated at the lower bounds of the spotted hyena preferred prey weight. Similar the bushbuck might not fall into the hyena's preferred prey weight; it is not often consumed. Other bovids in Kafue Region appear to play a less important role than puku in its diet, which emphasises the potential predation risk for puku by spotted hyenas.

Unfortunately, the diet of other large predator species in the study regions could not be assessed during this thesis. However, further large carnivore might prey on puku: leopards, cheetahs and wild dogs.

The leopard is reported to have an extremely catholic diet (Hunter at el. 2013), taking a much wider range of prey species than most other cats (Sun Quist & Sunquist 2002). Furthermore, it is able to adapt its diet to human influence on the environment (see Ott et al. 2007 or Ray 2011). Although probably not preferred, the leopard hunts puku in Zambia as shown by Ray (2011). Puku and impala are the main prey items in terms of a frequency of occurrence in the scats and consumed biomass, but putting in relation consumed and abundant biomass of impala, puku and bushbuck, only the bushbuck turned out to be taken more than available (Ray 2011, Stommel 2009). Similarly, leopards prey upon kob antelopes in Comoé NP, Côte d'Ivoire, but below the relative abundance of kob (Bodendorfer et al. 2006). The puku is too heavy according to the leopard's preferred weight of prey, 10-40 kg (Hayward et al. 2006a). Further, the puku's preference for grasslands (see Chapter 2) counteracts the predation by leopards. But as shown in this study puku can occur in miombo woodlands (see Chapter 2) and then might comply the hunting behaviour of leopards. In Kafue NP, high numbers of puku killed by leopards are explained by the proximity of woodland and riparian forests, habitats of leopards, in the habitat of puku, i.e. the floodplains and patches of grassland (Mitchell et al. 1965).

Cheetahs prey upon gazelles or gazelle-like antelopes (Sunquist & Sunquist 2002). Hayward et al. (2006b) found out that they kill and prefer to kill the most available prey within a body mass range of 23-56 kg. This is slightly below the puku's weight, but young puku might be hunted. The small size of prey is related to the cheetah's need to bolt down its meat before kleptoparasites, in particular lions and spotted hyenas, arrive (Hayward et al.

2006b). Cheetahs do not only occur in open plains, but also in miombo woodland areas (Caro 2013). However, although they suffer less from kleptoparasitism in closed habitats they do not shift their diet towards larger prey items (Hayward et al. 2006b). On the other hand, prey inhabiting open grasslands, as puku do, are suggested particularly susceptible to cheetah predation (Hayward et al. 2006b). Indeed Mitchell et al. (1965) found puku to be killed to considerable amounts by cheetahs in Kafue NP. The diet of the cheetah is not well studied in miombo areas and might need more attention in future studies.

Further, Kafue NP is home to wild dogs. Its most important prey species is the impala; the preferred weight of their prey ranges from 16-32 kg and from 120-140 kg (Hayward et al. 2006c). In southern Zimbabwe, Pole et al. (2004) found the diet of wild dogs to be composed almost entirely of impala (74%) and of greater kudu (22%) which were the most abundant antelopes in this area. Puku are abundant in Kafue Region, too; and also go into scrub- and woodlands (see Chapter 2), preferred habitat of this canid (Sillero-Zubiri 2009). Furthermore, in Faro NP, Cameroon, wild dogs consume kob antelopes to 55.6% (Breuer 2005). This altogether makes predation of wild dogs on puku probable. Contrarily, Mitchell et al. (1965) observed the wild dog to prey upon lighter and heavier species than puku and the amount of impala was low, too. Further research on the wild dogs' feeding habits in Zambia is needed.

Another member of the dog-family occurring in the two study regions (own. obs.) is the side striped jackal (*Canis adustus*). In Zimbabwe, they scavenge only occasionally from large carnivore kills; from this resource they are often outcompeted by black-backed jackals (Sillero-Zubiri 2009). At that site, their diet is composed of fruits, small and medium sized mammals, birds, invertebrates and grass (Sillero-Zubiri 2009). In Ngorongoro Crater, side striped and black-backed jackals (*Canis mesomelas*) compete for fawns of Grant's gazelle (Sillero-Zubiri 2009). Concerning black-backed jackals nearly all consumption of ungulates is due to active hunting rather than scavenging (Klare et al. 2010). This jackal does prey upon ungulates; irregardless of the ungulate's density, they hunt upon the young of those ungulate species that hide (Klare et al. 2010) like are puku. Side striped jackals are considered less predatory than other jackals (Sillero-Zubiri 2009). Only little research has been conducted on this medium-sized carnivore. In areas where it is not occurring sympatrically with the black-backed jackal as in Zambia, information about its diet is lacking. The question arises if side-striped jackals show hunting behaviour on ungulates in the absence of black-backed jackals.

4.4.4 Conclusion: Top down regulation of puku

Puku are very abundant in the study regions. This makes them a possible prey for every predator. Although not preferring puku, a lot of the large carnivores might prey upon puku just because it is abundant. Occurrence of large predators that probably kill puku was found to be higher in Kafue Region than in Kasanka NP. However, few sightings and hints are available for Kasanka NP, especially concerning the leopard (Frank Willems, pers. comm.). Systematic search for scats and also the camera trap study could not clearly prove the presence of large terrestrial predators, but revealed the presence of medium sized carnivore species. However, caracals and perhaps side striped jackals might exercise predation on (young) puku in Kasanka NP, but rather fractionally compared to Kafue Region. The occurring medium sized carnivore species, like mongooses or civet, consume meat of puku but without exercising a predation pressure on the puku's population. The abundance of puku influences the amount of available carrion.

The absence of predators enables herbivores to increase many more times than 'normal' which causes a trophic cascade (Terborgh et al. 2001). Intense grazing favours unpalatable grasses and thus increases the resistance of the vegetation which then reduces carrying capacity for grazers (Terborgh et al. 2001). Large predators do no longer occur on much of the Earth's surface: top-down regulation is replaced by bottom-up regulation becomes more and more widespread (Terborgh et al. 2001).

The characteristics of the puku's population were different in each study region (see Chapter 2). The puku's population in Kasanka NP was characterised by high densities at specific localities as well as generally in more open habitat than in Kafue Region. The males of various African ungulates have been shown to be especially vulnerable to predation (Pole et al. 2004) – and male groups of puku were observed more often in Kasanka NP. Moreover, zebra population in the Serengeti might be limited by the first year survival of zebra (Grange et al. 2004). Thus, the high numbers of male and juvenile puku in Kasanka NP might be a further indication of less predation pressure on the puku in Kasanka NP.

On the other hand, biodiversity of both bovid and carnivore species was apparently higher in Kafue Region. In systems with diversity of predators and prey, top-down and bottom-up regulation affect simultaneously herbivore populations (Sinclair et al. 2003). Thus abundance of herbivores is limited by predation and by resources (Sinclair et al. 2003). The presence of top predators can increase the diversity of prey species via intermediate disturbance effects (Sinclair & Byrom 2006). Despite that, predators can reduce the diversity as shown for lizards and spiders in the Caribbean (Sinclair & Byrom 2006). Taken as secondary prey, rare species are reduced by predators that depend on more common prey (Sinclair & Byrom 2006). Barida NP, Nepal, was resurveyed after 22 year of protection. The abundance of ungulates increased but this was mainly due to the increase of a few species (Wegge et al. 2009). The predators occurring on that site, namely tiger (*Panthera tigris*) and leopard, did not choose the most abundant prey. In this case, as with the lizard example, the large carnivore might not maintain or stabilize the ecosystem (Wegge et al. 2009). Wegge et al. (2009) recommend improving the habitat conditions that changed due to shifts in the ungulate society. Further, conservation planning needs to take into account the needs and impacts of predator and prey to prevent negative effects on ungulate populations (Wegge et al. 2009). This might take place similarly in Kasanka NP, if densities of predators increase due to conservation effort and management. Thus, this should encourage to monitor and survey population density and distribution of carnivore and herbivore species, not only in Kasanka NP but in all protected areas.

Each predator needs a specific amount of meat to fulfil its nutritional requirements. These amounts are different for each carnivore species (Hayward 2006, Hayward et al. 2006a, Hayward et al. 2006b, Hayward et al. 2006c, West & Packer 2013); generally they increase with increasing body size of the predator. This means that the predators have a different impact on puku in respect to their general preference of particular prey and to their amount of meat needed. This makes a general evaluation of the exact predation pressure difficult. Furthermore, ‘Predation needs to be analysed for each particular situation and its influence may vary not only spatially, but also temporally within a certain area’ (Smutz 1978, cited from Hayward & Kerley 2005). This citation summarises that predation upon puku as in general upon the antelope society changes in time and space. When looking at the distribution of the kills through the course of a year (Mitchell et al. 1965), puku appear to suffer more from predation during the dry season. On the one hand, during the rainy season the growing vegetation, as well as the wet soil, might generally reduce the carnivore’s hunting success. Further, puku in Kasanka NP showed different patterns in habitat use during the rainy season (see Chapter 2) which might affect positively their susceptibility. Additionally sexes might be killed differently because of weight constraints or because of differences in habitat use or sociability. This means that there are many aspects that need to be assessed about the relation of predator and herbivore population. Dietary analyses of nearly all predator species are rather lacking in the miombo ecoregion. This research should be emphasized as one basis for the understanding of the animal community in Zambia.

5 Activity patterns of puku

Abstract

The aim of this study was to find out about different behavioural patterns of puku (*Kobus vardonii*) in the course of a day, during different seasons and in different study regions. This was complemented by behavioural observations of impala (*Aepyceros melampus*) to check for a possible interference competition.

Observations were conducted from viewpoints at Kabwe Plain in Kasanka NP during the cool dry season 2009, the hot dry season 2010 and the late rainy season 2011 and at Puku Pan in PPKR during the cool dry season 2010. This was complemented by data from transect line sampling. At the viewpoints behaviour was measured every 10 minutes in a way that all hours of a day were covered twice. Behaviours were measured by scan sampling and the recording rule was instantaneous sampling.

Distribution of grazing and resting was rather similar in all study regions, especially during the cool dry season. In all study regions and seasons, puku were found active and thus grazing mainly at dawn and at night, confirming earlier statements by de Vos & Dowsett (1964). Puku were not dayactive, although some diurnal activity took place. During the main parts of day, puku rested. Results implied peaks of resting during the morning, around midday and during the afternoon that were more or less pronounced in the different surveys. This might be related to increasing temperatures but also to the need to ruminate. The need to ruminate, which, at least in Kasanka NP, appears higher during the hot than during the dry season. A probable explanation might be the food quality, which is suggested to be lower during the hot dry season and which makes puku spend more time on resting.

Impala were found to move more than puku, reducing by this interference competition. The two species were observed grazing only. In contrast to puku, impala are predominantly diurnal and forage mainly during the day, although some foraging behaviour can happen at night (Jarman 2011). Although not observed at night during this study, the time schedule might be the main difference in activity patterns between these antelope species.

Concerning resting behaviour, puku were observed very often lying down while resting in contrast to impala that kept standing. Unlike puku, impala are a preferred prey of several predators which might justify this behaviour. Although more possible predators are available in PPKR, puku there did not show any increased vigilant behaviour in comparison to the findings from Kasanka NP.

As puku exhibit differences between sexes according to habitat choice (see Chapter 2) and also concerning their diet (see Chapter 3). Further, the territoriality might influence the behaviour. Dimorphism in behaviour patterns between sex and age classes are expected as well as a particular activity patterns in the rainy season which would underline the need for further analysis of the available data as well as for expanded observations.

5.1 Introduction

Hoofed animals are reported to spend most of their lifetime on feeding, reproducing and avoiding to be eaten (Macdonald 2004). Most bovids feed and ruminate by turns both day and night (Estes 1991). While some bovids are more active during the night (buffalo, bushbuck, reedbucks), bovids are generally more active at daytime (Estes 1991). Peaks of feeding and of social activities are at times early and late in the day, whereas most species are relatively inactive during the hottest hours (Estes 1991). However, many authors have commented on the existence of well-defined daily activity patterns in African ruminants, but factual information is still relatively insufficient; this applies especially for observations of nocturnal activity (Wronski et al. 2006).

Knowledge of activity patterns in puku (*Kobus vardonii*) is rather anecdotic than based on standardised observations. De Voss & Dowsett (1964) stated that “they seem most active from sometime before until several hours after sunrise, and from about two hours before sunset until about one hour after sunset”. Further, they found actively feeding puku between 20:00 and 24:00, when they crossed the puku’s range by a vehicle (de Vos & Dowsett 1964). Grazing and moving could be observed at daytime, but puku tend to rest through the day (de Vos & Dowsett 1964). This statements contrast Estes (1991) reporting that *Kobus* species were dayactive and likely to hide into cover by night. However, the closely related reedbucks are reported to emerge from cover at night in order to graze (Estes 1991).

Since food can only be consumed once, the periodicity of foraging activities in different bovids should only have little impact on exploitative competition (Belovsky & Slade 1986). However, interference competition can be influenced by differences or similarities in activity patterns of bovids through the day as this regulates the degree to which different herbivores have access to the same food plants (Belovsky & Slade 1986). Impala (*Aepyceros melampus*) have the highest degree of spatial overlap with puku in Kafue Region (see Chapter 2). They are reported to forage mainly during the day interrupted by a peak of rumination around midday. They rest mainly at night when few foraging takes place (Jarman 2011). Based on the results of dietary overlap, exploitative competition between puku and impala is considered minimal in the cool dry season (see Chapter 3), but interference competition might still take place. This study intends to investigate the puku’s circadian behaviour patterns. Mainly, the behaviour of puku in a defined area was observed from selected viewpoints. Nocturnal observations were made possible by a night vision device. Observations on the impala's behaviour patterns are supposed to allow for more insights into the syntopic occurrence of these two antelope species.

- At which time of the day are puku most active? Following de Vos & Dowsett (1964) puku might be active especially at dawn and in the early hours of the night, while resting behaviours occur around midday.

- Do puku show differences in activity budgets and patterns in the different study areas? General patterns of activity in the same season are suggested to be similar between study regions. However, the presence of impala and of larger carnivore species in Kafue Region (see Chapter 4) might affect the puku's behaviour.

- Are there any differences in activity budgets and activity patterns between seasons? As shown for lechwe (*Kobus leche*) (Williamson 1993), puku are suggested to increase feeding time in the hot dry season because of decreased food quality.

- Do puku and impala differ in their activity patterns and their activity budgets? Suggesting a minimal interference competition and because of a different diet activity budget and patterns might be different in these antelope species.

Data of the observations at the waterhole at Puku Pan Lodge were used by Christine Haunhorst for her Diplomarbeit (Haunhorst 2011). Due to differences in data analysis and to ensure comparability between the different surveys, I reanalysed the raw data for this thesis.

5.2 Methods

Data collection took place at Kasanka NP and at Puku Pan Lodge in PPKR. Observations on behavioural patterns were conducted at restricted sites. In Kasanka NP, observations took place at Kabwe Plain. The viewpoint of the observer (GPS coordinates: 36L 197038 8612011) was next to Kabwe Camp. The study area was situated in north/north-eastward direction of the northern border of the river (Figure 5-1 A). All puku that came into the study area were sampled. The area sampled by the transect lines and by this data collection did not overlap and could be conducted at the same time. Further, as puku were used to human activities at Kabwe Camp, they were considered not influenced by human activities. The same was assumed for the waterhole at Puku Pan Lodge. Here, the viewpoint of the observer (GPS coordinates: 35L 390309 8317739) was situated near the lodge and the area situated in eastern direction from the lodge was sampled (Figure 5-1 B). All antelopes that came into the study area were sampled. Data collection took place while sitting on a chair or in the vehicle which was used especially at night for safety reasons. Further, data of behaviours were collected for all antelope species encountered during transect line sampling (see Chapter 2).

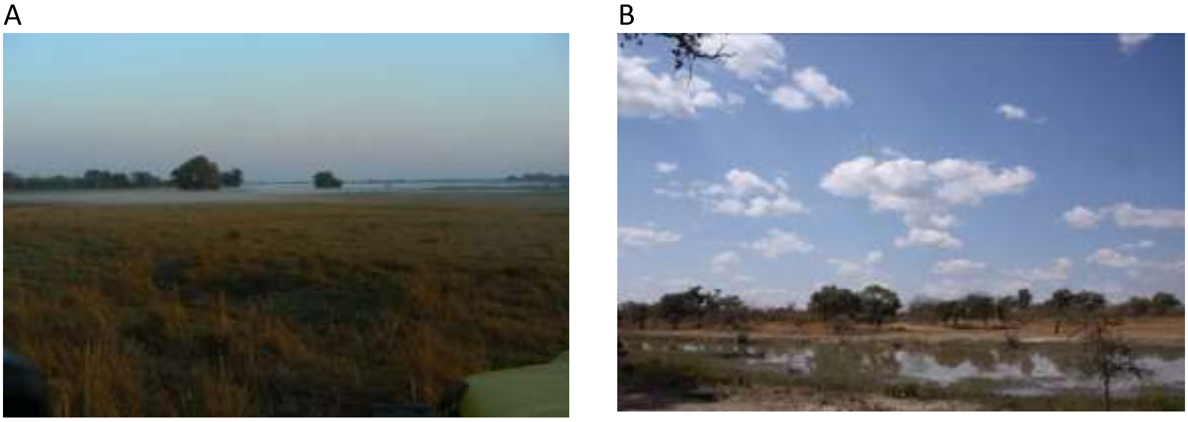


Figure 5-1: Study areas for behaviour sampling. Kabwe Plain in Kasanka NP during the hot dry season 2010 (A) and the waterhole at Puku Pan Lodge during the cool dry season 2010 (B).

Preliminary to the data collection, an ethogram was established that defines categories of behaviours (see Appendix Table A. 13). The categories are self-evident: While the activities classified as 'resting' are 'inactive' behaviours the remaining categories can be summarised as 'active' behaviour patterns. Behaviour was measured by scan sampling and the recording rule was instantaneous sampling following (MARTIN & BATESON 2007). This method can be used to obtain data from a large number of animals (ALTMANN 1974). All antelopes present in the study area, were rapidly scanned once every 10 minutes, beginning at the full hour. A beeper gave an alarm call. This method is preferable for to record behavioural states instead of recording discrete events of short location (Martin & Bateson 2007). The obtained data give information about the time distribution of behaviours (Altmann 1974). Additionally, all territorial whistles of puku were noted together with their time of occurrence.

During a scan, every animal within the study area was related to one of the behaviour categories. Further, it was intended to differentiate between sex and age classes. Data collection of behaviours covered day- and night-time. All hours of the day were sampled twice. Sessions of data collection lasted 2 to 11.5 hours. However, observer related, data collection was carried out during the presence of two observers (one to observed, the other to write down) and a single observer never carried out data collection for more than 3 hours. This was done in order to ensure a good data collection. The time of day referred to is Zambian local time (UTC+2). Observations were carried out with binoculars (Steiner, SkyHawk 10x42). At nighttime, the study areas were scanned and behaviours were observed with a night vision device (Carl Zeiss, Victory 5,6x62 T* with reticule). Air temperature and relative air humidity were noted once every 30 minutes. Only in Kasanka NP, the puku on the study area were subdivided into groups. In order to evaluate movements of the groups, their possibly changing distance to the observer was assessed with a range finder (Carl Zeiss, Victory 8x26 T* PRF) and the angle with the northern direction set as 0°.

Data collection took place in Kasanka NP during all three field trips: in the cool dry season 2009 (from 14th to 28th August 2009), in the hot dry season (from 18th to 23th October 2010) and in the late rainy season (from 12th to 24th April 2011). In the late rainy season, observations at nighttime were abandoned as considered not feasible, due to high grass and increased vegetation cover. At Puku Pan Lodge, data collection took place in the cool dry season 2010, from 21th to 27th July 2010. For the data collection I was assisted by students of biology.

The data collected during the scans as well as the events of territorial whistles were pooled into intervals of 30 minutes that subdivide the twenty-four hours of the day into 48 intervals. Concerning the data collected at Puku Pan, only the observation of puku and impala were considered sufficient for data analyses. Further, as the data collection was not sufficient to assess behaviour patterns of puku and impala to the same extent, behavioural data from the transect lines was included in order to assess synchronity of behavioural patterns. The behaviours collected during transect line sampling were assigned to the starting time of the transect line, i.e. to 07:00, 10:00, 13:00 and 16:00.

Relying on all observations made during the 30 minutes-intervals, the percentage amount of each behaviours category was calculated. Thus, activity budgets were assessed for each of the 30 minutes intervals. Although resulting from a slightly different method of data collection in field, the raw data collected in Luambe NP during the cool dry season 2007 for my diploma thesis (Rduch 2008) were pooled into 30 minutes intervals and compared with the data of this study. Per definition “day” was set the time between 07:00 and 16:59, “night” was defined the time between 19:00 and 4:59 and “dawn” is determined as the time from 05:00 to 6:59 and from 17:00 to 18:59. I only calculate activity budgets if a minimum of 5 observations was done during the 30 minutes intervals. Activity budgets were also calculated for all observations in the respective survey. Circadian activity budgets were possible for the surveys in Kasanka NP only. To allow comparison between surveys in Kasanka NP and other study regions, diurnal activity budgets were calculated which encompass the time between 6:00 and 17:59.

In order to make general activity patterns visible, the behaviours were pooled into six categories: grazing, moving, vigilant, resting and other behaviours. Pearson correlations were used in order to check for connections between behaviours or between behaviours and air temperature/humidity. General patterns of activity at day, night and dawn were checked for significance via the Kruskal-Wallis-test (KW-test) or the Mann-Whitney-U-test (U-test) if only two times of the day were compared. To check differences in the activity budgets between surveys or within the course of a day during each survey, the Wilcoxon ranked signed test was used. To check for differences in the amount of resting behaviours and territorial whistles the Chi^2-test was used. All statistics were carried out with SPSS 13.0. also used to create the boxplots. Other figures were created using Microsoft Excel 2010.

5.3 Results

The amount of puku on the surveyed area changed within the course of the day. Further, the data layer was different between the surveys (see also Figure A. 24 and Figure A. 25). During the data collection in the cool dry season 2009 in Kasanka NP, 7,498 observations were made which was the highest amount of observations during a survey. During each 30-minutes interval, 8 to 394 observations were made. Generally, the more observations could be made during daytime. None of the intervals covered remained with less than 5 observations so that all of them could be considered for the evaluation of the puku's behaviours. Concerning the survey in the hot dry season 2010 in Kasanka NP, a single interval (4:30-4:59) remained without enough observations for an evaluation. A total of 5,426 observations was made; a maximum of 200 observations was made per 30-minutes interval. Unlike the survey in Kasanka NP in 2009, puku were present in the area at night, even though numbers were fluctuating and lower than at daytime. Although puku were present almost all the time at Puku Pan, during nighttime, the numbers were two low for analyses during nighttime; one male puku stayed at the waterhole the whole night, mostly grazing. During daytime, puku were present at rather constant numbers. Up to 155 observations were made per 30-minutes interval. Impala were present at the waterhole at Puku Pan between 8:00 and 12:29 mainly. During the remaining time of the day, impala were absent except for two further 30-minutes-intervals. In the survey during the late rainy season 2011 in Kasanka NP, only one single adult male was observed once walking at the edge of the miombo. No other observations could be made on the surveyed area.

During transect line sampling, it was not possible to assess the behaviour of all sighted individuals. Between 190 and 250 puku were detected, with the lowest number of detections at 10 am and 1 pm. The amount of individuals not assessed for behaviours ranged between 16 and 23% being at its minimum at 10 am and 4 pm. Concerning impala, between 182 and 357 detections of animals were made. Highest numbers of observations were made at 7 am and 1 pm. At 7 am, the behaviour of 36% of the animals could not be assessed, hereby highest amount of this category through the times of the day. A low number of detected impala went hand in hand with a high number of individuals with assessed behaviours (see also Table A. 14).

The amount of observed sex and age classes on the survey areas changed as well as this was the case along the transect lines in Kafue Region. However, the evaluation presented here does not consider sex and age classes separately.

Air temperature rose from about 6:00 where they reached their lowest values to maximum values mostly around midday. They fell in the following course of the day until about 19:30. During the night, temperatures continued to fall until 6:00. Concerning relative air humidity, values were highest at night and lowest during the early afternoon. Air temperature and relative air humidity showed a similar course during the time of the day (see also Figure A. 26). During all surveys, their showed a very strong negative correlation (Pearson correlation air temperature vs. relative air humidity: Kasanka cool dry season 2009: r=-0.860, p<0.001, N=44; Kasanka hot dry season 2010: r=-0.978, p<0.001, N=48; survey Kasanka late rainy season 2011: r=-0.978, p<0.001, N=30; Puku Pan cool dry season 2010: -0.916, p<0.001, N=48). In the following, behaviours were related to air temperature only.

Generally, there was a weak negative correlation between the activity of puku and the air temperature during all surveys conducted during this study, which was significant for the surveys in Kasanka NP only (Pearson correlation: Kasanka NP 2009: r=-0.447, p=0.002, N=44; Kasanka NP 2010: r=-0.319, p=0.029, N=47, Puku Pan 2010: r=-0.310, p=0.109, N=28).

Puku showed a circadian rhythm in their activity patterns. Generally, puku were found to be more active at night than at daytime, but they were especially active at dawn (Figure 5-2). This was a common feature for all surveys conducted in the course of this study. But the differences were more pronounced in the cool dry season 2009 in Kasanka NP. During all surveys these differences were significant in Kasanka NP (KW-Test: cool dry season 2009 in Kasanka NP: p<0.001, N(day/night/dawn)=20/20/8; hot dry season 2010 in Kasanka NP: p=0.001, N(day/night/dawn)=20/19/8) and at Puku Pan (U-Test: p=0.010, N(day/dawn)=20/5). Further, this trend was as well reflected by the data collected in Luambe NP, which were not tested due to weak data layer.

When active, puku were very often observed grazing, so that these categories of behaviour showed a very strong correlation (Pearson correlation: Kasanka NP 2009: r=0.918, p<0.001, N=48; Kasanka NP 2010: r=0.940, p<0.001, N=47, Puku Pan 2010: r=0.972, p<0.001, N=28, Luambe NP: r=0.948, N=23). Thus, puku grazed to a high extent at night and especially at dawn.

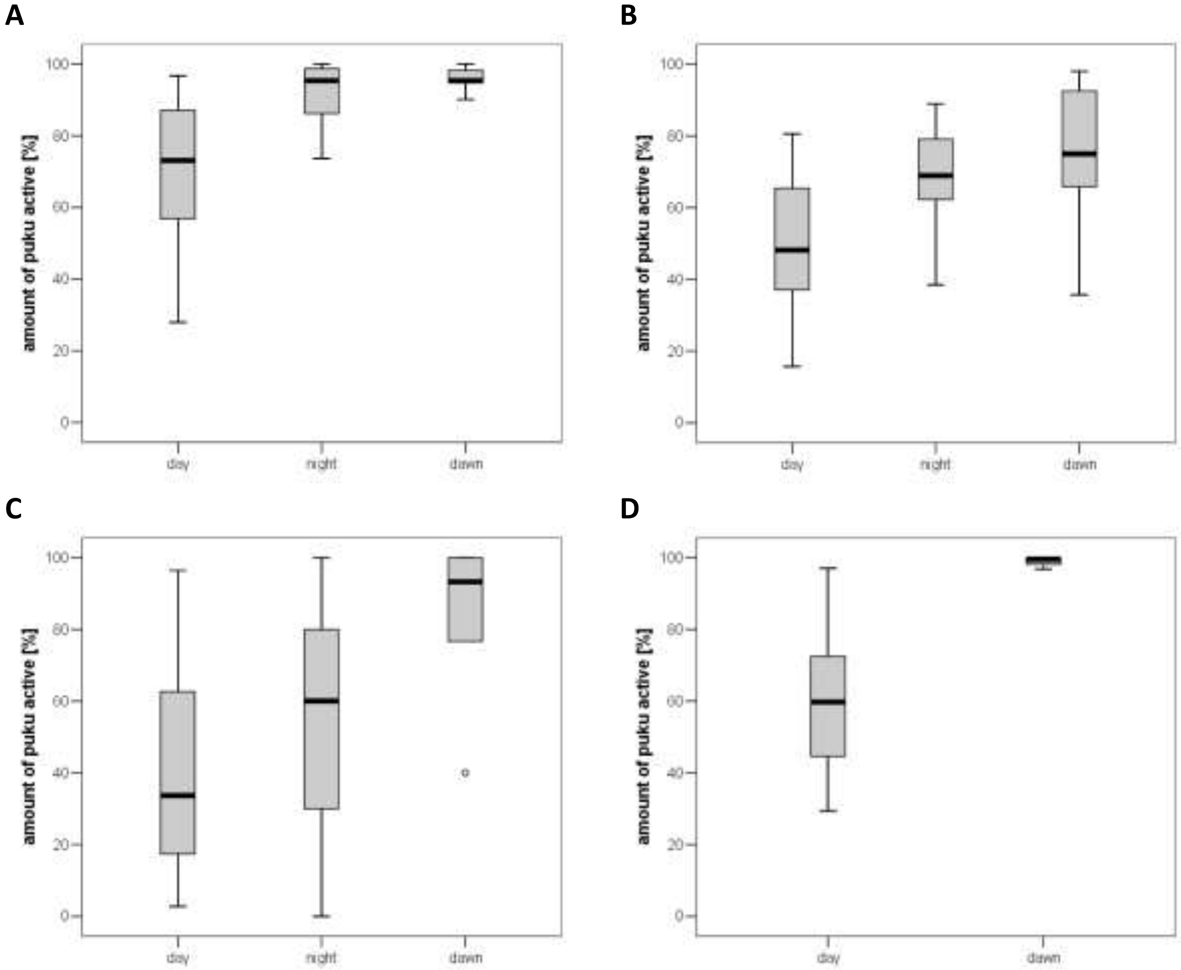


Figure 5-2: Boxplots showing the activity rates of puku (*Kobus vardonii*) at daytime, at night and at dawn in the different surveys: in Kasanka NP in the cool dry season 2009 (A) and in the hot dry season 2010 (B), at Puku Pan in the cool dry season 2010 (C) and in Luambe NP in the cool dry season 2007 (D). Differences were significant for A-C (see text). In the order of day, night and dawn N=20/20/8 for A, N=20/19/8 for B, N=20/3/5 for C and N=20/-/3 for D.

Grazing and resting behaviours were observed most often. Further, moving and vigilant behaviours were observed less often. During the observations of animals from a fixed viewpoint, browsing was observed neither in puku nor in impala. The different behaviours were observed to different amounts during the surveys (Figure 5-3). As observation at night did not always result in enough data for an evaluation, the behaviours observed between 06:00 and 17:59 were pooled into diurnal activity budgets. Generally, during all surveys, the amounts of moving and vigilant behaviours were similar, reaching amounts between about 3 and 6% or 2 and 4%, respectively. Territorial and reproductive behaviours were observed to very few amounts only. Grazing and resting made up the bulk of the observed behaviours. Grazing was observed to very high amounts during the cool dry season 2009 in Kasanka NP, but to the minimal amounts in the cool dry season 2010 at Puku Pan. Contrarily, the amount of resting behaviour was highest at Puku Pan in 2010 and lowest in Kasanka NP in 2009. The differences in these diurnal activity budgets were not significant between surveys (Wilcoxon Singed Rank Test: Kasanka NP 2009 vs. Kasanka NP 2010: Z=-0.105, p=0.917, N=6; Kasanka NP 2009 vs. Puku Pan 2010: Z=-0.105, p=-0.917, N=6; Kasanka NP 2009 vs. Luambe NP 2007: Z=-0.405, p=0.686, N=5; Puku Pan 2010 vs. Luambe 2007: Z=-0.135, p=0.893, N=5). Only for Kasanka NP, the evaluation of a complete circadian activity budget was possible for each survey. While grazing made up about 70% of the behaviours observed in the cool dry season 2009, it covers only about 53% in the hot dry season 2010. Contrarily, resting behaviours reached higher amounts in the hot dry season 2010 than in the cool dry season 2009. The other observed behaviours reached similar low amounts: the amount of moving was about 5% and the amount of vigilant behaviours was 2%, respectively. However, the differences in the circadian activity budget between the two surveys in Kasanka NP were not significant (Wilcoxon Singed Rank Test: Kasanka NP 2009 vs. Kasanka NP 2010: Z=-0.314, p=0.753, N=6).

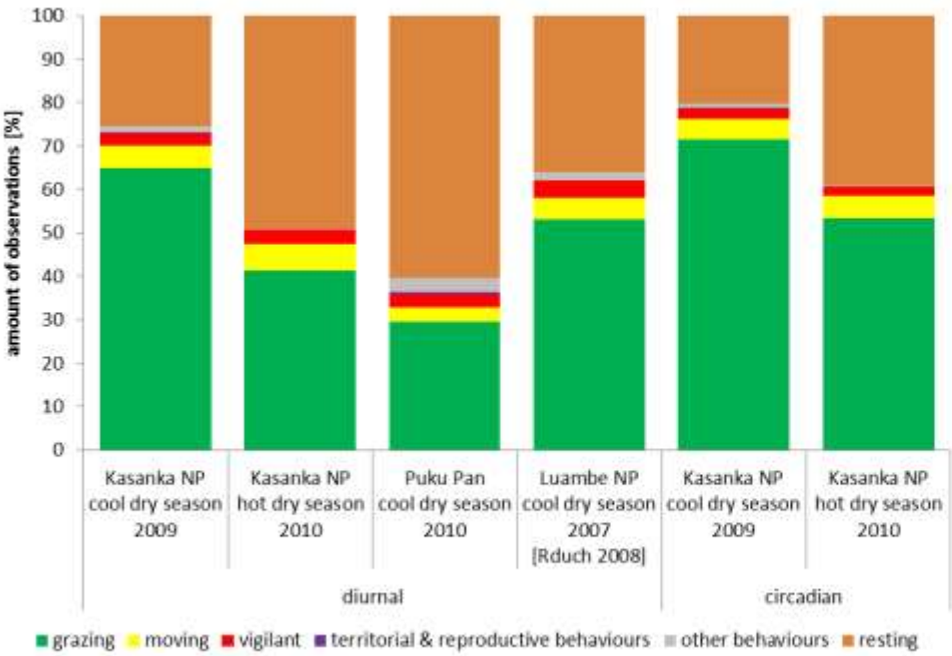


Figure 5-3: Comparison between activity budgets of puku (*Kobus vardonii*): Diurnal activity budgets from 6:00 to 17:59 for all surveys (left) and circadian activity budgets for the surveys in Kasanka NP (right). Differences in the activity budget between surveys were not significant (see text).

During all surveys, the amount of the observed behaviours changed within the course of the day (Figure 5-4, Figure 5-5, Figure 5-6). In the morning, puku had a first period of resting. A relative maximum of resting behaviours was reached between 8:00 and 10:30, depending on the survey. Then, grazing activity increased towards midday; this was especially pronounced in Kasanka NP and less pronounced at Puku Pan or in Luambe NP where activity rates remained low. In Kasanka NP, resting behaviours increased in the early afternoon and in the late afternoon. The resting peak in the late afternoon was also to be found at Puku Pan, but not in Luambe NP. In all four surveys, puku grazing activity increased in the afternoon and was highest at dawn and during the night. In Kasanka NP, grazing activity during the night was generally higher in the cool dry season 2009 than in the hot dry season 2010. During all surveys, moving took place especially at dawn. Territorial and reproductive behaviours were observed above all in the survey in the cool dry season 2009 in Kasanka NP, especially during the night.

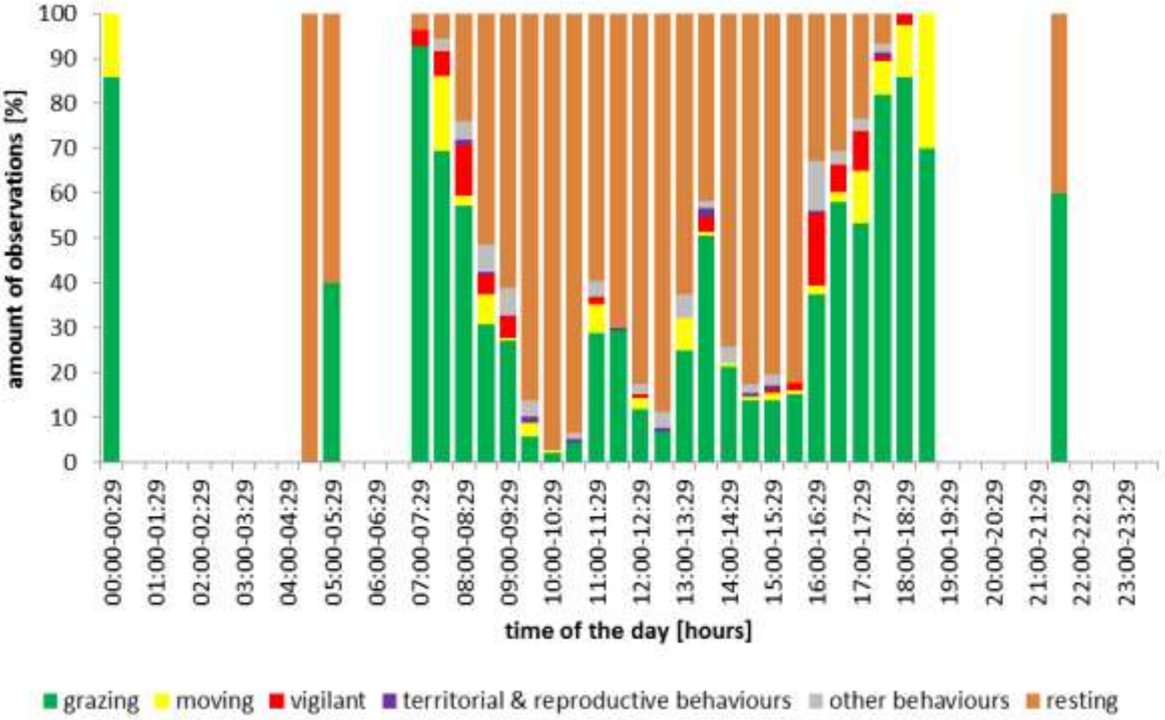
The observed differences in the patterns of active behaviours in the course of a day were significant between the surveys in Kasanka NP (Wilcoxon Signed Ranks Test: Z=-5.016, p<0.001, N=47), between the surveys in the cool dry season in 2009 in Kasanka NP and in 2010 at Puku Pan (Wilcoxon Signed Ranks Test: Z=-3.712, p<0.001, n=28) and between Puku Pan 2010 and Luambe NP 2007 (Wilcoxon Signed Ranks Test: Z=-2.763, p=0.006, N=21). They were not significant between the survey in the cool dry season 2009 in Kasanka NP and in 2007 in Luambe NP (Wilcoxon Signed Ranks Test: Z=-1.430, p=0.153, N=23).

Through all surveys, grazing and resting always showed a significant strong negative correlation (Pearson correlation: Kasanka NP 2009: r=-0.918, p<0.001, N=48; Kasanka NP 2010: r=-0.940, p<0.001, N=47; Puku Pan 2010: r=-0.972, p<0.001, N=28; Luambe NP 2007: 0.948, p<0.001, N=23).

Comparing different surveys, resting behaviours showed a significantly positive weak correlation between the surveys in Kasanka NP (Pearson correlation: r=0.364, p=0.012, N=47), and between the surveys in the cool dry season in Kasanka NP 2009 and at Puku Pan 2010 (Pearson correlation: r=0.420, p=0.026, N=28). Grazing patterns correlated significantly positive to medium degree between the surveys in Kasanka NP (Pearson correlation: r=0.550, p<0.001, N=47) and significantly positively weakly between the cool dry season in Kasanka NP 2009 and at Puku Pan 2010 (Pearson correlation: r=0.424, P=0.025, N=28). There were no significant correlations in that concern between the data of this study and the data collected in Luambe NP 2007.

Figure 5-4: Activity patterns of puku (*Kobus vardonii*) in the course of the day during the different surveys in Kasanka NP. In the cool dry season (A) and in the hot dry season (B).

A



B

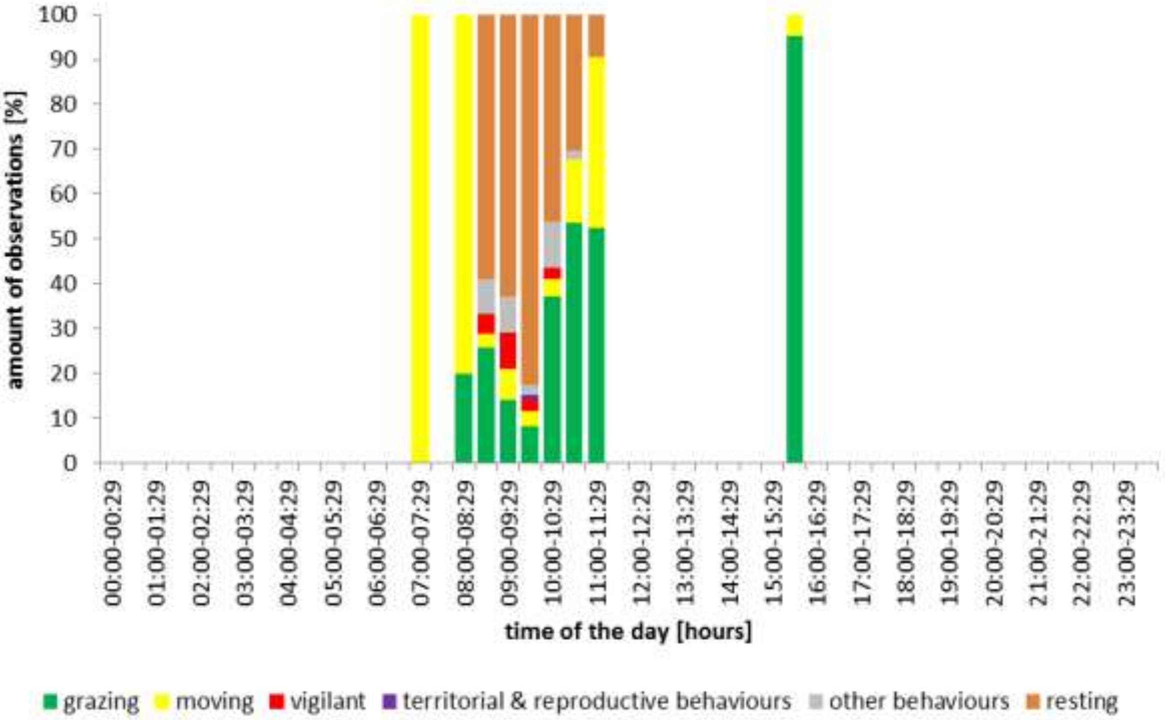


Figure 5-5: Activity patterns of puku (*Kobus vardonii*) (A) and impala (*Aepyceros melampus*) (B) in the course of the day during the cool dry season at Puku Pan.

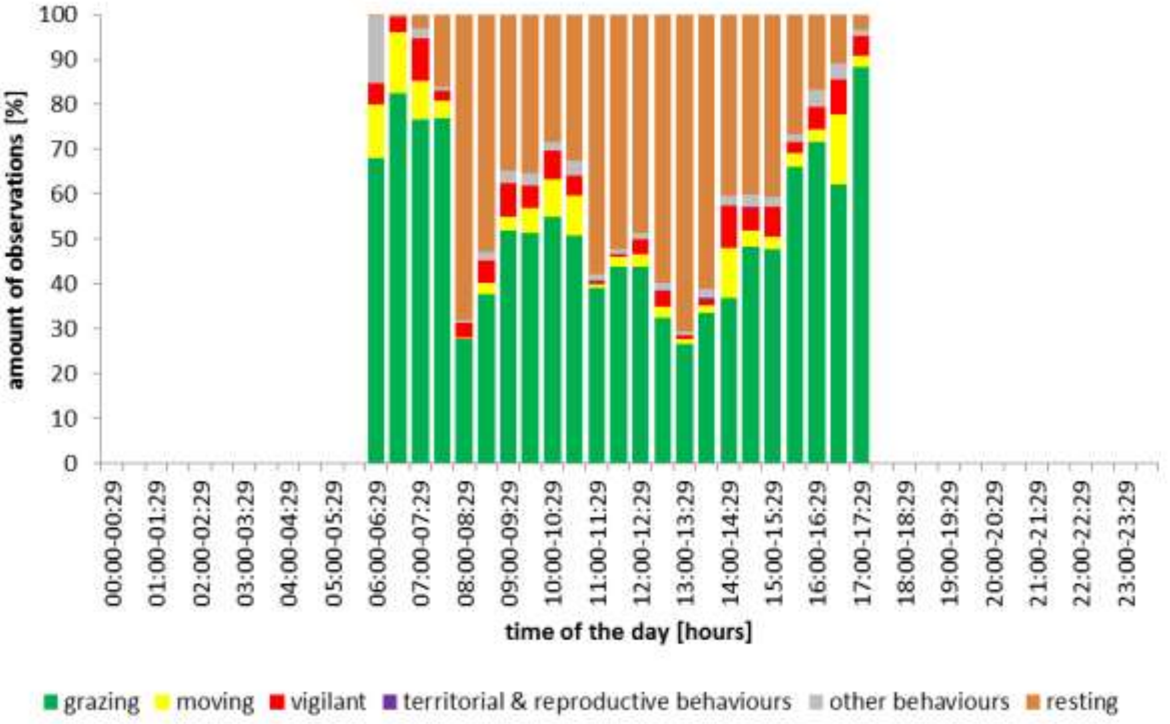


Figure 5-6: Activity patterns of puku (*Kobus vardonii*) in the course of the day in Luambe NP during the cool dry season 2007.

When coming into the area surveyed during the morning, impala showed a high amount of resting behaviours between 8:30 and 9:59 (Figure 5-5 B). Further they showed high amounts of moving, which is unlike to puku. The differences between the activity patterns of puku and impala at Puku Pan were significant (Wilcoxon Signed Ranks Test: Z=-2.073, p=0.038, N=9). There were no significant correlations between grazing (Pearson correlation: r=-0.484, p=0.187, N=9) and resting activities (Pearson correlation: r=0.475, p=0.197, N=9) of these antelope species at Puku Pan. To assess further differences and similarities in activity patterns, the data of activities collected on the transect lines were used (Figure 5-7). Pooled over all analysed times of the day, it turned out that these antelopes had a similar amount of grazing. In contrast to puku, impala showed more moving behaviour and less resting behaviours. These differences in the general diurnal patterns of behaviours were not significant (Wilcoxon Signed Ranks Test: Z=-0.105, p=0.917, N=6). During the course of the day, puku showed the peak of resting behaviours in the morning, at 10 am. Impala never showed more than 25% of resting behaviours but moved to a high amount at 1 pm. Both puku and impala showed highest amounts of grazing at 7 am and 16 pm. Over the course of the day, the differences in the behaviour patterns of puku and impala were not significant (Wilcoxon Signed Ranks Test: Z=-0.806, p=0.420, N=24).

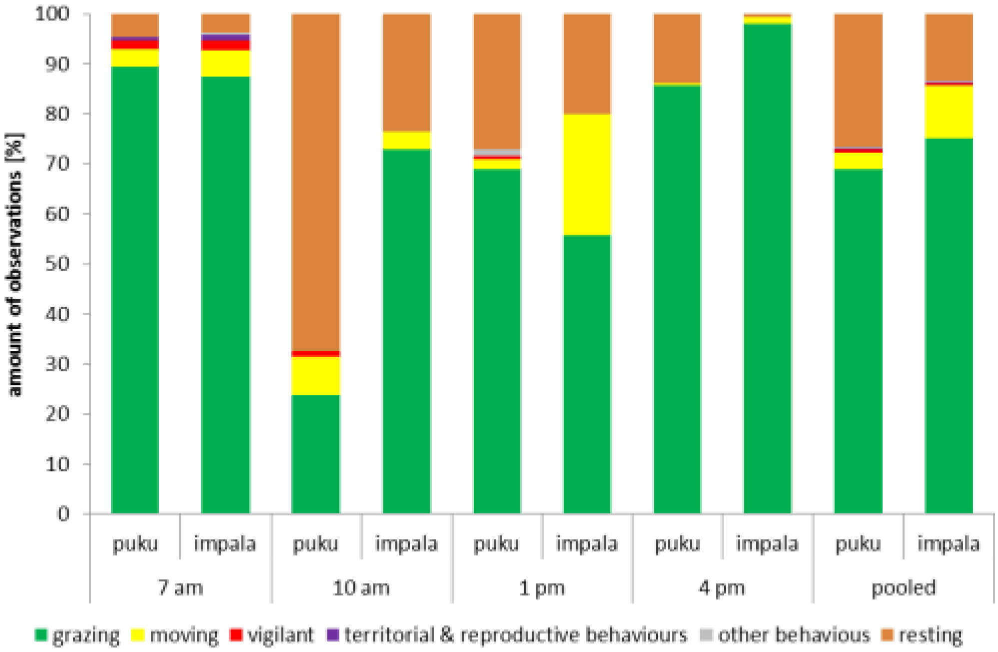


Figure 5-7: Activity budgets of puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) based on the observations along the transect lines. Activity budgets are presented for each of the surveys during the day and pooled for all the data collected during transect line sampling.

The resting behaviour was further differentiated (Figure 5-8). Puku showed relatively low amounts of resting while standing. This behaviour reached 10% of all resting behaviours in the cool dry season 2009 in Kasanka NP, including both circadian and diurnal observations. In more than 80% of the observed resting behaviours, puku lay down with the head held up. This behaviour decreased in amounts in the hot dry season in Kasanka NP. Differences in the amounts of resting behaviours in the surveys were significant for the circadian data (Chi²-test: p=0.001, N(Kasanka 2009/Kasanka 2010)=7370/5370) as well as for diurnal data (Chi²-test: p=0.010, N(Kasanka 2009/Kasanka 2010/Puku Pan 2010)=5314/2820/2583).

During transect line sampling, only ‘resting while standing’ and ‘resting while lying’ were differentiated without further attention of the position of the head. Here, differences between puku and impala were visible (Figure 5-8 B): while puku lay down in 2/3 of the observed resting behaviour, impala were detected standing while resting in 90% of the observations. These differences were significant (Chi²-test: p<0.001, N(puku/impala)=697/837). However, concerning impala, in about 3% of the resting observations the exact resting behaviour could not be assessed.

In the rainy season 2011 in Kasanka NP, a number of 5 territorial whistles only was noted during the day and dawn where the data collection took place; they were not further assessed for a circadian patterns. In Kasanka NP, 103 whistles were noted in the cool dry season 2009 and 118 territorial in the hot dry season, respectively. At Puku Pan, 94 territorial whistles was less but still in the same range as in Kasanka NP during the surveys in the dry seasons. Generally, during all of these surveys, when taking into consideration the average number of whistles per hour in the respective times of the day, territorial whistles were observed rather at nighttime than during day or dawn (Figure 5-9), but these patterns were not significant (Chi^2-test: p=0.688, N=9).

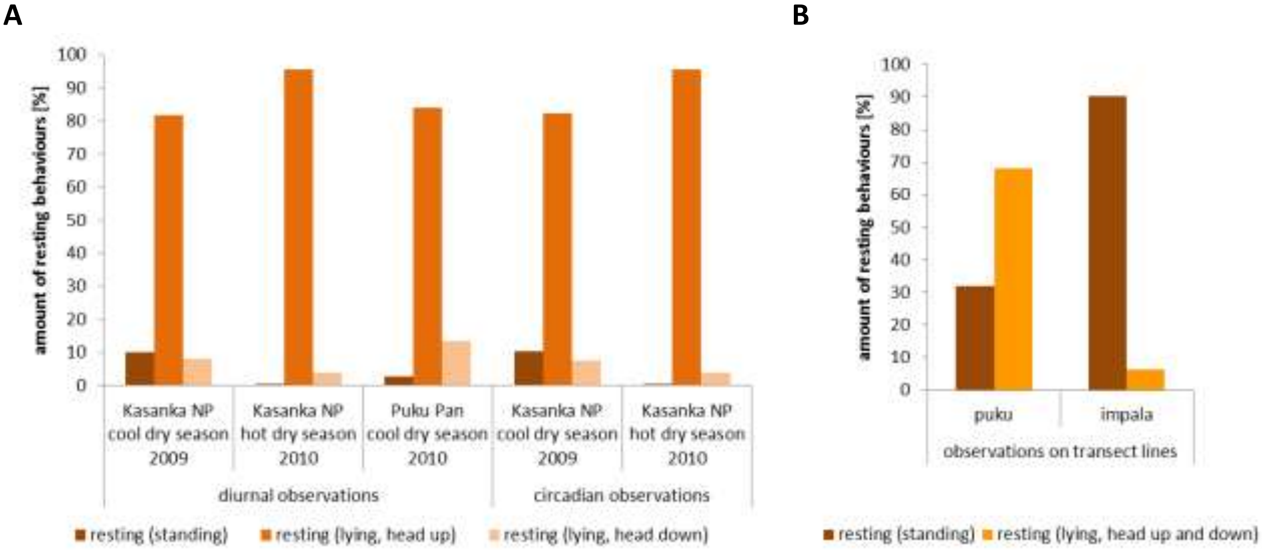


Figure 5-8: A closer look at the different resting behaviours: observed in puku (*Kobus vardonii*) during the different surveys from the viewpoints (A) and observed in puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) while transect line sampling (B).

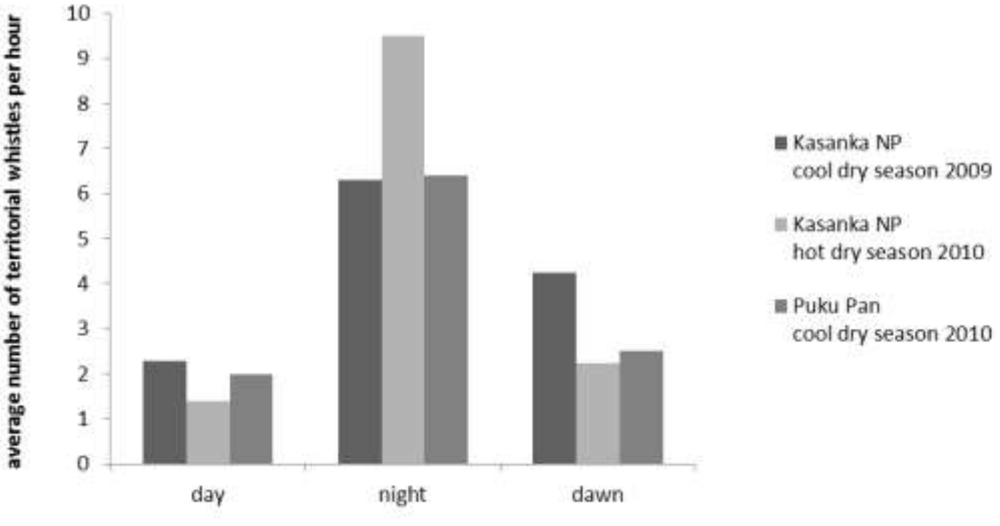


Figure 5-9: Number of events of territorial whistles of puku (*Kobus vardonii*) at different times of the day during different surveys. Differences in distribution of whistles over the day were not significant (see text).

5.4 Discussion

The observations on Kabwe Plain in Kasanka NP turned out into a very high number of observations during both the cool dry season 2009 and the hot dry season 2010. Although many puku left Kabwe Plain during the night (cool dry season 2009) or during parts of the night (hot dry season 2010), puku were present to a sufficient number for reliable findings during the analysis. At Puku Pan, puku were present to a sufficient number for reliable results at daytime, but unfortunately left the area at night, except for a probably territorial male. The impala at Puku Pan just were present a few hours only, so that the data collected along the transect lines turned out to be the only source of information to assess and to compare activity budgets and patterns of puku and impala. It is unsure whether the approaching of the vehicle influenced behaviours: while puku were considered rather unaffected, impala often reacted with escape especially when their original position was near to the road. Further, at high distances from the lines, exact behaviours of animals were sometimes difficult to assess. The antelopes were used to human presence and activities at Kabwe campsite or at Puku Pan Lodge. In consequence, this form of data collection is considered to influence less the natural behaviour patterns and therefore might represent the antelope's activity to a more reliably degree. However, as the puku left the area surveyed at night to different numbers, the question remains if the puku show the same behaviours observed at Kabwe Plain over all of their range. Williamson (1993) found lechwe to show different behaviour patterns depending on their whereabouts.

Puku were most active at dawn and in consequence showed grazing then. This confirms earlier statements by de Vos & Dowsett (1964). Their general activity at day, at night and at dawn is comparable to the activity patterns of bushbuck (*Tragelaphus scriptus*) found by Wronski et al. (2006). However, the range of the puku's activity was wider than in bushbuck, which means that a high amount of active or inactive puku can be found at daytime. This makes the general patterns of activity less distinct in puku than in bushbuck. Comparisons with other bovids are rather difficult in this context as other studies are mostly limited to daytime activities. The general activity patterns of puku confirm statements in Estes (1991) that bovids would be generally active especially early and late in the day. However, statements about the genus *Kobus* tell that these mainly dayactive (Estes 1991), whereas the findings of this study indicate that puku are predominantly not dayactive!

Although not significant in their distribution over the day, territorial whistles of puku were observed most often at dawn and above all at night. Beside the neckpatch, the whistles emitted by adult males are one sign for the ownership of a territory (ROSSER 1990). Only during times of activity the territorial males need to attract females and display against other males.

In the cool dry season 2009, high levels of grazing activities took place in the first half of the night and thus confirm earlier statements by DE VOS & DOWSETT (1964). However, in the hot dry season at Kabwe Plain activity patterns were less distinct. Nevertheless, the puku's grazing activity was higher in the early hours of the night than at daytime, but highest grazing activity still took place at dawn.

Puku rested to high amounts at daytime. In all surveys puku showed peaks of resting behaviours: during the morning, which was mostly the more pronounced resting peak, around midday and during the afternoon. These peaks were well defined especially in the surveys of the dry season, but still existed in the hot dry season. However, these patterns did not result in significant differences when comparing the cool dry season in Kasanka NP and Luambe NP only; results can rather be considered as trends. Resting at midday, hence during the hottest hours of the day, is a common feature of bovid activity patterns. Black wildebeest (*Connochaetes gnou*) were observed lying down most of the time at daytime (VRAHIMIS & KOK 1993) and also beira (*Dorcatragus megalotis*) show more inactive behaviours at midday and in the early afternoon (GIOTTO et al. 2008). Antelopes might try to avoid active behaviours in the hottest time of the day, which might also be related to feeding activity oscillations that are related to the rumen volume and the need to ruminate (TWINE 2002). The antelope might take advantage of these energetically expensive hours to lie down and ruminate rather than forage (TWINE 2002). Yet, puku rarely choose the shade but rested in the middle of Kabwe Plain; this was also observed at Puku Pan (own obs.) This astonishing behaviour was already noted by DE VOS & DOWSETT (1964).

Ruminating was not included in this behaviour as it not easy to survey: The slight movement of jaws might be overseen when animals rest too far from the observer or when the hot air is shaking because of the heat of the day. However, ruminating might take place while resting. The total amount of resting in Kasanka NP was higher in the hot dry season than in the cool dry season, while the total amount of observed grazing decreased in the hot dry season. Implying ruminating in resting behaviours, the question arises if spending more time ruminating at this time of the year is a consequence of poorer food quality. This would contrast to the observations of Williamson (1993) on the related red lechwe that increase the time of feeding in the hot dry season.

The distribution of grazing and resting was rather similar in all surveys. However, the total amount of these behaviours was different; moving and vigilant behaviours only contributed to smaller amounts to the activity budgets. The data at puku Pan were collected in the cool dry season, but interestingly, higher amounts of resting in the diurnal activity budget were shown than the hot dry season at Kabwe Plain. The differences in the activity budgets in the cool dry seasons were not significant, but Kasanka NP and Luambe NP diurnal activity budgets resembled more one to another than to Puku Pan. These differences could be related to the location of the survey area. Near to a lodge, not only to a simple campsite, puku might feel safe from predators. However, these differences might also be justified by the smaller sample size at Puku Pan. The amount of vigilant behaviour was similar in the diurnal activity budgets in all surveys. Differences in the occurrence of predators existed between the study areas with probably less predator presence in Kasanka NP than in the other regions (see Chapter 4). The presence of more predators did not appear to influence the puku's attention, in contrast impala that are more vigilant with increasing predator density (Skinner & Chimimba 2005).

In Kasanka NP, territorial and reproductive behaviours could be observed most often in the surveys during the cool dry season 2009, but less often in the hot dry season 2010. Assuming a gestation length of eight months (Huffman 2011), this would imply that in March and April young puku are born to higher amounts than in July and August. This fits to the observation of the social organisation of puku (Chapter 2). Neonate puku occurred during the line transect survey in the cool dry season 2009 but most of them had already reached the juvenile status.

Unfortunately, impala could not be observed during a circadian or over the complete times of the day. On the one hand this might implement that impala roam more through the area than puku and by this reduce the mutual overlap and thus interference competition with puku. Impala showed a higher amount of moving at both Puku Pan and in the area covered by the transect lines. Concerning the area at Puku Pan, impala showed a high amount of resting behaviours during the morning. These patterns were reflected by the data from the transect lines, where resting behaviour of impala increased at 10 am and 1 am. These patterns of resting at midday were already documented for impala (Jarman 2011). Also in Luambe NP, impala were found to have a resting peak between 10:00 and 10:59 (Simon 2008). Impala are suggested to be rather sensitive to high temperatures (Klein &

Fairall 1986) which might explain these patterns. However, impala spent more time than puku on being active with about equal amount of grazing and higher amounts of moving, while browsing was not observed. This might be based on the intermediate feeding strategy of impala (see Chapter 3) searching for food of high quality. Generally, impala are suggested to have an energetically demanding lifestyle (Klein & Fairall 1986). In contrast to puku, impala are predominantly diurnal and forage mainly during the day, although some foraging behaviour can happen at night (Jarman 2011). Further, Simon (2008) reported that in Luambe NP, impala rest at night. Although not observed during this study, this might be the main difference in activity patterns between these antelope species.

The survey of impala's activity patterns resulted in high amounts of grazing activity while browsing was not observed. This appears to conflict with the results of the impala's diet (see Chapter 3) showing an amount of about 2/3 of browse in Kafue region. Grazing defined as 'feeding with the head close to the ground' can imply feeding on both grasses and herbs. The question arises if browsing is easy to oversee or not to distinguish if impala are discovered but partly hidden behind scrubs. Bushfires in the dry season, as they did happen in the study regions, inducing growth of fresh grass can reduce the amount of time browsing for impala (Wronski 2003) and thus might increase the potential dietary overlap between puku and impala in the dry season. Observations of activity patterns for impala did not cover the entire day however, this might need further attention.

Another difference between these bovids was their exact resting behaviour. In most occasions and during all surveys puku lay down while resting; they even were observed with the head on the ground, apparently completely relaxed. Even if along the transect lines, impala were observed lying down, in most cases they were observed resting while standing up. Furthermore, impala rest often at shady places (Jarman 2011) maybe as a consequence of less heat tolerance (Klein & Fairall 1986). This was also observed during this study (own obs.), whereas puku searched the sun. Impala, unlike puku, are a preferred prey of several predators as leopards (*Panthera pardus*) (Hayward et al. 2006a), cheetahs (*Acinonyx jubatus*) (Hayward et al. 2006b) or wild dogs (*Lycaon pictus*) (Hayward et al. 2006c), which might affect their resting behaviour in favour of a quick flight. However, impala and puku were found to have similar amounts in vigilant behaviour.

Activity patterns might influence detection probability of the antelopes. Puku were observed less at 10 am which was their resting peak. Impala showed high amounts of vigilant behaviours at 7 am when their highest amount of behaviour could not be determined because they interrupted their normal activity or even ran away. This could imply that predation takes place more likely in the morning when temperatures are lower and the first daylight facilitates vision. In addition to the differences in habitat choice through the day activity patterns might influence detection probability. This might confirm the decision to sample the transect lines four times a day (see Chapter 2) in order to get a daily average of animal density.

The investigation of behaviour of puku made during this study could confirm earlier statements that were based on free observations (DE VOS & DOWSETT 1964). Further, knowledge was improved as patterns of activity could be revealed; information on resting behaviour could be gained. Differences in diurnal behaviour between puku and impala were detected. However, although aimed, no data could be gained from the late rainy season. Because of increased grass quality and quantity but also related to differences in habitat choice and distribution, the puku’s behaviour patterns might alter between wet and dry seasons.

Beside differences in relation to time of the day and year, activity patterns might be different according to age and sex classes as shown in some ungulates from temperate latitudes (WRONSKI et al. 2006). Although the collected data were distinguished between sex and age classes for puku as well as for impala, they were pooled for the analyses in the context of this thesis. Sexual dimorphism in body size, as present in puku, leads to sexual dimorphism in foraging behaviour (RUCKSTUHL 1998). In bighorn sheep (*Ovis canadensis*) females spend less time lying and ruminating but have greater movement rates than males; with regard to females this is justified by less energy requirements and the need to reduce the predation risk for the juveniles (RUCKSTUHL 1998).

Puku were already shown to exhibit differences according to sexes concerning habitat choice (see Chapter 2) as well as diet (see Chapter 3). Furthermore, male puku differentiate into those owning a territory and those without territory, while the latter can move rather freely within a certain area, the territorial males are restricted to a limited area. Differences in behavioural patterns are expected as well are in the activity budgets. Thus, this might need further analyses of the available data as well as observations differentiating the males according to their territorial status.

6 General Synthesis

At first sight one might see the puku (*Kobus vardonii*) as a nondescript, non-charismatic antelope, incomparable to impressive sable antelopes or to smart gazelles. It does not attract attention as large carnivores, primates or elephants do. However, the puku emerged as a very fascinating study animal.

Road surveys allowed estimations about numbers and occurrence of different antelopes, revealed information about distribution patterns, habitat choice and population structure. The overall population size of puku in Kasanka NP could be estimated. Microhistological analyses of faecal samples of bovids have not been carried out before on species occurring in the miombo ecoregion. Diets of puku and of other bovid species in the study regions in Zambia were assessed for the first time in Zambia and represent new knowledge. The study areas were checked for signs of predators and scats of carnivore species were investigated. Further, activity patterns of puku, so far not observed via standardised methods, were assessed.

Puku were found to be distributed unequally within the study regions. During the dry season, local population densities in the study regions ranged up to 149.39 puku/km² in Kasanka NP and up to 110.64 puku/km² in Kafue Region. These spots were generally characterised by their proximity to water. The puku's density was highest in open grasslands where an average density of 36.15 animals/km² was reached in Kasanka NP compared to only 14.66 animals/km² in Kafue Region. In intermediate habitats, i.e. at the edge of woodlands and in light wood- and shrublands, the puku's density was higher in Kafue Region than in Kasanka NP. In the two study regions puku were observed in miombo woodlands, but at low densities only. The densities of puku along rivers and lakes increased with the progression of the cool dry season: observations to that effect were made in both study regions. These patterns were further amplified in the hot dry season during which sampling was carried out in Kasanka NP, only. Miombo is suggested to be used more intensely during the rainy season. In the dry season, the puku's distribution is affected by water: they occurred especially in grasslands, but also in wooded areas, near to water, whereas grasslands remote from water were not occupied. Following this, the abiotic factor water appears to have a direct impact on the puku's distribution. However, in grasslands distant to the river, but sometimes providing waterholes, reedbuck (*Redunca arundinum*) and Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*) might occur. Interactions between these antelopes that might further affect the distribution patterns remained obscure. In Kasanka NP spatial overlap of puku with other antelopes was minor: they overlap slightly with sitatunga (*Tragelaphus spekii*). Otherwise, spatial overlap existed rather between reedbuck, Lichtenstein's hartebeest and sable antelope (*Hippotragus niger*) than between those and puku. In Kafue Region, puku and impala (*Aepyceros melampus*) occurred syntopicly. They distributed similarly over the transect lines but impala were encountered to a higher extent in miombo woodlands and especially in intermediate habitats.

General traits of the population structure were alike in the study regions. Group sizes of puku were generally small to medium. Very large groups were observed in Kasanka NP only. However, the puku's populations showed differences in their structure: In Kasanka NP, the amounts of juveniles and subadult males was higher than in Kafue Region. The most common group compositions were single males and females groups, accompanied by young puku end eventually by a male. Kasanka NP had an uncommonly high amount of male groups. Further, the sex ratio in Kasanka NP tended to be not generally biased towards the females. These differences might be a result from higher juvenile survival.

Puku fed predominantly on grasses. They fed especially on *Panicum* ssp. *Brachiaria* sp., *Sporobolus* spp., *Hyparrhenia*/*Andropogon*-grasses and on *Eragrostis* ssp. Puku consumed the same grasses in all surveyed seasons, but their amounts changed which might be due to the water level in the floodplain where different grazing grounds are available during the course of a year. Furthermore, differences between sexes were observed. Territorial males exclude bachelor males from specific areas which might be the reason for the observed differences. The results of the diet of puku in Kasanka NP revealed that although characterised by a small niche breadth on a small-scale, puku exhibit an opportunistic choice of grass species. Food plants and their amounts were found to differ considerably between sites in Kasanka NP, between the study regions in Zambia and protected areas in southern Africa. For one thing, this might render the puku less vulnerable to food shortages of whatever origin, e.g. bushfires or lack of precipitation. For another thing, this might enable puku to live in different areas characterized e.g. by different vegetation and grass species. In Kasanka NP, overlap between reedbuck, sable, hartebeest, buffalo and sitatunga was highest in the hot dry season, while in this season overlap between these bovids and puku was lowest. Thus, in difference to the other bovid species in Kasanka NP, puku experienced only little competition for food in the hot dry season form other bovids. Syntopic occurrence of puku and impala at similar population densities in Kafue Region can be explained by dietary differences that were revealed especially for the dry season when impala browsed to considerable amounts.

Puku and impala showed differences in activity patterns that might reduce interference competition. Puku exhibit foraging behaviour especially at dawn but also during the night. Although grazing took place during daytime, too, the puku showed high amounts of resting behaviour during the day. These activity patterns were similar for puku in all study regions. In Kafue Region, impala were found to show more moving during daytime than puku do, which is confirmed by data from Luambe NP (Simon 2008). Generally, and in contrast to puku, impala are predominantly diurnal and forage mainly during the day (Jarman 2011). Although impala were not observed at night during this study, this might constitute the main differences in activity patterns between these antelopes.

In Kasanka NP, large terrestrial predators were found to be rather absent or might occur in very low densities. In Kasanka NP, puku were prey of Nile crocodile (*Crocodylus niloticus*) that further occurred next to the places where puku occurred at high densities. In the course of the study, puku were found to be an important prey of spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*) in Kafue Region. No diets of other large terrestrial predators could be evaluated within this study. However, leopards (*Panthera pardus*), wild dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*) were considered important predators on puku even though facts about their exact diet in the study regions are lacking. Puku were consumed by medium sized carnivores in Kasanka NP, namely white-tailed mongooses (*Ichneumia albicauda*) and African civets (*Civettictis civetta*), but most probably the latter carnivores did not kill the puku by themselves.

Explorative competition might play a minor role concerning food availability for puku. During this study, in times of food scarcity it was not affected by dietary competition. This could be proven for the bovid society in Kasanka NP as well as for the coexistence of puku and impala in Kafue Region. Food resources of puku might thus be affected in quality and quantity by rainfall and by soil nutrients. These abiotic factors are suggested to have limiting effects on ungulates (Fritz & Duncan 1994). In a study on zebras in Kenya, their population was assumed to be limited by rainfall and especially by its variability (Georgiadis et al. 2003). Rainfall determines the amount of food available in the dry season when lack of food and mortality are most severe (Sinclair 1979b). With respect to the findings about the body conditions of puku in Kasanka NP, bottom-up regulation via rainfall and food is very likely to affect the puku, but further research is needed to confirm this assumption. However, it is supported by the differences in rainfalls in Kasanka NP. In 2008/2009 there was less precipitation than in 2009/2010 (Frank Willems, pers. comm.). This might have led to a higher amount of puku with a poor body condition in 2009 than in 2010. While rainfall and soil nutrients act density-independently the amount of food is density-dependent. With respect to the high population densities puku are also influenced by intra-specific competition. This might apply especially for the puku in Kasanka NP reasoned by the density of puku in the openland areas being considerably higher in Kasanka NP than in Kafue Region.

This study considers bovids only. However, it has to be mentioned that also other herbivores might affect the populations of antelopes. Megaherbivores, i.e. rhinoceroses, hippopotamuses, giraffes and especially elephants, influence food and the availability of food for mesoherbivores (Fritz et al. 2002). Mesograzers appear unaffected by the activities of megaherbivores (Fritz et al. 2002) or as shown for puku in Chobe NP can even increase in numbers due to increased habitat and food (Dipotso & Skarpe 2006). Contrarily, elephants might compete with mesobrowsers and mesomixed feeders (Fritz et al. 2002) like impala. Bulk feeders as zebra, buffalo or hippopotamuses reduce the height of grass. In the absence of larger herbivores, Tom Heineken (pers. comm.) prefers the clipping of grasslands to bushfires in order to simulate their grazing activity. This causes the grasses to produce new green shots and thereby attracts smaller herbivores. Comparable to early burning, this reduces the risk of heavy fires, as height of dry grass and thus dry biomass is reduced. The presence or absence of large herbivores affects the whole ecosystem and thus also the antelope community.

Similar to puku in Zambia, zebra in Serengeti give birth in every month of the year. This makes zebra foals more available to predators than young of wildebeest or buffalo and leads to a limitation of zebra by predators (Grange et al. 2004), thus from top-down, in contrast to the findings of Georgiadis et al. (2003). Nevertheless, top-down limitation is less common in tropical ungulates, but it interacts with food availability as often malnourished individuals are killed (Bolger et al. 2008). Thus, injured and hobbling puku in Kasanka NP would perhaps not occur if more terrestrial predators were around. The very relaxing resting behaviour observed in puku lets suggest that they feel rather safe in all study regions. But puku were consumed but not preferred by the predators studied.

Surveys assessing a population status should always take into consideration the social organization and demography of the target animal. Changes might indicate development in both negative (FISCHER & LINSENMAIR 2006, FISCHER & LINSENMAIR 2002) and positive directions: The results of this study showed a high amount of juvenile and subadult-male puku in Kasanka NP. It is suggested that a higher juvenile survival affects both these amounts and generally the number of puku in Kasanka NP. Generally, juvenile survival, beside age of first reproduction, is a parameter most sensitive to environmental variation and density-dependence (BOLGER et al. 2008). In Kasanka NP, competition among puku might be relatively high with their increasing number; however, the puku did not appear to be affected by competing bovid species. Furthermore, the number of puku in Kasanka NP is positively influenced by the low number of terrestrial predators. Nevertheless, predators that prevent substantial increase or cause substantial decrease in abundance of herbivore populations are the exception rather than the rule (WHITE 1978). In systems with and without predators, food is considered the most common resource (BOLGER et al. 2008) and thus food probably also affects the puku in Kafue Region.

No matter what natural cause might influence the puku in the selected areas, the human influence also has to be considered. All study areas experience a status of protection. Although poaching occurred in both study regions, it was considered more present in Kasanka NP; human settlements are closer. In this context, a great credit for anti-poaching measures has to be given to Kasanka Trust Ltd. One proof for the purposeful conservation measures of Kasanka Trust is the development of the population size of puku: for the survey period 2009/2010 in Kasanka NP, a population size of 5,038 (3,268-7,238) puku was estimated. This is an eightfold increase within 15 years, since the survey in July 1994 done by GOLDSPINK et al. (1998). Nevertheless, the general distribution patterns of puku avoiding areas at the national park’s border might indicate a possible consequence from poaching. This appears to be common in the two surveys separated by 15 years. If and how numbers of puku in Kafue Region develop or developed in the last years is difficult to evaluate. An extrapolation of population size as carried out for Kasanka NP was not intended for Kafue NP, as the study area did not cover enough of its surface and not all habitat types. Due to the presence of larger predators, the population of puku might be more affected by predation than in Kasanka NP.

It is in the nature of the beast that a PhD project is limited in both time and space. This study investigated aspects of the puku's ecology in Kasanka NP, in Kafue NP and adjacent GMAs in Zambia. Hence, it involved only a fraction of the protected areas in Zambia. No other antelope is more Zambian than the puku which may be encountered in different protected areas in Zambia e.g. in the national parks of Luangwa Valley in the east, in West Lunga NP in the west, in Mweru Wantipa NP or Nsumbu NP in the north (EAST 1998). What about the recent population status and ecology of puku in all these regions? In 2007, an estimation resulted in 2081±501 puku in the western half of Luambe NP close to Luangwa River (RDUCH 2008). Current data about the puku's populations are not available for other protected areas in Zambia. Moreover, this study collected data during three field trips. Thus, a real long-term and Zambian wide monitoring would obviously go beyond the scope of this study. Nevertheless, it might be needed to assess future trends and threats in the puku's populations. In the rainy season, differences in the distribution of puku might act on the competition for habitat and diet among puku and other antelope. In Kasanka NP, puku showed shifts in distribution and habitat use during the wet season which is suggested for Kafue Region as well. Interference with humans might be increased and thus constitute a potential threat for puku (JENKINS 2013) which underlines the still existing need to assess the aspects of the puku's ecology in the rainy season. Furthermore, in the course of this study, both distribution patterns of antelopes and their dietary competition could not be analysed or did not comprise the whole bovid society in the rainy season. The reference collection of leaf epidermises of grasses can provide the basis to evaluate the diet of antelopes in other regions of Zambia. Grasses not included in the collection but present in the other regions of Zambia should then be added. Further, it is recommended to discriminate the genera *Andropogon* and *Hyparrhenia*. The method of microhistological analyses was shown to be budgetary friendly, requiring rather more than microscope and well trained eyes to distinguish the epidermal fragments and the dung of antelopes. By this, diets and dietary overlap of puku and other antelopes can be evaluated in other regions of Zambia as well as in other regions in Southern Africa. Knowledge about how sympatric occurrence of bovids will be gained that further might help to improve conservation measures. During the research I also could point out that although knowledge about the diets of large carnivore species, as lion, spotted hyena and cheetah is generally available, the data mostly come from southern, eastern and sometimes western Africa. Data from Zambia, that builds the junction between the eastern and southern Africa and that is further part of the miombo ecoregion, are mostly lacking. This applies generally to both carnivore and herbivore species. It should be an incentive to improve research on wildlife in Zambia, in terms of involving more species and encompassing larger periods of time. Ecosystems always change and conservation should take into account the processes that determine the dynamics of the system (Sinclair & Byrom 2006). Furthermore, ecosystems must be considered dynamic and management should resist the temptation to maintain a status quo (Sinclair 1979a). But the status quo has to be assessed regularly in order to point out differences that emerge over time. Therefore populations have to be monitored regularly and data about sex and age classes, group-sizes, group composition and also body condition shall be collected. They can reveal important information about the status of a population as shown by this study. Populations are influenced by a host of biotic and abiotic factors (Hunter & Price 1992). Many potential forces determine the population change and the community structure (Hunter & Price 1992). Thus, it can only be attempted to include as many factors as possible into such investigations.

Our ability to protect species depends on the knowledge of relative strength and interactions in the ecosystem (Wegge et al. 2009) and this study has made first attempts to identify and to describe interactions in selected excerpts of the Zambian ecosystem with the puku being the hub of this research. While researching about the puku, it turned out to be a real umbrella species. A lot of insight into the Zambian ecosystem could be gained reaching from grasses to antelopes and to carnivores. This study yielded interesting findings: besides confirming the few existing knowledge, it revealed new facts about the puku’s ecology and its population status in the study regions in Zambia.

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Abbreviations

AIC	Akaike's Information Criterion
ANOVA	analysis of variance
$B_{standard}$	standardised diet breadth
CDS	Conventional Distance Sampling Engine
D	population density (density of individuals) [animals/km^2]
D%CV	% coefficient of variation of the population density
D_S	estimated cluster density
E(S)	expected cluster size
E(S) %CV	% coefficient of variation of expected cluster size
ER	Encounter rate [number of observed objects/total length of transect lines]
ER %CV	% coefficient of variation of ER
FO	'frequency of occurrence' (the percentage of scats in which a particular item was found)
g(y)	detection function
GMA	game management area
GPS	global positioning system
IUCN	International Union for Conservation of Nature
KW-test	Kruskal-Wallis-test
MCDS	Multiple Covariates Distance Sampling
MRT	mean retention time
N	population size
NP	national park
P-0, P-A, P-B, P-C, P-D, P-E, P-F	different sites where puku regional dung samples were collected
PCA	principal component analysis
PO	'percentage occurrence' (the number of times a prey item was found, expressed as a percentage of all items recorded)
PPKR	PukuPan & Kaingu Region (the study region situated in the GMA adjacent to Kafue NP)
RAI	relative abundance index
SE	standard error
SSC	Species Survival Commission
TN	trap-night
UTC	Coordinated Universal Time
U-test	Mann-Whitney-U-test
WPO	wildlife police officer
ZAWA	Zambian Wildlife Authority
ZFMK	Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany Zoological Research Museum Alexander Koenig, Bonn, Germany

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Appendix

Table A. 1: Information on the transect lines in Kasanka NP

At the one end the transect line **Luwombwa** starts at the turnoff to Luwombwa Lodge in the western part of Kasanka NP near to Luwombwa River. It stretches into north-southwards direction and leads entirely through miombo woodlands. The floodplains of Luwombwa River are thus not sampled.	
The transect line **Chikufwe** goes around the Chikufwe Plain situated in the middle of the western part of Kasanka NP. The transect line goes along the margin of miombo woodland so that one observer scans the plan and the other one the woodland. An exception is the northern part of the transect line where the road goes through the plain. Here lie a waterhole and an airstrip.	
Coming from Chikufwe Plain the transect line **Nafulwe** starts at a fallen tree where the miombo woodland opens on a plain on the western side. It goes in southward direction along the plain, leads through miombo and turns in eastern direction parallel to the Kasanka NP's border.	
The transect line **Katwa** starts at the one end at the main road that connects Luwombwa to Pontoon. Mostly leading through miombo woodlands it gives sight onto dambo areas on the west hand side and on floodplains on the northwest hand side. It ends on a small floodplain area near a waterhole.	
The transect line **Kafubashi** starts at the one end at the main road at the crossing to Kabwe Camp. But the transect lines goes into southwards direction. Starting with both sides looking into miombo the eastern side shortly gives sight on a plain/dambo, marked by grassland and by light woodlands and shrubs.	

to be continued

Table A. 1 continued

The transect line **Puku**-**Loop** is situated in the centre of Kasanka NP. It starts at the one end where a small road leaves the main road and ends at the driveway to Kabwe Camp. Arc shaped, it goes along and through the floodplains of Kasanka River situated at its western border. While one observer always has sight onto the floodplains, the other observer also has view into the margin of miombo woodland or into the end of Kafubashi dambo.	
	
The transect line **Mulembo** goes into east-western direction. It begins at the western end where the road along the eastern Kasanka River border turns west into the miombo. Leading mainly towards miombo woodland, the transect line gives sight in the northern, hence on floodplains of Mulembo River which constitutes the northern border of Kasanka NP.	
This transect line **Fibwe** leads into nearly north-southwards direction through Fibwe Plain. It begins at the one end at Chisamba Waponde where a road turns off from the main road and leads towards Fibwe. There, the transect lines goes through miombo woodland. On the grassland covered Fibwe Plain, there is a small moist patch. The transect lines reaches miombo again and ends at the crossing near Fibwe Camp.	
The transect line **Wasa** begins at a crossing near Wasa III. Is goes mainly through miombo woodland at the southern waterside of the Wasa Lakes. Thus, it often gives sight on the lakes, dambo and floodplain areas. It ends at a crossing of roads between Wasa I and Wasa II.	

Table A. 2: Information on the transect lines in PPKR

The transect line **Kafue South** goes parallel but at a certain distance to Kafue River. It starts at a broken tree near Puku Pan Lodge. The road crosses a small river but the transect lines ends just before. It leads though open scrubland with a grass understory and along open grasslands. The western side of the line is often burned whereas the eastern side is not.	
The transect line **Kafue North** is very close to Kafue River. Leading through open grasslands, open scrublands, along riverine thickets, and at its northern end, along a small river. It starts at the turnoff from the main road and ends near the small river.	
Arc shaped, the transect line **Between** goes through several narrow clearings, dambos, grassland stripes, and miombo woodland. Some of the grassland areas provide small waterholes.	
The transect line **miombo west** goes along the main road that connects Puku Pan Lodge to the Ithezi-thezi road. It goes entirely through miombo woodland in western-eastern direction. It starts at a small hill and ends at the crossing at the airstrip.	
The transect line **miombo east** also goes along the main road that connects Puku Pan Lodge to the Ithezi-thezi road. It goes entirely through miombo woodland in western-eastern direction. It starts at a tree marked by a signpost and ends at the turnoff to Kaingu-Lodge. It is situated at a certain distance from Kafue River.	

to be continued

Table A. 2 continued

In north-southwards direction, the transect line **Kopje** goes through miombo woodland, parallel to but at remote from Kafue River. Startpoint and endpoint are two dambos that cross the transect line.	
The transect line **River** goes along the riverside road, very close to Kafue River. Leading through open grasslands, dambos, open scrublands and riverine thickets. Some of the grassland areas provide waterholes. It starts after the crossing of a small riverbed and ends at a scrub.	
The transect line **Main Road** goes along the main road that connects Kaingu-Lodge in a northerly direction with the Ithezi-thezi road. It starts at a wooden bridge and ends at a tree. Near the bridge, there is the only small open area, otherwise it leads through miombo.	
The transect line Plains goes into west-eastern direction along a dambo remote from Kafue River. It gives mainly sight onto grasslands, but also onto scrubland or miombo and light woodlands. It starts at a turnoff and ends where the road goes into the miombo. One waterhole provides water.	

Table A. 3: Information on the transect lines in Kafue NP

The transect line **Dambo** goes into west-eastern direction, rather remote from Kafue River but close to a small riverbed providing some water. On the northern side, there is miombo. On the southern side lies a vast dambo area.	
The transect line **Hippo** goes along the riverside road very close to Kafue River which is situated north of the transect line. It leads through scrublands, riverine thickets (more or less dense) and along some dambo areas. It starts near Hippo Lodge and ends where the road turns away from the river.	
The transect line **Camp** starts at the thicket at McBrides' Campsite near Kafue River. Leading through dambo areas and open woodlands it ends at the first crossing situated at a certain distance from the River.	
The transect line **Airstrip** leads into west-eastern direction and through miombo woodlands interrupted by one clearing only. The transect line starts at the Airstrip and ends at the dambo near the old mine.	

Table A. 4: Parameter setting in DISTANCE for the different estimations for Kasanka NP.

study region	No	data basis	right truncation	engine	covariate (factor)	post-stratification	estimation of encouter rate	estimation of detection probability	expected cluster size	cluster size estimation method
Kasanka	1	all detections of antelopes	8%	CDS	-	observation: species	by stratum	for all data combined	by stratum	default setting
	2	all detections of antelopes	8%	MCDS	habitat (1,2 and 3)	observation: species	by stratum	for all data combined	by stratum	default setting
	3	all detections of puku	10%	CDS	-	-	for all data combined	for all data combined	for all data combined	default setting
	4	all detections of puku	10%	MCDS	habitat (1,2 and 3)	-	for all data combined	for all data combined	for all data combined	default setting
	5	all detections of puku	0%	MCDS	habitat (1,2 and 3)	Sample: label (transect line)	by stratum	for all data combined	for all data combined	default setting
	7	all detections of puku	0%	MCDS	habitat (1,2 and 3)	Observation: habitat	by stratum	by stratum	by stratum	default setting

Table A. 5: Parameter setting in DISTANCE for the different estimations for Kafue Region.

study region	No	data basis	right truncation	engine	covariate (factor)	post-stratification	estimation of encouter rate	estimation of detection probability	expected cluster size	cluster size estimation method
Kafue	1	all detections of antelopes except the revision of September (river and plains)	8%	MCDS	habitat (1,2 and 3)	observation: species	by stratum	for all data combined	by stratum	simple average
	2	all detections of puku – except the revision of September (river and plains)	0%	MCDS	habitat (1,2 and 3)	-	for all data combined	for all data combined	for all data combined	simple average
	3	all detections of puku – except the revision of September (river and plains)	10%	MCDS	habitat (1,2 and 3)	Sample: label (transect line)	by stratum	for all data combined	for all data combined	simple average
	5	all detections of puku – including the revision of September (river and plains)	8%	MCDS	habitat (1,2 and 3)	Sample: label (transect line)	by stratum	for all data combined	for all data combined	simple average
	6	all detections of impala – except the revision of September (river and plains)	1%	MCDS	habitat (1,2 and 3)	-	for all data combined	for all data combined	for all data combined	simple average
	7	all detections of impala – except the revision of September (river and plains)	1%	MCDS	habitat (1,2 and 3)	Sample: label (transect line)	by stratum	for all data combined	for all data combined	simple average
	9	all detections of impala – including the revision of September (river and plains)	8%	MCDS	habitat (1,2 and 3)	Sample: label (transect line)	by stratum	for all data combined	for all data combined	simple average
	10	all detections of antelopes – except the revision of September (river and plains)	8%	CDS	-	observation: species	by stratum	for all data combined	by stratum	simple average
	11	all detections of puku – including the revision of September (river and plains)	0%	CDS	-	-	for all data combined	for all data combined	for all data combined	simple average
	12	all detections of impala – except the revision of September (river and plains)	1%	CDS	-	-	for all data combined	for all data combined	for all data combined	simple average
	21	all detections of puku – except the revision of September (river and plains)	10%	MCDS	habitat (1,2 and 3)	Observation: habitat	by stratum	for all data combined	by stratum	simple average
	22	all detections of impala – except the revision of September (river and plains)	5%	MCDS	habitat (1,2 and 3)	Observation: habitat	by stratum	for all data combined	by stratum	simple average

Table A. 6: Sightings of the antelope species on the different transect lines and in the different survey periods in Kasanka NP. * transect line surveyed twice in July 2009 – comparably value (half of the sum of the observations) in brackets ** transect line not surveyed at 16h

survey	transect line	puku (*Kobus vardonii*)	sitatunga (*Tragelaphus spekii*)	buschbock (*Tragelaphus scriptus*)	riedbock (*Redunca arundinum*)	Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*)	orebi (*Ourebia ourebi*)	bush duiker (*Sylvicapra grimmia*)	sable (*Hippotragus niger*)	total
2009-July	Luwombwa	1	-	-	-	-	-	-	-	1
	Chikufwe	-	-	-	-	-	1	-	-	1
	Nafulwe	-	-	-	-	1	-	-	-	1
	Katwa	6	-	-	-	-	-	-	-	6
	Kafubashi	2	-	-	-	-	-	2	-	4
	Puku-Loop*	312 (161)	7 (3.5)	2 (1)	-	-	-	-	-	321 (165.5)
	Mulembo**	5	-	1	-	-	-	-	-	6
	Fibwe**	28	-	1	-	-	-	-	-	29
	Wasa**	21	2	-	-	-	-	2	-	25
	total	375 (224)	9 (5.5)	4 (3)	-	1	1	4	-	394 (238.5)
2009-August	Chikufwe	1	-	-	9	2	-	-	-	12
	Katwa	1	-	-	-	-	-	-	-	1
	Puku-Loop*	185	8	3	-	-	-	-	-	196
	Fibwe**	27	1	1	-	-	-	-	-	29
	total	214	9	4	9	2	-	-	-	238
2010-October	Luwombwa	-	-	-	-	-	-	-	-	-
	Katwa	8	-	-	-	-	-	-	-	8
	Chikufwe	-	-	-	3	2	-	-	-	5
	Kafubashi	5	-	-	-	-	-	-	-	5
	Puku-Loop	150	10	7	-	-	-	-	-	167
	total	163	10	7	3	2	-	-	-	185
2010-November	Luwombwa	-	-	1	-	-	-	-	-	1
	Chikufwe	-	-	-	10	2	-	1	1	14
	Nafulwe	-	-	-	-	-	-	-	-	-
	Katwa	16	-	-	-	-	-	1	-	17
	Kafubashi	2	-	-	-	-	-	-	-	2
	Puku-Loop	198	15	6	-	-	-	-	-	219
	Fibwe	60	-	5	-	-	-	1	-	66
	Wasa	54	3	1	-	-	-	-	-	58
	total	330	18	13	10	2	-	3	1	377

Table A. 7: Observed animals for the antelope species on the different transect lines and in the different survey periods in Kasanka NP. * transect line surveyed twice in July 2009 – comparably value in brackets
** transect line not surveyed at 16h

survey	**transect line**	**puku (*Kobus vardonii*)**	**sitatunga (*Tragelaphus spekii*)**	**buschbock (*Tragelaphus scriptus*)**	**riedbock (*Redunca arundinum*)**	**Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*)**	**orebi (*Ourebia ourebi*)**	**bush duiker (*Sylvicapra grimmia*)**	**sable (*Hippotragus niger*)**	**total**
2009-July	Luwombwa	1	-	-	-	-	-	-	-	1
	Chikufwe	-	-	-	-	-	1	-	-	1
	Nafulwe	-	-	-	-	5	-	-	-	5
	Katwa	11	-	-	-	-	-	-	-	11
	Kafubashi	5	-	-	-	-	-	2	-	7
	Puku-Loop*	3,895 (1,947.5)	10 (5)	2 (1)	-	-	-	-	-	3,907 (1,953.5)
	Mulembo**	14	-	1	-	-	-	-	-	15
	Fibwe**	327	-	2	-	-	-	-	-	329
	Wasa**	133	2	-	-	-	-	2	-	137
	total	4,386 (2,438.5)	12 (7)	5 (4)	-	5	1	4	-	4,413 (2,459.5)
2009-August	Chikufwe	3	-	-	20	14	-	-	-	37
	Katwa	3	-	-	-	-	-	-	-	3
	Puku-Loop*	2,496	13	4	-	-	-	-	-	2,513
	Fibwe**	462	1	1	-	-	-	-	-	464
	total	2,964	14	5	20	14	-	-	-	3,017
2010-October	Luwombwa	-	-	-	-	-	-	-	-	-
	Katwa	39	-	-	-	-	-	-	-	39
	Chikufwe	-	-	-	5	11	-	-	-	16
	Kafubashi	29	-	-	-	-	-	-	-	29
	Puku-Loop	1,846	20	9	-	-	-	-	-	1,875
	total	1,914	20	9	5	11	-	-	-	1,959
2010-November	Luwombwa	-	-	1	-	-	-	-	-	1
	Chikufwe	-	-	-	16	16	-	1	19	52
	Nafulwe	-	-	-	-	-	-	-	-	-
	Katwa	85	-	-	-	-	-	1	-	86
	Kafubashi	4	-	-	-	-	-	-	-	4
	Puku-Loop	1,630	33	7	-	-	-	-	-	1,670
	Fibwe	547	-	5	-	-	-	1	-	553
	Wasa	442	4	1	-	-	-	-	-	447
	total	2,708	37	14	16	16	-	3	19	2,813

Table A. 8: Number of sightings for the antelope species on the transect lines in Kafue-Region.

	transect line	**puku (*Kobus vardonii*)**	**impala (*Aepyceros melampus*)**	**bushbuck (*Tragelaphus scriptus*)**	**greater kudu (*Tragelaphus strepsiceros*)**	**reedbuck (*Redunca arundinum*)**	**waterbuck (*Kobus ellipsiprymnus*)**	**Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*)**	**Sharpes grysbok (*Raphicerus sharpei*)**	**bush duiker (*Sylvicapra grimmia*)**	**total**
PPKR	Kafue North	32	13	-	-	-	-	-	-	-	45
	Kafue South	11	8	-	4	-	-	-	-	-	23
	Between	8	2	-	-	1	-	-	-	-	11
	Miombo East	-	1	-	1	-	-	-	-	-	2
	Miombo West	-	1	-	-	-	-	-	-	-	1
	River	8	9	2	-	-	-	-	-	-	19
	Main Road	3	1	2	-	-	-	-	1	-	7
	Plains	5	9	-	3	-	4	2	-	-	23
	Kopje	-	2	-	-	-	-	-	-	-	2
	total	67	46	4	8	1	4	2	1	-	133
Kafue-NP	Dambo	17	20	-	-	-	2	-	-	1	40
	Hippo	41	32	8	-	-	1	-	-	-	82
	Camp	19	2	1	-	-	-	-	-	2	24
	Airstrip	2	2	-	-	-	-	-	-	1	5
	total	79	56	9	-	-	3	-	-	4	151

Table A. 9: Distribution of the number of observed individuals of the antelope species on the different transect lines in the Kafue-Region.

	transect line	**puku (*Kobus vardonii*)**	**impala (*Aepyceros melampus*)**	**bushbuck (*Tragelaphus scriptus*)**	**greater kudu (*Tragelaphus strepsiceros*)**	**reedbuck (*Redunca arundinum*)**	**waterbuck (*Kobus ellipsiprymnus*)**	**Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*)**	**Sharpes grysbok (*Raphicerus sharpei*)**	**bush duiker (*Sylvicapra grimmia*)**	**total**
PPKR	Kafue North	223	105	-	-	-	-	-	-	-	328
	Kafue South	24	125	-	20	-	-	-	-	-	169
	Between	30	20	-	-	1	-	-	-	-	51
	Miombo East	-	1	-	1	-	-	-	-	-	2
	Miombo West	-	4	-	-	-	-	-	-	-	4
	River	65	61	2	-	-	-	-	-	-	128
	Main Road	24	4	2	-	-	-	-	1	-	31
	Plains	31	273	-	12	-	21	3	-	-	340
	Kopje	-	14	-	-	-	-	-	-	-	14
	total	397	607	4	33	1	21	3	1	-	1067
Kafue-NP	Dambo	84	282	-	-	-	6	-	-	1	373
	Hippo	222	214	11	-	-	1	-	-	-	448
	Camp	127	18	1	-	-	-	-	-	3	149
	Airstrip	15	8	-	-	-	-	-	-	1	24
	total	448	522	12	-	-	7	-	-	5	994

Table A. 10: Sighting on the transect lines River and Plains in the re-survey in the progressing dry season in September 2010. * The transect line River was only driven thrice in September

	transect line	**puku (*Kobus vardonii*)**	**impala (*Aepyceros melampus*)**	**bushbuck (*Tragelaphus scriptus*)**	**greater kudu (*Tragelaphus strepsiceros*)**	**reedbuck (*Redunca arundinum*)**	**waterbuck (*Kobus ellipsiprymnus*)**	**Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*)**	**total**
sightings	River*	11	3	-	3	-	-	-0	17
	Plains	4	14	-	1	1	2	1	23
total		15	17	-	4	1	2	1	40
observed animals	River*	79	20	-	11	-	-	-	110
	Plains	10	317	-	3	2	9	3	344
total		89	337	-	14	2	9	3	454

Table A. 11: Comparison of CDS and MCDS engine estimation results for Kasanka NP. The densities given represent the densities in the area surveyed by the transect lines. All compared datasets were treated each with the same data filter to ensure comparability via the AIC.

estimation for	Kasanka-Estimation No. (CDS and MCDS)	CDS			MCDS		
		AIC	D	%CV	AIC	D	%CV
all antelopes	1 and 2	13308.98	43.58	32.07	13274.20	44.18	31.91
puku (*Kobus vardonii*)	3 and 4	11660.92	43.67	32.77	11642.24	44.58	32.64

AIC: Akaike's Information Criterion; D: estimate of population density (density of individuals) [animals/km^2]; %CV: % coefficient of variation of D

Table A. 12: Comparison of CDS and MCDS engine estimation results for Kafue Region. The densities given represent the densities in the area surveyed by the transect lines. All compared datasets were treated each with the same data filter to ensure comparability via the AIC.

estimation for:	Kafue-Estimation No. (CDS and MCDS)	CDS			MCDS		
		AIC	D	%CV	AIC	D	%CV
all antelopes	10 and 1	2652.49	60.85	25.3	2639.79	65.18	24.9
puku (*Kobus vardonii*)	11 and 2	1585.36	25.50	34.7	1567.62	29.94	35.2
impala (*Aepyceros melampus*)	12 and 6	1106.01	30.43	34.9	1095.40	30.33	35.8

AIC: Akaike's Information Criterion; D: estimate of population density (density of individuals) [animals/km^2]; %CV: % coefficient of variation of D

The densities of all antelopes, puku and impala that result from these general estimations represent the population densities in the area surveyed by the transect lines. A transfer of these numbers to the entire study areas or even entire Kasanka NP or Kafue Region would not be reliable.

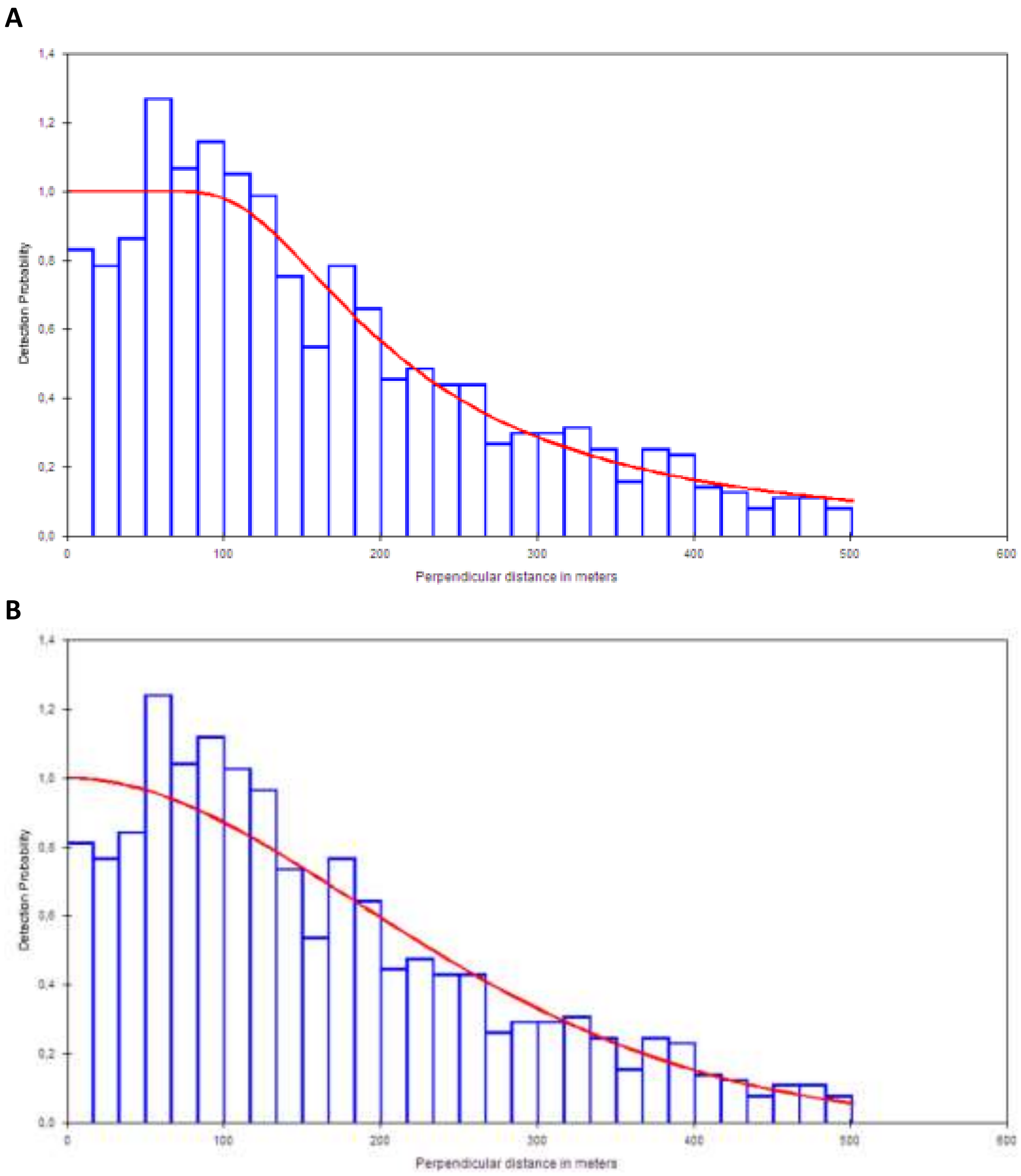
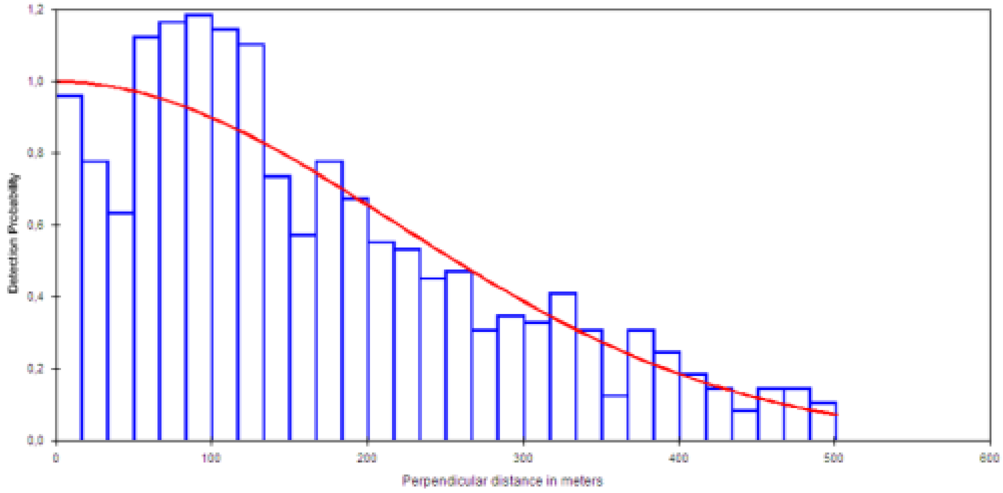
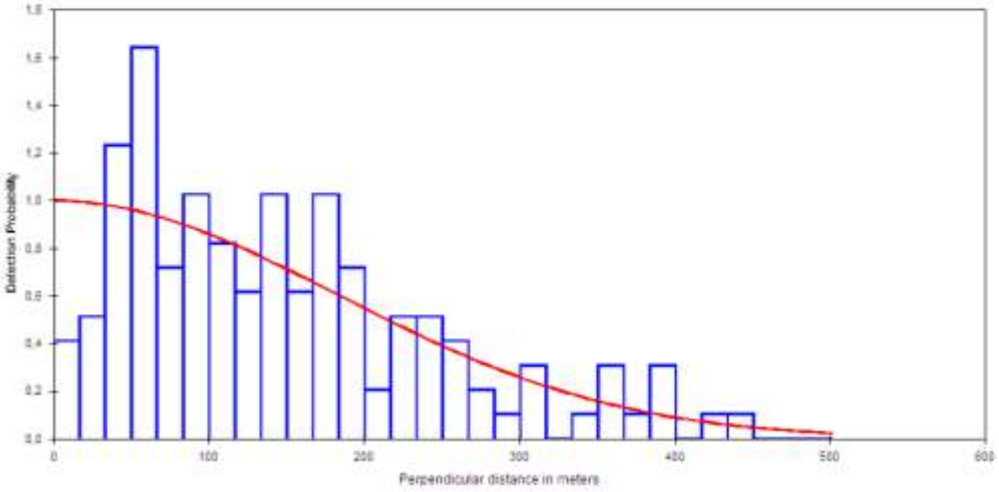


Figure A. 1: Models of detection function (red) of the estimation of puku (*Kobus vardonii*) in Kasanka NP as given by DISTANCE: CDS (hazard-rate/cosine) (A) and MCDS engine (half-normal/cosine, overall detection function) (B). The amount of detections is plotted in intervals.

grassland



intermediate habitats



woodland

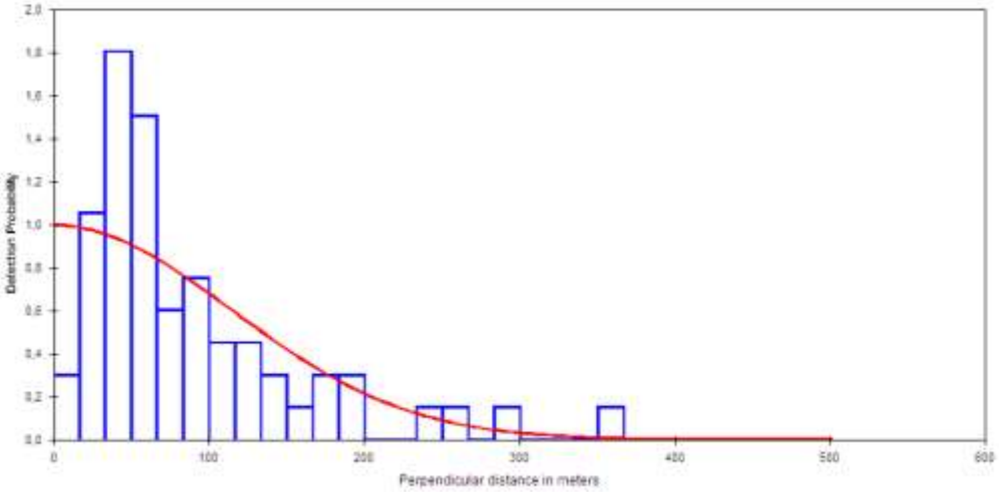


Figure A. 2: Models of half-normal/cosine detection function (red) of the MCDS estimation of puku (*Kobus vardonii*) in Kasanka NP as given by DISTANCE for the different habitat categories (grassland, intermediate habitats, woodland). The amount of detections is plotted in intervals.

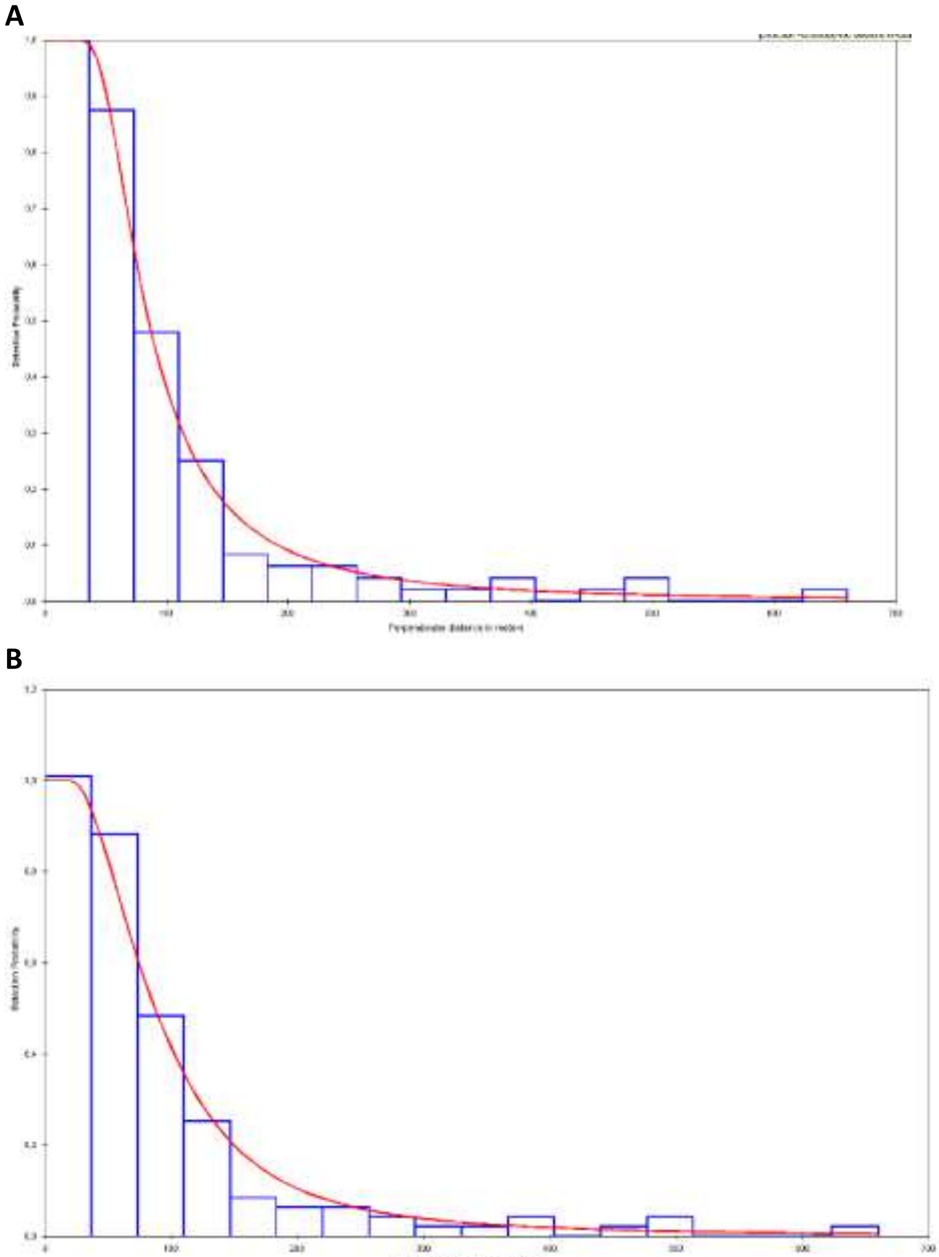
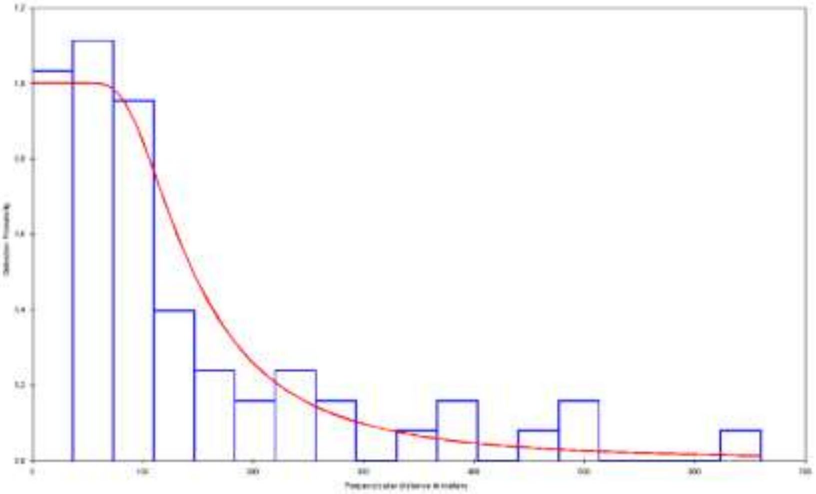
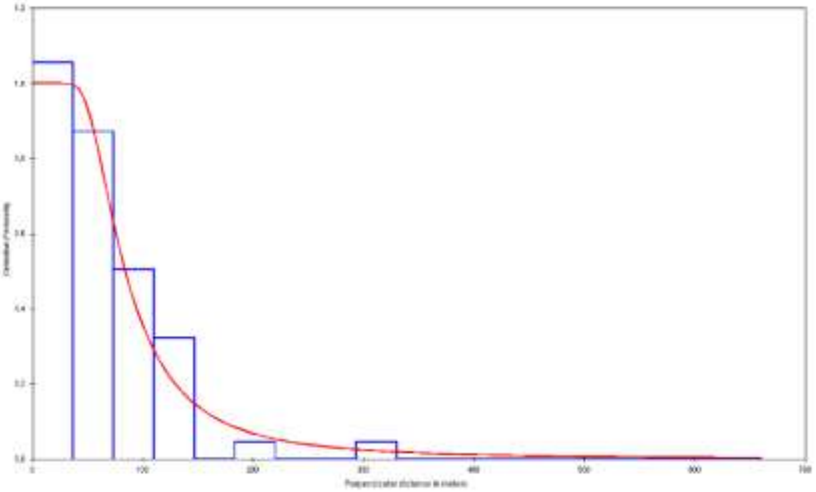


Figure A. 3: Models of detection function (red) of the estimation of puku (*Kobus vardonii*) in Kafue Region as given in DISTANCE: CDS engine (hazard-rate/cosine) (A) and MCDS engine (hazard-rate/cosine, overall detection function) (B). The amount of detections is plotted in intervals; the x-axis shows the perpendicular distance in metres, the y-axis shows the detection probability.

grassland



intermediate habitats



woodlands

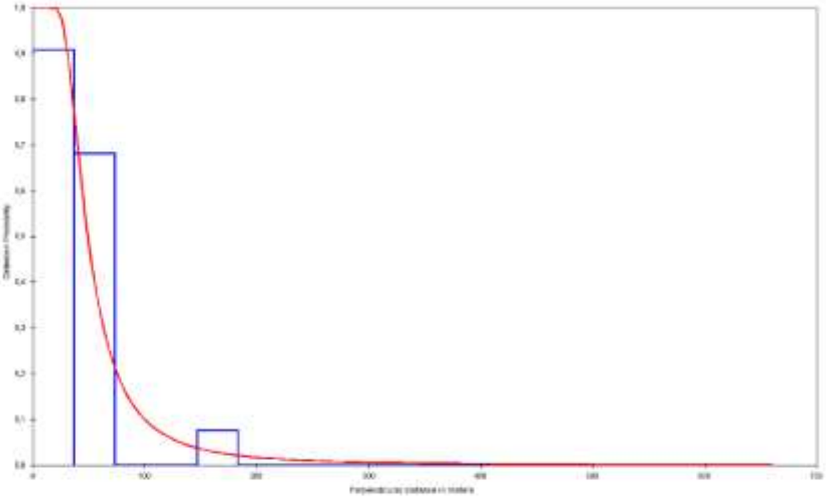


Figure A. 4: Models of detection function (hazard-rate/polynomial) (red) of the MCDS estimation of puku (*Kobus vardonii*) in Kafue Region as given in DISTANCE for the different habitat categories (grassland, intermediate habitats, woodland. The amount of detections is plotted in intervals; the x-axis shows the perpendicular distance in metres, the y-axis shows the detection probability.

Reference Guide on Epidermal Structures of Grasses

Generally, epidermal cell patterns are difficult to describe which makes illustrations (drawings, photographs) necessary. Useful information provided by the cell patterns are the width of the costal and intercostal (measured in the number of cell rows) and the special distribution and abundance of trichomes, shorts cells, papillae and stomata.

The terms and definitions of epidermal characteristics in this reference collection as follow BARTHLOTT & MARTENS (1979). Leaves of grasses have leaf veins parallel to the long axis– this arrangement is followed by the epidermal cell rows. Cell rows above the veins are called 'costal' whereas cell rows between veins are called 'intercostal'. Generally, the long cells in the costal are narrower and have thicker cell walls than the bigger long cells in the intercostal. Stomata are only found in the intercostal.

Long cells build the basis of the epidermis. They can be characterised by the presence of one or more papillae. The anticlinal cell walls are mostly toothed. This undulation can be strong or broad and S or U sharped. Short cells occur mostly in pairs: one is suberinised, the other is silicified. In the costal, they can occur in long rows of pairs. The silica bodies are completely silicified short cells in the costal. Because of their specific form and situation within the epidermis silica bodies are an important characteristic and very typical for the Poaceae. Trichomes are hairs and of great taxonomic importance: A) Micro hairs are composed of two cells, an important information is the ratio the length of the basal and the distal cell. B) Pickle hairs are composed of one cell with a thick wall. Its tip can jut out its basis. Hook hairs are a special kind of pickle hairs in the intercostal: they are smaller and have a very short tip. C) Long or macro hairs, composed of one long cell, occur mostly in the intercostal. Papillae are outward turnings of the cell walls. Many, small papillae can be arranged on all long cells or a single bigger papillae occurs on a long cell at a time. Interstomal papillae occur on long cells between stoma, only. Stomata can be round or triangular shaped. Diagnostic important information concerning all these features are (relative) length or ratio as well as (relative) abundance.

BARTHLOTT, W. & B. MARTHENS (1979): Cuticula-Taxonomie der Gräser eines westafrikanischen Savannengebietes unter dem Aspekt der Futterpräferenz-Analyse wildlebender Großsäuger. Tropische und Subtropische Pflanzenwelt 30. Akademie der Wissenschaften und der Literatur, Mainz. Franz Steiner Verlag GmbH, Wiesbaden.

Description of epidermal characteristics of Poaceae

***Brachiaria* sp.**

Grasses determined as a member of the genus *Brachiaria* ((Trin.) Griseb.) and used for reference were found in Kasanka NP and collected under the field names Z and Kas-20. A determination to species level was not possible, different species might be collected.

Silical bodies in the short cells of the costal are cross shaped or short dump-bell shaped. Costal short cells are separated into rows, 1 to 2 rows were observed per costal, but these rows can be absent. Stomata are triangular sharped. There are 1 to 2 rows of stomata in the intercostal. Relative distance between two stomata is generally 1 to 3 length of stoma. Micro hairs are present and shorter than stomata. Pickle hairs were not observed in the costal. Hook hairs are present in the intercostal. Long hairs are present in combination with cells in a circle around the basal end. Papillae were not observed. Long cells in the intercostal with strong and broad (U) undulating cell walls, generally rectangular shaped, but rows of long cells can be wave-like in the mid-intercostal. If not separated from each other by trichomes, long cells are often separated by short cells (Figure A. 5 A).

***Cynodon* sp.**

The grass determined as a member of the genus *Cynodon* (Rich.) and used for reference was found in Kafue Region (PukuPan & Kaingu-Region) and collected under the field name Kaf-10. A determination to species level was not possible. Preparation of the epidermis for reference was rather difficult. Not all characteristics could be properly evaluated. Further, an intergeneric hybridization with the genus *Chloris* is possible (Watson, L., & M.J. Dallwitz (1992 onwards). Thus, epidermal structures of these genera might resemble to each other.

Silical bodies in the short cells of the costal are like sharp-edged dump-bells, with sometimes with a knot in the middle. Costal short cells are in rows, 1 to 3 rows were observed per costal. Stomata are round. There are 2 to 3 rows of stomata in the intercostal. Relative distance between stomata is 1 to 2 relative length of stoma. Neither micro hairs, pickle hairs in the costal, hook hairs in the intercostal nor long hairs were observed. Papillae are round and smaller than stomata, situated singly on cells between stomata as well as on almost every other long cell and often at the far end of the cells. Long cells in the intercostal are rectangular shaped with strong undulating cell walls (Figure A. 5 B).

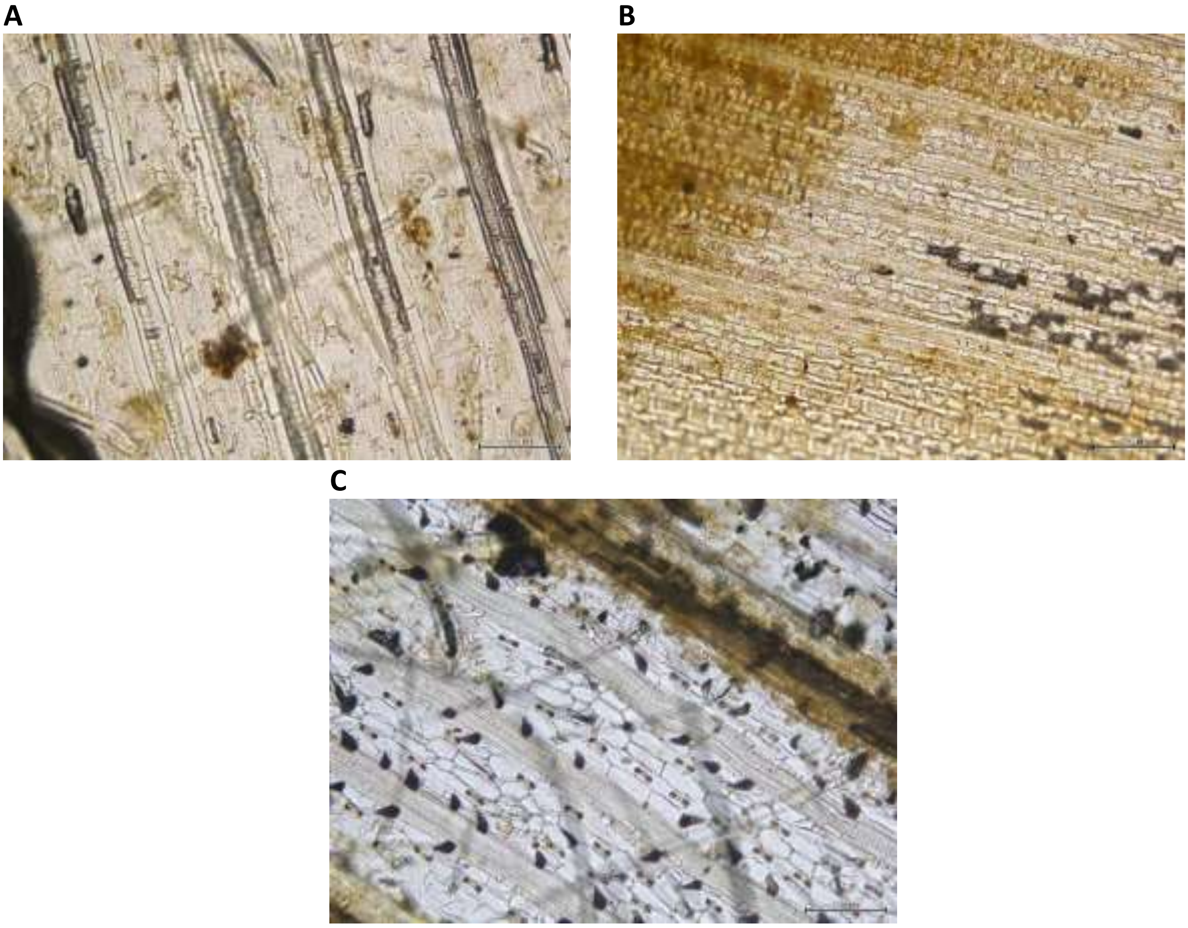


Figure A. 5: Epidermal structures of different grass species 1.
A: Abaxial epidermis of *Brachiaria* sp. (field name: Z); B: Abaxial epidermis of *Cynodon* sp. (field name: Kaf-10); C: Abaxial epidermis of *Digitaria* sp. (field name: Kaf-16). The scale is the same for all pictures giving 100 µm.

***Digitaria* sp.**

Grasses determined as a member of the genus *Digitaria* (HALLER) and used for reference were found in Kasanka NP and in Kafue Region (PukuPan & Kaingu-Region) and collected under the field names W, Kaf-11, Kaf-16 and Kaf-23. Different species might be collected, only Kaf-23 could be determined to species level: *D. monodactyla*.

Silical bodies in the short cells of the costal are short but relatively thick and dump-bell shaped. Costal short cells are in rows, 1 to 9 rows were observed in the costal. Stomata are triangular, sometimes round. There are 1 to 4 rows of stomata in the intercostal. Relative distance between two stomata is 1 to 3 lengths of stoma. Micro hairs can be present and are shorter than stomata. Pickle hairs in the costal, with a round basis, are frequent as well as hook hairs in the intercostal. Long hairs can be present in the intercostal. Papillae were not observed. Long cells are rectangular to square shaped, sometimes alveolate, with undulating cell walls. Short cells were rarely observed in the intercostal (Figure A. 5 C).

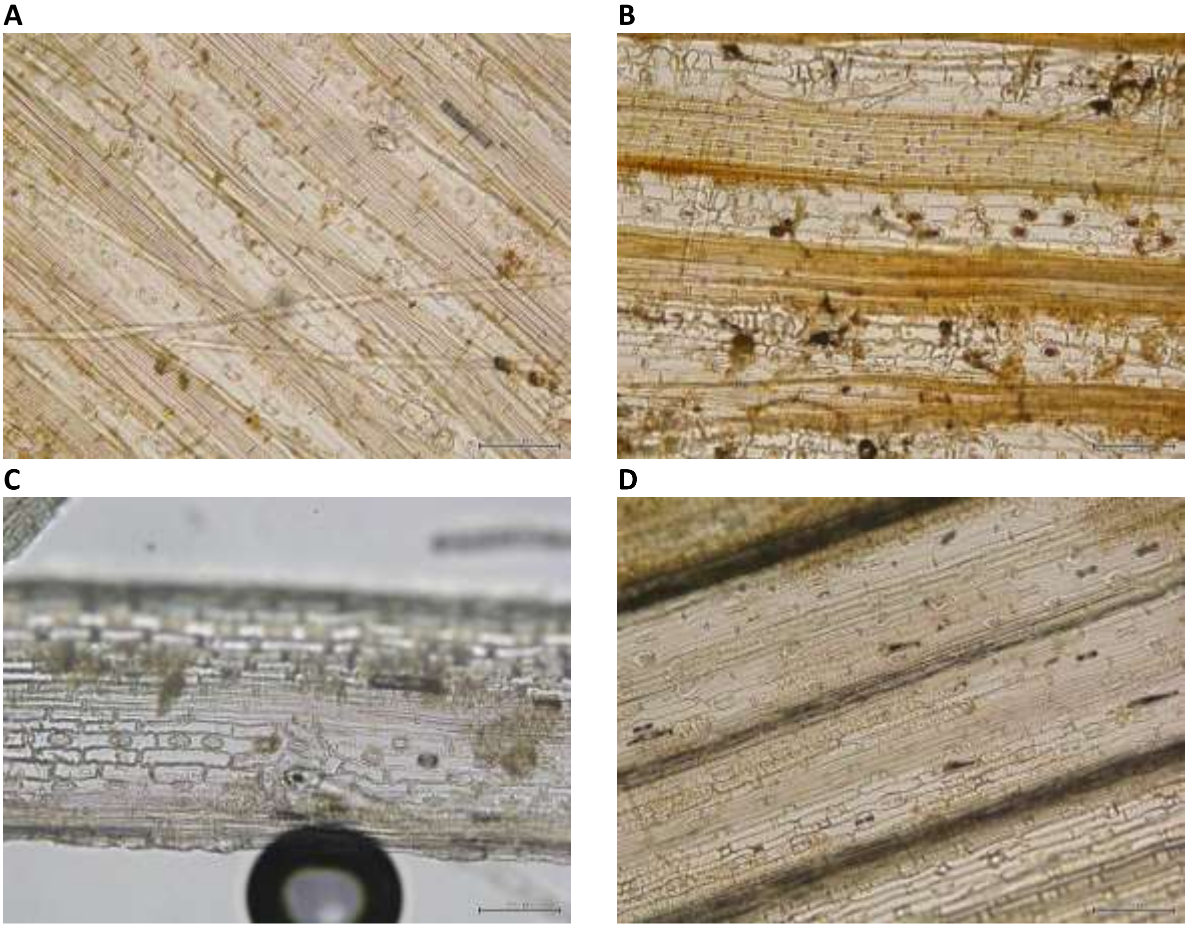


Figure A. 6: Epidermal structures of *Eragrostis*.
A: Abaxial epidermis of *E. congesta* (field name: AE); B: Abaxial epidermis of *E. chapelleri* (field name: AB); C: Abaxial epidermis of *E. racemosa* (field name: Kas-1); D: Abaxial epidermis of *Eragrostris sp.* (field name: Kas-3). The scale is the same for all pictures giving 100 µm.

Eragrostis spp.

Grasses determined as a member of the genus *Eragrostis* (N.M. WOLF) and used for reference were found in Kasanka NP and Kafue Region (PukuPan & Kaingu-Region) and collected under the field names J, AB, AE, Kas-1, Kas-2, Kas-3, Kas-14, Kaf-7, Kaf-12, Kaf-15, Kaf-28 and Kaf-30. Following species could be identified: *E. congesta* (AE), *E. chapelleri* (AB, Kaf-15) and *E. racemosa* (Kas-1, Kas-2, Kas-14). A determination to species level was not possible for the remaining grasses but Kaf-28 and Kaf-30 appear to belong to one species as well as J and Kas-3.

Silical bodies in the short cells of the costal are round, stick shaped (straight or curved). Pairs of short cells are separated by long cells. Rarely two or three pairs are strung together. Stomata are mostly round but can be triangular shaped (*E. chapelleri*, Kaf-12). There are 1 to 3 rows of stomata in the intercostal. Relative distance between stomata is 1 to 5 (mostly 1 to 3) relative length of stoma. Micro hairs are present and as long or longer than stomata. They were not observed in *E. chapelleri*, Kaf-7 or Kaf-12. Pickle hairs in the costal and Hook hairs in the intercostal were not found except in Kaf-28, Kaf-30, J and Kas-3 where they are frequent or present, respectively. Pickle hair have a rather round basis. Long hairs were observed only in *E. congesta* and *E. chapelleri* where they were frequent or present in the intercostal with cells in a circle around the basal end. Papillae were not observed. Long cells in the intercostal with strong undulating cell walls are rectangular shaped and often separated from each other by short cells. Long cells in the costal look alike (Figure A. 6:).

Hemarthria altissima

The grass determined as *Hemarthria altissima* ((Poir.) Stapf and C.E. Hubbard) and used for reference was found in Kasanka NP and collected under the field name A.

Silical bodies in the short cells of the costal are short and dump-bell shaped. Costal short cells are in rows, 1 to 2 rows were observed per costal. Stomata are triangular shaped and can be relatively large. There are 1 to 4 rows of stomata in the intercostal. Relative distance between two stomata is <0.5 to 1 length of stoma. Neighbouring rows with stomata are entwined. Micro hairs, pickle hairs in the costal and hook hairs in the intercostal were not observed. Long hairs were rarely observed in the intercostal with cells in a circle around the basal end. Papillae were not observed. Long cells in the intercostal are rectangular or rather square-alveolate towards the middle of the intercostal, cell walls are (sinus) undulating. Long cells in the costal are rectangular but narrow. Long cells are separated often from each other by short cells (Figure A. 8 A).

‘*Hyparrhenia-Andropogon*-group’

The genera *Hyparrhenia* (Anderss.) and *Andropogon* (L.) can resemble to each other not only in general appearance (see van Oudtshoorn 2009) but also in their epidermal characteristics (see Barthlott & Martens 1979). These two taxa belong to the *Andropogonoidae-Andropogoneae* group of grasses (Barthlott & Martens 1979). Since *Andropogon* was not surely identified within the grasses collected in field a wrong determination cannot be excluded. Van Outshoorn (2009) reported about possible hybridisation between several species in *Hyparrhenia*. A doubtless discrimination of between these two genera and within *Hyparrhenia* is not possible and thus they are listed together as ‘*Hyparrhenia- Andropogon*-group’.

Grasses determined as members of this group used for reference were found in Kasanka NP and Kafue Region (PukuPan & Kaingu-Region) and collected under the field names E, I, K, Q, Y-1, AA, AG, AH, AP, Kas-18, Kas-22, Kaf-2, Kaf-2 aus Kas, Kaf-3, Kaf-19, Kaf-21, Kaf-25, Kaf-29 and Kaf-31. The grasses Q, AP and Kaf-3 were determined as *H. tamba*. The grasses E, I, AG, Kaf-2 aus Kas and Kaf-2, were determined as *H. nyassae*. The grasses K, Kas-18 and Kas-22 were determined as *H. hirta*.

Silical bodies in the short cells are all dump-bell shaped, not sharp-pointed and very good to detect. They are mostly large and thick, sometimes with a knot in the middle. The short cells in the costal are in rows. 1 to 4 rows were observed. Stomata are more or less triangular. There are 1 to 4 rows of stomata in the intercostal. Relative distance between stomata is 0.5 to 2 length of stoma. Micro hairs are either present and longer than stomata (*H. tamba*, *H. nyassae*) or not observed (*H. hirta*). Pickle hairs are mostly present and have an oval basis. Hook hairs are present or frequent. Mostly long hairs were not observed, but can be present (*H. tamba*). Papillae are situated in the interstomal: only on cells between two stomata, a big round papilla (about the size of the stomata) can be found. Papillae were not observed in some species (*H. hirta* and AA, Kaf-19, Kaf-14). The long cells in the intercostal are rectangular and have a strong, sometimes sinus undulation (*H. hirta* and AA, Kaf-19, Kaf-14). If not separated by trichomes, long cells are often separated from each other by short cells (Figure A. 7).

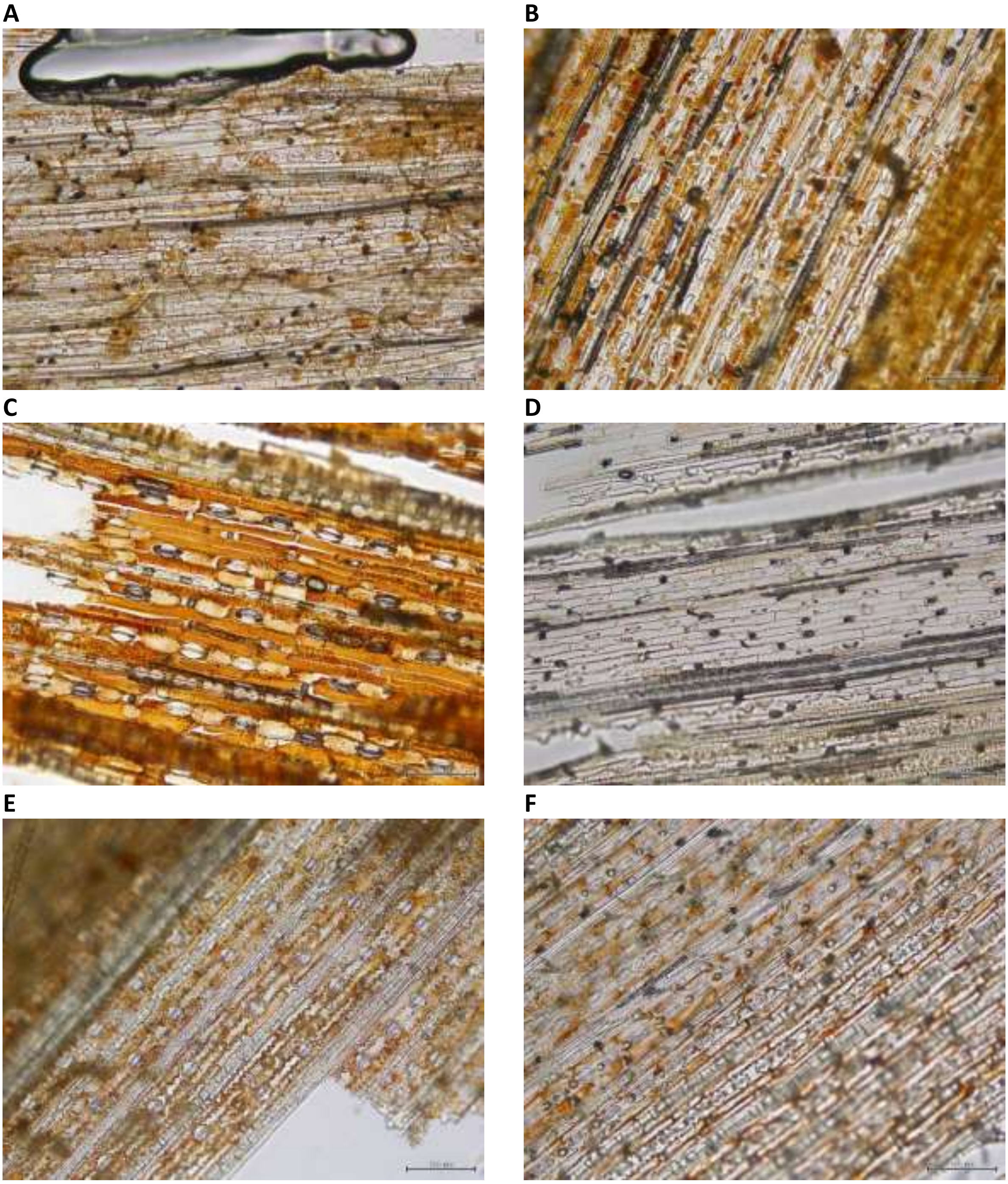


Figure A. 7: Epidermal structures of members in the *Hyparrhenia*/*Andropogon*-Group.
A: Abaxial epidermis of *H. tamba* (field name: AP); B: Abaxial epidermis of *H. nyassae* (field name: AG); C: Abaxial epidermis of *H. nyassae* (field name: Kaf-2); D: Abaxial epidermis of *H. nyassae* (field name: Kaf-2 aus Kas); E: Abaxial epidermis of *H. hirta* (field name: K); F: Abaxial epidermis of another grass in the '*Hyparrhenia-Andropogon*-group' (field name: Kaf-25). The scale is the same for all pictures giving 100 µm.

Loudetia sp.

The grass determined as *Loudetia sp.* (HOCHST.) and used for reference was found in Kasanka NP and collected under the field P. A determination to species level was not possible.

Silical bodies in the short cells of the costal are long and thick and dump-bell shaped, not sharp-pointed. Costal short cells are in rows, 1 to 3 rows per costal were observed. Stomata are triangular shaped and flat. There are 1 to 2 rows of stomata in the intercostal. Relative distance between stomata was between 1.5 to 3 lengths of stoma. Micro hairs longer than stomata were observed. Pickle hairs in the costal were not observed. Hook hairs are frequent in the intercostal. Long hairs are present in the intercostal. Papillae are not present. Long cells are rectangular shaped and if not separated by trichomes often separated from each other by short cells (Figure A. 8 B).

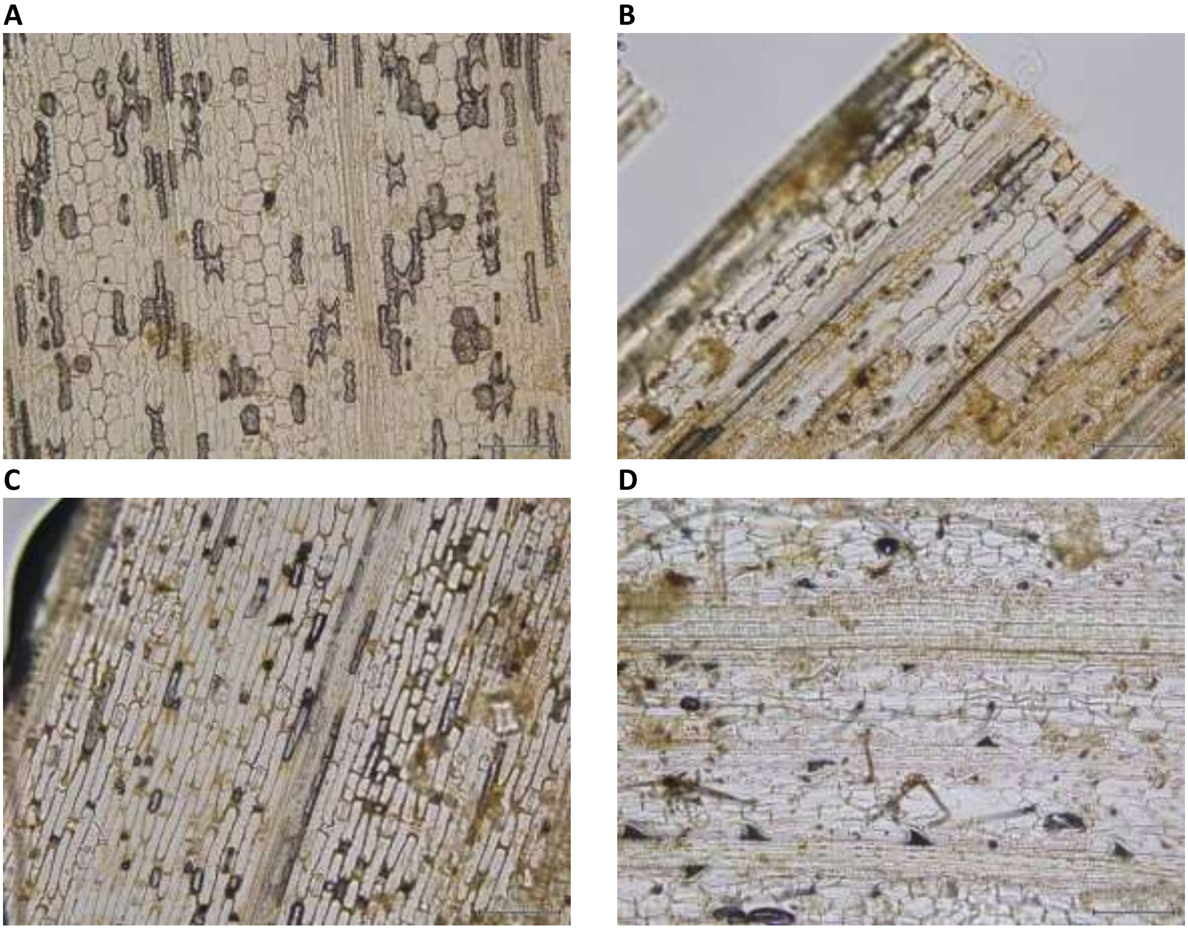


Figure A. 8: Epidermal structures of different grass species 2.
A: Abaxial epidermis of *Hemarthria altissima* (field name: A); B: Abaxial epidermis of *Loudetia sp.* (field name: P); C: Abaxial epidermis of *Melinis nerviglumis* (field name: Kas-11); D: Abaxial epidermis of *Oryza sp*. (field name: AI). The scale is the same for all pictures giving 100 µm.

Melinis nerviglumis

The grasses determined as *Melinis nerviglumis* ((Franch.) Zizka) and used for reference were found in Kasanka NP and collected under the field names Kas-11 and Kas-21.

Silical bodies in the short cells of the costal are long and not sharp-pointed dump-bell shaped. Costal short cells are in rows, 1 row per costal was observed. Stomata are slightly triangular shaped. There are 1 to 5 rows of stomata in the intercostal. Relative distance between stomata is 2 to 6 lengths of stoma. Micro hairs present, shorter than stomata. Pickle hairs in the costal are absent. Hook hairs in the intercostal are frequent. Long hairs are absent. Papillae are absent. Long cells are rectangular and have strong undulating cell walls. If not separated from each other by hook hairs they are often separated by (pairs of) short cells (Figure A. 8 C).

Oryza sp.

Grasses determined as a member of the genus *Oryza* (L.) and used for reference were found in Kasanka NP and in Kafue Region (PukuPan & Kaingu-Region) and collected under the field names AI and Kaf-33. A determination to species level was not possible. Different species might have been collected. Preparation of the epidermis for reference was rather difficult. Not all characteristics could be properly evaluated.

Silical bodies in the short cells of the costal are thick dump-bell shaped, rather long, not sharp-pointed, sometimes with a knot in the middle. Costal short cells are in rows, 1 to 3 rows were observed in the intercostal. Stomata are rather triangular. There are 1 to 4 rows of stomata in the intercostal. Relative distance between two stomata is 0.5 to 3 length of stoma. Cell rows with stomata are entwined. Micro hairs are present and as long as stomata. Pickle hairs in the costal are frequent, with oval basic. Hook hairs are present. Long hairs were not observed. Papillae were not observed. Long cells in the intercostal are rectangular or square and alveolate in the middle of the intercostal, cell walls are undulating. Long cells were not observed to be separated from each other by short cells (Figure A. 8 D).

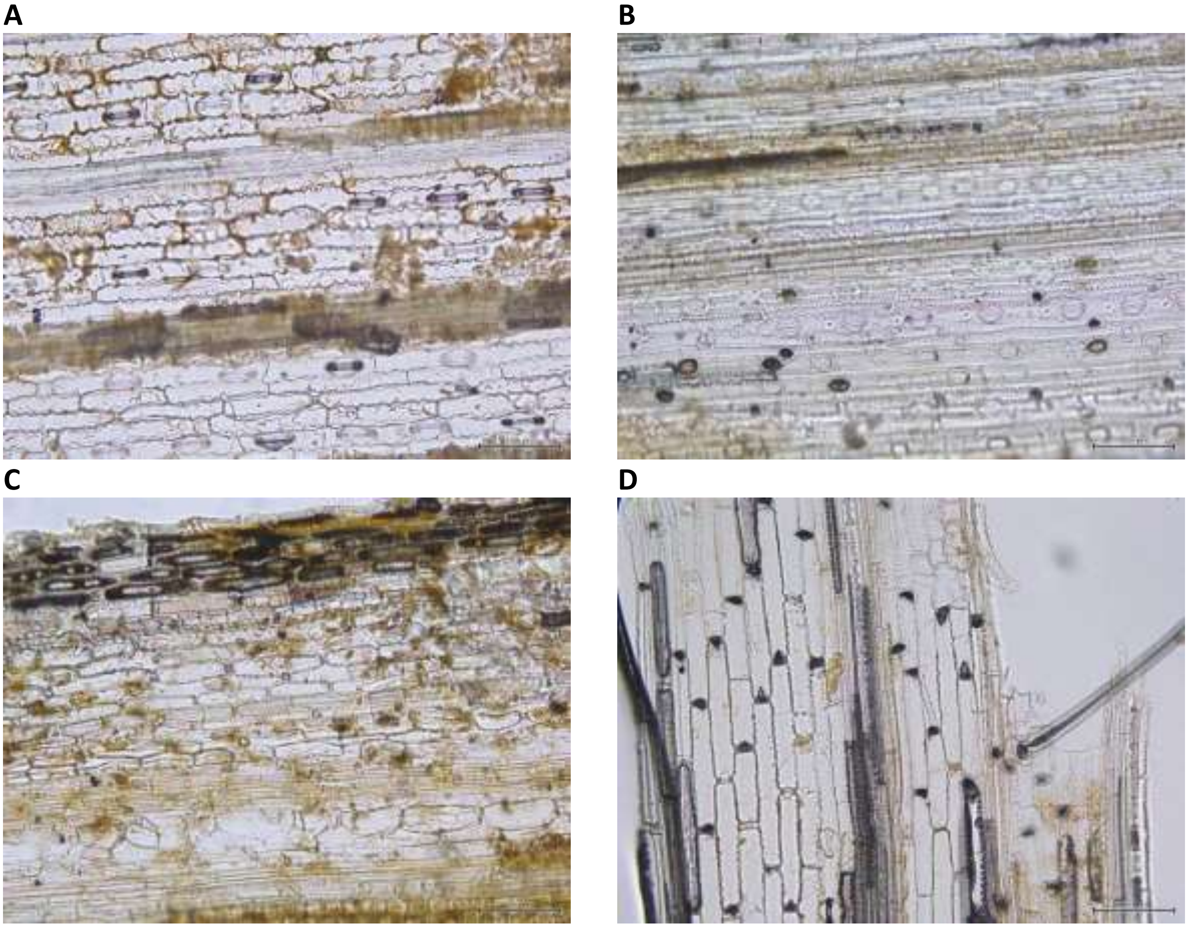


Figure A. 9: Epidermal structures of *Panicum* spp
A: Abaxial epidermis of *Panicum sp.* (field name: Kaf-17), B: Abaxial epidermis of *Panicum sp.* (field name: Y-2); C: Abaxial epidermis of *Panicum maximum* (field name: AQ), D Abaxial epidermis of *Panicum maximum* (field name: Kas-12). The scale is the same for all pictures giving 100 µm.

***Panicum* spp.**

Grasses determined as members of the genus *Panicum* (L.) and used for reference were found in Kasanka NP and Kafue Region (PukuPan & Kaingu-Region) and collected under the field names H, Y-2, AQ, Kas-7, Kas-12, Kas-17 and Kaf-17. AQ, Kas-12 and Kas-17 were all defined as *P. maximum*. A further determination of the remaining grasses to species level was not possible. Different species might be collected. The structural differences in the epidermis did not allow a reliable discrimination between taxa at microscopic level. Preparation of the epidermis for reference was rather difficult for H and Kas-7. Not all characteristics could be properly evaluated.

Silical bodies in the short cells are long or short and dump-bell shaped, sometimes with a knot in the middle, but they were poorly visible (especially for *P. maximum*). Costal short cells were observed in 1 to 2 rows per costal. Sometimes the costal appeared to be composed only of long cells separated from each other by thin stick shaped short cells (Kas-12, Kas-17). Stomata are triangle shaped. There are 1 to 3 rows of stomata in the intercostal. Relative distance between stomata is 1 to 5 length of stoma. Micro hairs are present and are shorter or about as long as stomata, they were not observed in Y-2 and Kas-7. Pickle hair in the costal can be either frequent with a round (AQ) or oval (Y-2) basis or absent. Hook hairs in the intercostal can be frequent (Y-2, AQ, Kas-12, Kas-17) or absent. Long hairs were present in Kas-7, AG, Kas-12 and Kas-17, only in the latter three mentioned species they have a circle of cells at the basal end. Papillae are absent. Long cells in the intercostal can resemble to those in the costal (Kas-12, Kas-17). Generally, long cells in the intercostal are rectangular shaped. The rows are wave-like in Kas-7. All long cells have cell walls with strong undulation, a sinus-undulation is found in Kaf-17 and H. If not separated from each other by hook hairs, the long cells are often separated from each other by short cells (Figure A. 9).

Pennisetum sp.

Grasses determined as a member of the genus *Pennisetum* (Rich.) and used for reference were found in Kasanka NP and in Kafue Region (PukuPan & Kaingu-Region) and collected under the field names G and Kaf-24. A determination to species level was not possible.

Silical bodies in the short cells of the costal are dump-bell shaped and rather thin. Costal short cells are in rows, not always continuously, 1 to 5 rows were observed per costal. Stomata are triangular. There are 1 to 5 rows of stomata in the intercostal. Relative distance between stomata is 1 to 3 length of stoma. Micro hairs, shorter or about as long as stomata, are present. Pickle hairs in the costal are absent. Hook hairs in the intercostal are frequent. Long hairs are absent. Papillae are absent. Long cells are rectangular and have strong (sinus) undulating cell walls (Figure A. 10 A).

Pogonarthria sp.

Grasses determined as a member of the genus *Pogonarthria* (Stapf) and used for reference were found in Kasanka NP and Kafue Region (PukuPan & Kaingu-Region) and collected under the field names U and Kaf-27. A determination to species level was not possible.

Silical bodies in the short cells of the costal are round to kidney-shaped. The costal short cells are in pairs, which are separated from each other by long cells. Stomata are round. There are 1 to 2 rows of stomata in the intercostal. Relative distance between stomata is 1 to 7 length of stoma. Micro hairs are present and about as long as stoma. Pickle hairs, hook hairs and long hairs were not observed. Papillae are absent. Long cells in the intercostal are rectangular with strong undulating cell walls, often separated from each other by short cells (Figure A. 10 B).

Phragmites australis

The grass determined as *Phragmites autralis* ((CAV.) TRIN. EX STEUD.) and used for reference was found in Kasanka NP and collected under the field names Kas-10.

Silical bodies in the short cells of the costal are round. Costal short cells are in rows, 1 to 2 rows were observed per costal. Stomata are round. There are 6 to 12 rows of stomata in the intercostal. Relative distance between stomata is 0.5 to 2 length of stoma. Stomata are abundant. Micro hairs are present and slightly longer than stomata. Pickle hairs in the costal were not observed. Hook hairs in the intercostal are frequent. Long hairs are absent. Papillae are absent. Long cells are rectangular and wave-like. If not separated from each other by hook hairs, cells in the intercostal are separated always by short cells. Rows in the intercostal are entwined and except for some few rows at the border, all contain stomata (Figure A. 10 C).

***Setaria* spp.**

Grasses determined as members of the genus *Setaria* (P. BEAUV.) and used for reference were found in Kasanka NP and Kafue Region (PukuPan & Kaingu-Region) and collected under the field names Kas-5, Kas-16, Kaf-6, Kaf-13 and Kaf-34. *S. incrassata* could be determined (Kas-16, Kaf-34), further different other species might have been collected.

Silical bodies in the short cells of the costal are cross or short dump-bell shaped. Costal short cells are in rows, 1 to 4 rows were observed per costal. Stomata are triangular. There are 1 to 3 rows of stomata in the intercostal. Relative distance between stomata is 1 to 6 lengths of stoma. Micro hairs can be present and are about half as long as stomata. Pickle hairs in the costal are present, basis is oval. Hook hairs in the intercostal are present. Long hairs were not observed. Papillae were not observed. Long cells are rectangular, sometimes getting narrow towards their ends, with a strong undulating cell wall. If not separated from each other by hook hairs, the long cells are separated from each other (often) by short cells (Figure A. 10 D).

***Sporobolus* spp.**

Grasses determined as members of the genus *Sporobolus* (R. Br.) and used for reference were found in Kasanka NP and Kafue Region (PukuPan & Kaingu-Region) and collected under the field names T, AK, AL, AS, Kaf-4 and Kaf-36. *S. centrifugus* (T) could be determined as well as *S. africanus* (AS).

Silical bodies in the short cells are round, straight or curved and stick shaped. In *S. centrifugus* they are dump-bell shaped. Costal short cells are in pairs, sometimes in double pairs that are separated by long cells. In *S. centrifugus* costal short cells are in rows. Stomata are round. There are 1 to 2 rows of stomata in the intercostal. Relative distance between stomata is <0.5 to 2 length of stoma. Micro hairs are present and about as long as stomata. Pickle hairs in the costal were not observed, except in *S. centrifugus* where pickle hairs have an oval basis. Hook hairs in the intercostal can be present. Long hairs are absent. Papillae are absent. Long cells in the intercostal are rectangular with strong undulating cell walls. Cells in *S. centrifugus* have a broader (sinus) undulation. They are often separated from each other by short cells (Figure A. 10 E).

***Tristachya* sp.**

The grass determined as members of the genus *Tristachya* (Nees) and used for reference was found in Kasanka NP and collected under the field name N. A determination to species level was not possible. Preparation of the epidermis for reference was rather difficult. Not all characteristics could be properly evaluated.

Silical bodies in the short cells are thin and dump-bell shaped. Costal short cells are in in rows. Stomata are rather triangular. There are rather rare – situated at relatively far distances from each other (in regard to within and between rows). Micro hairs are present, about as long as stomata. Pickle hairs in the costal as well as long hairs were not observed. Hook hairs in the intercostal are present. Papillae are absent. Long cells in the intercostal are rectangular with strong undulating cell walls and are sometimes separated from each other by short cells (Figure A. 10 F).

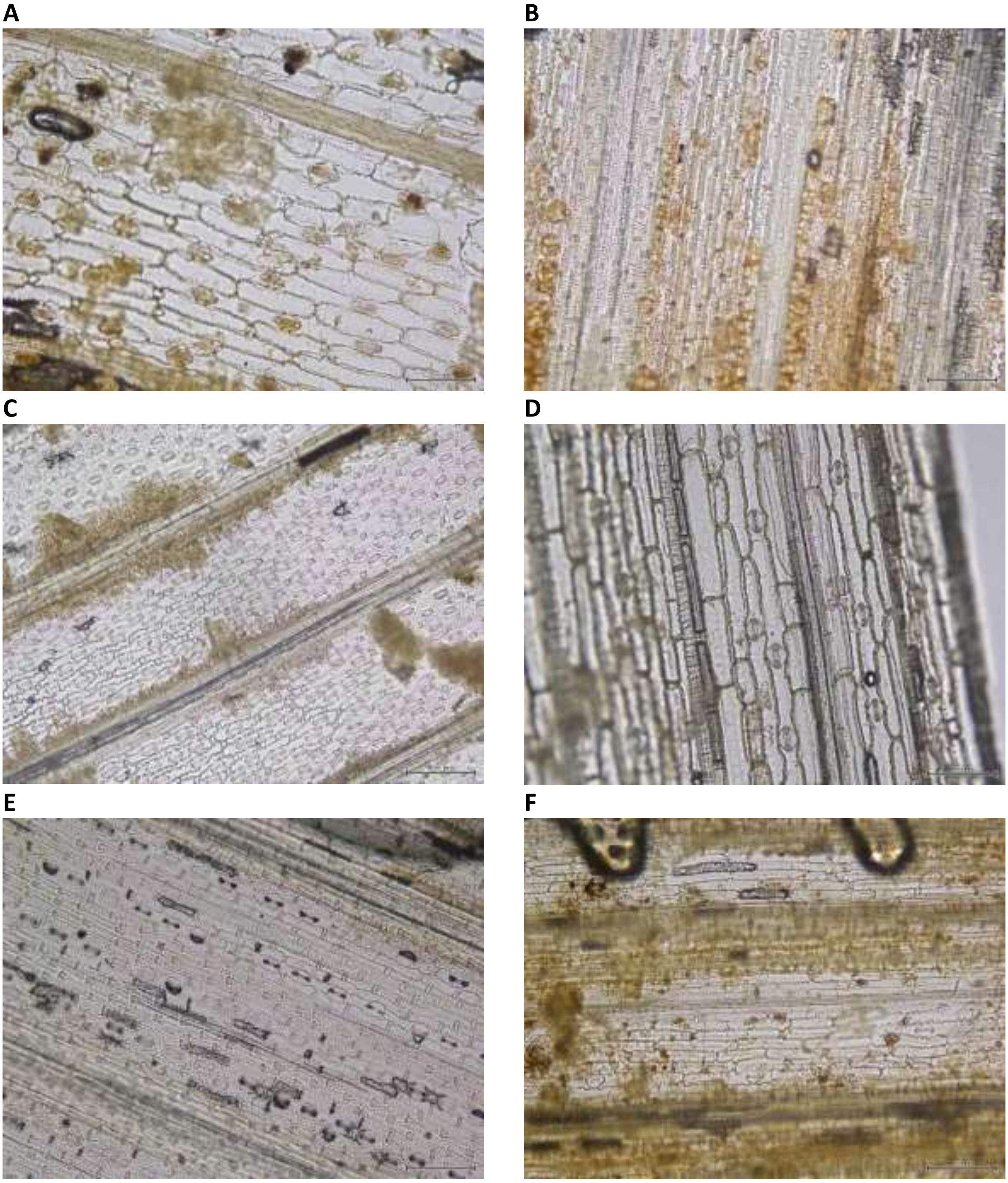


Figure A. 10: Epidermal structures of different grass species 3.
A: Abaxial epidermis of *Pennisetum sp.* (field name: Kaf-24); B: Abaxial epidermis of *Pogonarthria sp.* (field name: U); C: Abaxial epidermis of *Phragmites australis* (field name: Kas-10); D: Abaxial epidermis of *Setaria sp.* (field name: Kaf-6); E: Abaxial epidermis of *Sporobolus africanus* (field name: AS); F: Abaxial epidermis of *Tristachya sp.* (field name: N). The scale is the same for all pictures giving 100 µm.

Description of epidermal characteristics of Cyperaceae

Cyperus papyrus (21)

Cyperus papyrus (L.) belonging to the Cyperaceae, the sedges, is the only non-poaceae in this reference collection. It was found and collected in Kasanka NP (Kas-9).

Silica bodies as well as micro hairs or long hairs were not observed. Stomata are round and rather big. There are 1 to 2 rows of stomata in the intercostal. Relative distance between stomata is not above 1.5 length of stoma. Stomata are abundant. Pickle hairs are sometimes present in the costal. Costal and intercostal are not clearly separable. Long cells in costal and intercostal are rectangular with undulating cell walls. Long cells in the costal are rectangular but shorter and thinner than in the intercostal. Cell walls are often (very) angular (not rectangular) to neighbouring cells in a row. No short cells were observed (Figure A. 11).

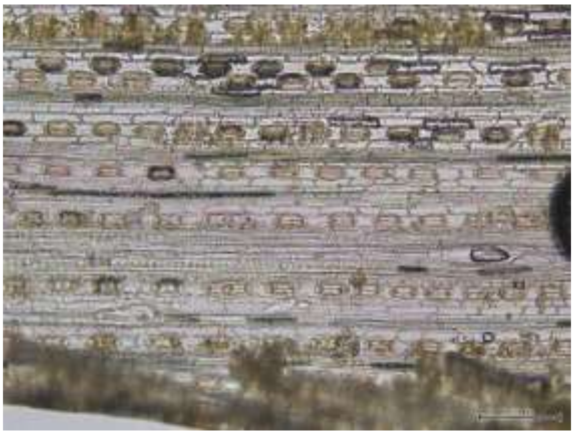


Figure A. 11: The abaxial epidermis of *Cyperus papyrus* (field name: Kas-9). The scale gives 100 µm.

Distribution of different grasses in Kasanka NP

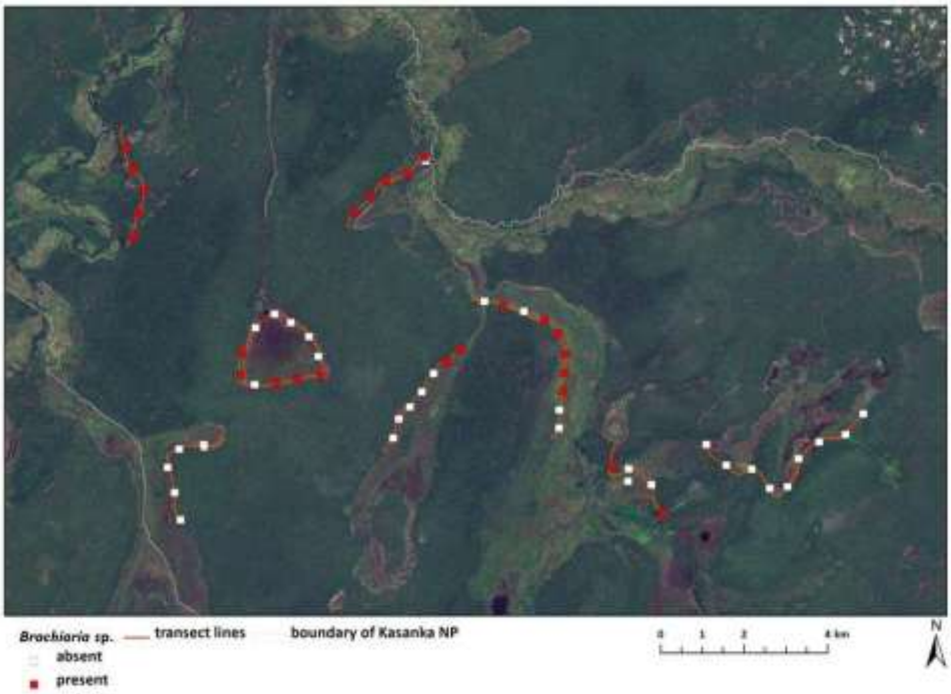


Figure A. 12: Distribution of *Brachiaria* sp. along the transect lines in Kasanka NP.

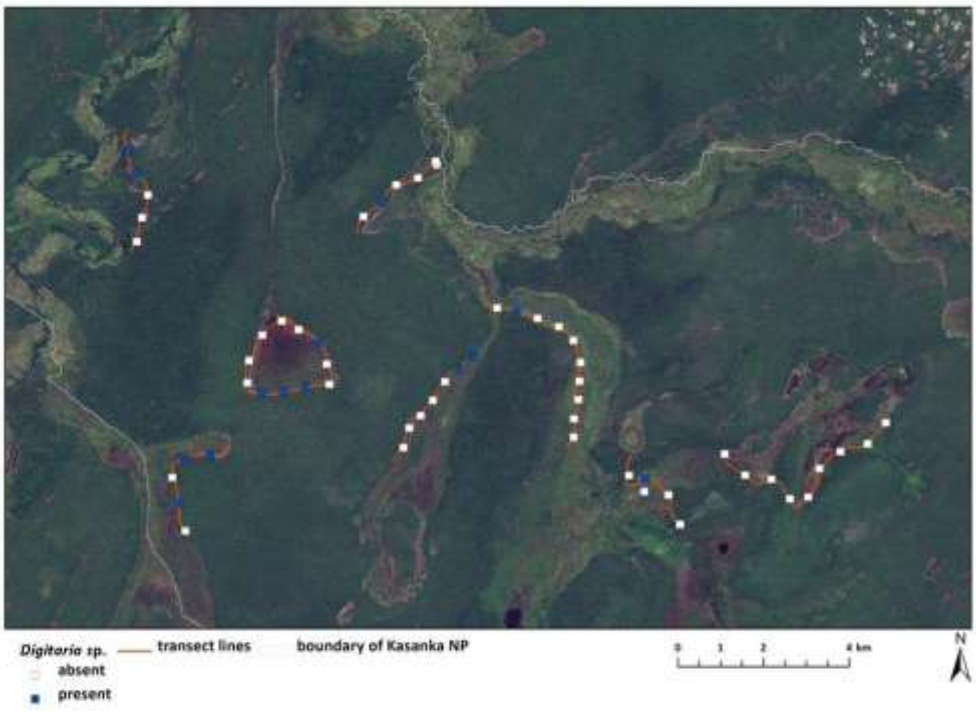


Figure A. 13: Distribution of *Digitaria* sp. along the transect lines in Kasanka NP.

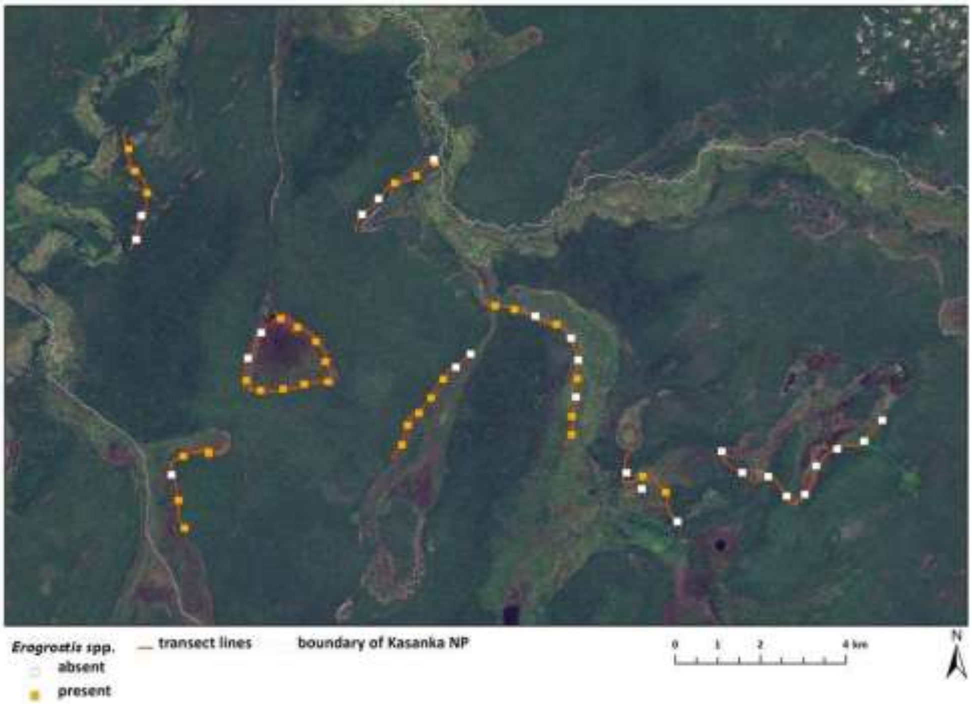


Figure A. 14: Distribution of *Eragrostis* spp. along the transect lines in Kasanka NP.

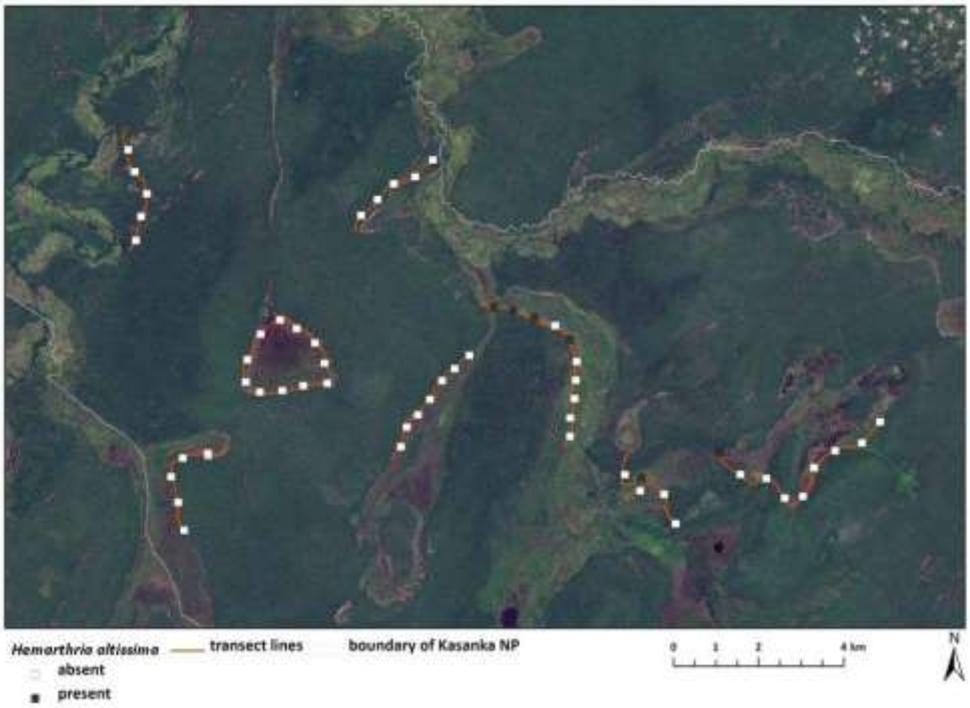


Figure A. 15: Distribution of *Hemarthria altissima* along the transect lines in Kasanka NP.

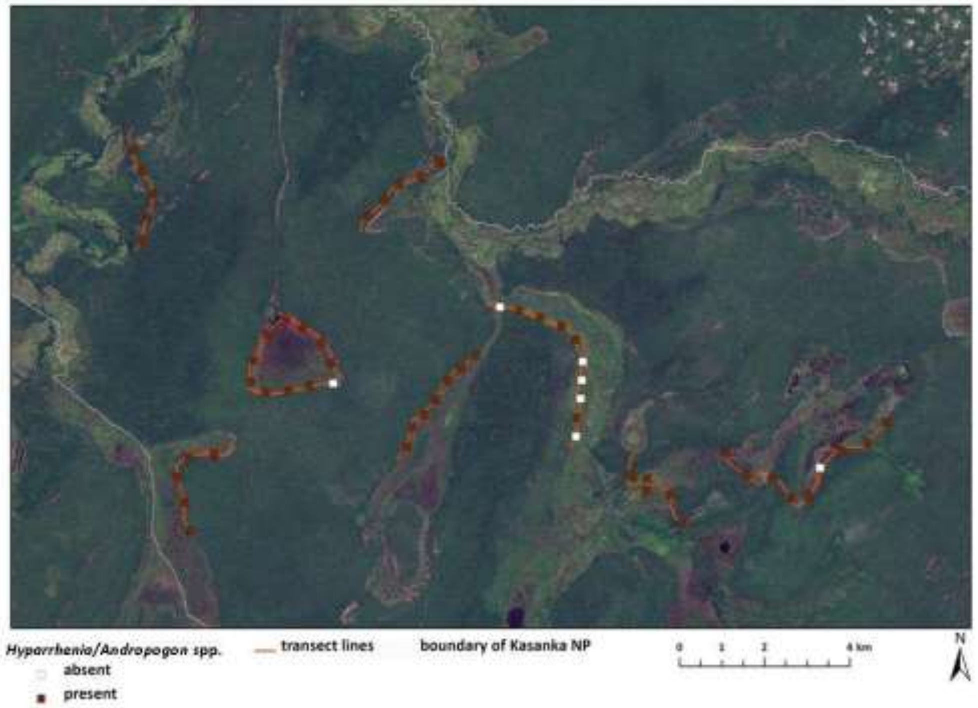


Figure A. 16: Distribution of grasses of the *Hyparrhenia/Andropogon*-Group along the transect lines in Kasanka NP.

Figure A. 17: Distribution of *Loudetia* sp. along the transect lines in Kasanka NP.

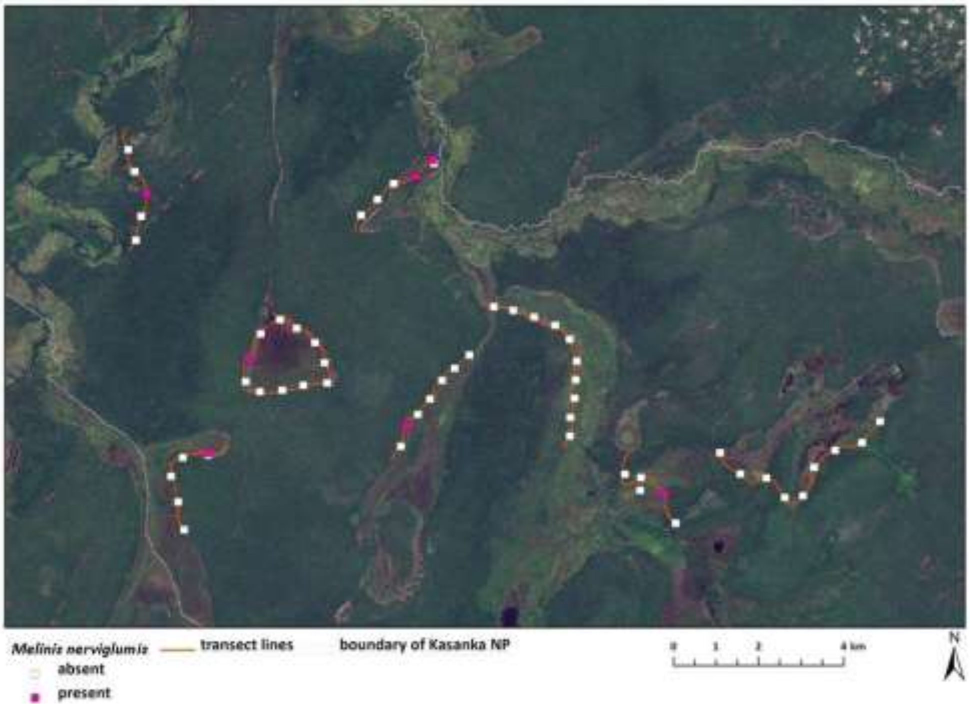


Figure A. 18: Distribution of *Melinis nerviglumis* along the transect lines in Kasanka NP.

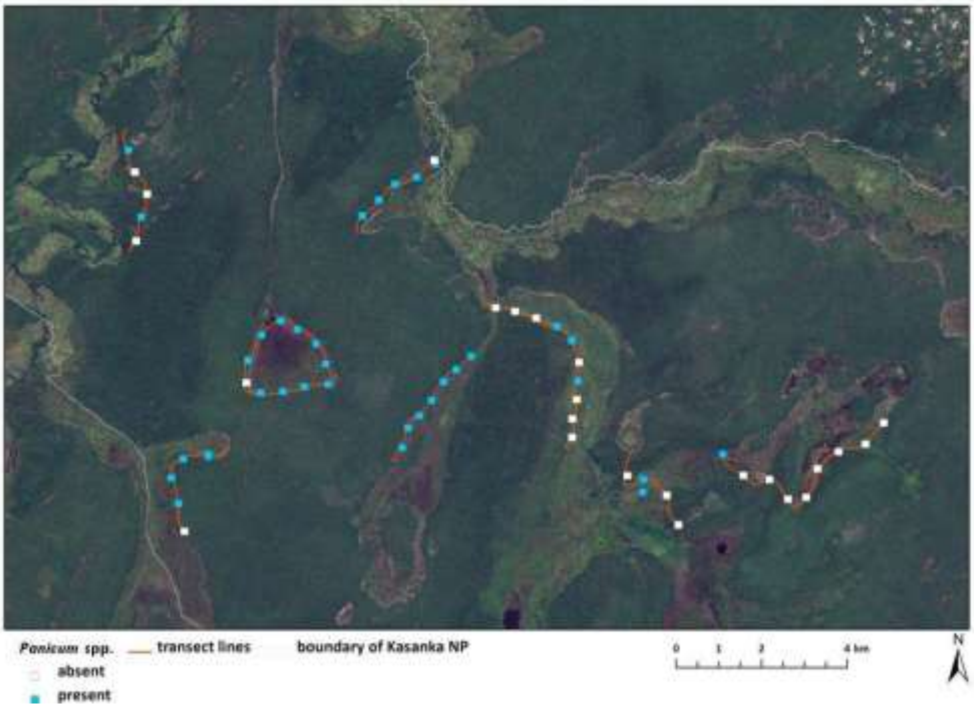


Figure A. 19: Distribution of *Panicum* spp. along the transect lines in Kasanka NP.

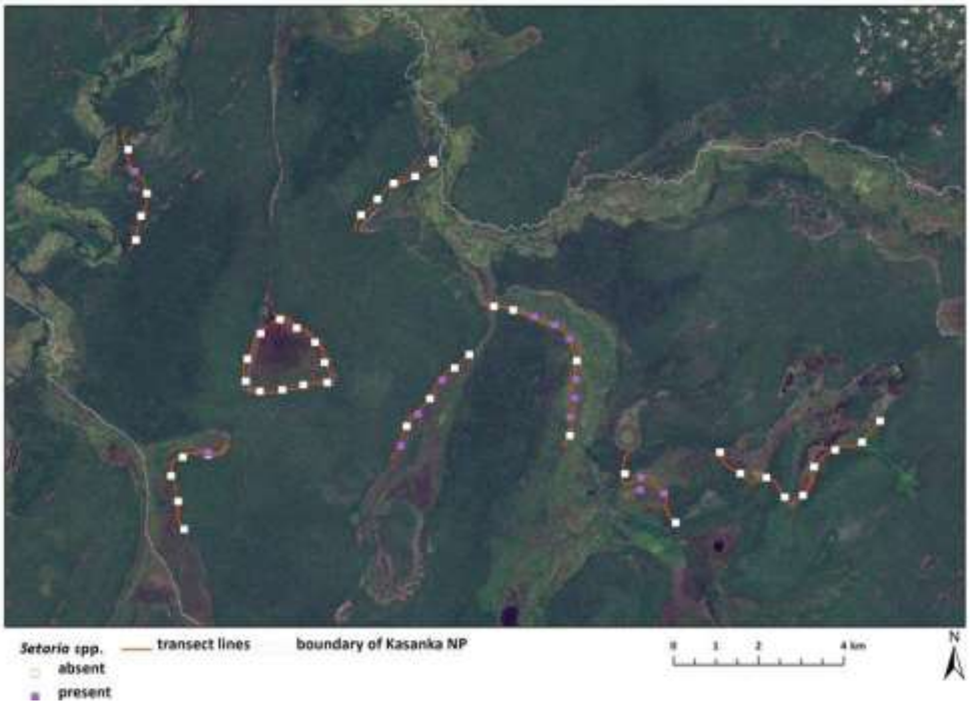


Figure A. 20: Distribution of *Setaria* spp. along the transect lines in Kasanka NP.

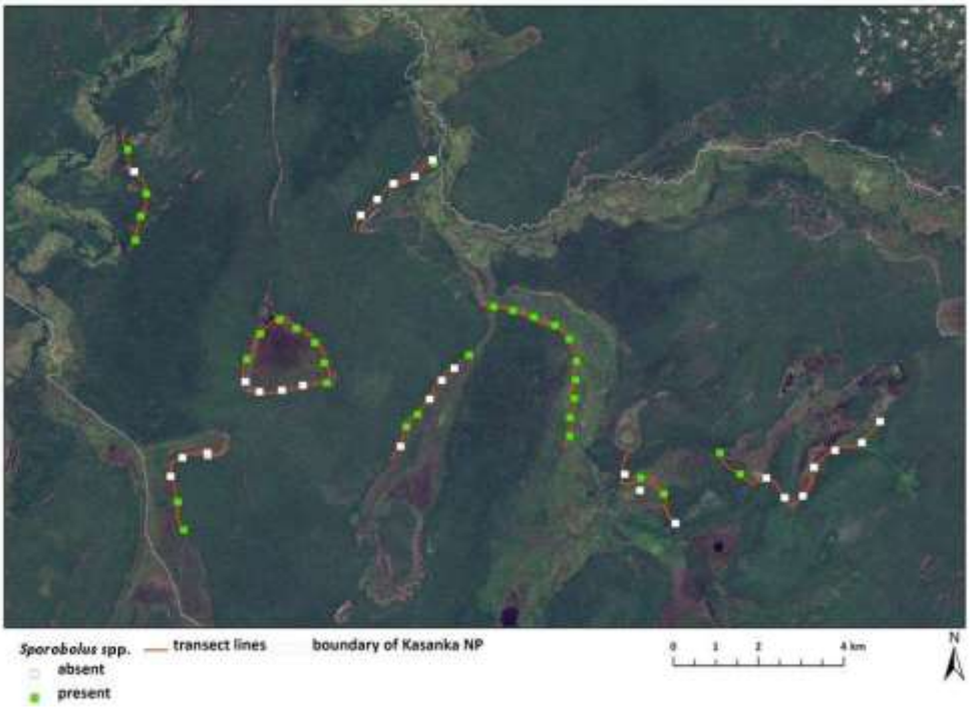


Figure A. 21: Distribution of *Sporobolus* spp. along the transect lines in Kasanka NP.

Description of the “Study regions for Predators” in Kasanka NP

A – grid 1 B – grid 2

C – grid 3 D – grid 3

E – grid 4 F – grid 5

Figure A. 22: Examples of habitats covered by the grids. Miombo woodland covered by grid 1 (A), grid 3 (C) and grid 5 (F), types of grasslands covered by grid 2 and 4 and floodplain habitat covered by grid 3 (D).

Grid 1 (Figure A. 22 A) is situated in the western part of Kasanka NP close to Luwombwa River and Luwombwa Lodge although the floodplain or the borders of the river are not covered. It covers an area west from the transect line and comprises miombo woodland. The rock appeared close to the surface as a least in some parts small clearings with rocky ground and few soil are present. Some parts of the area were burnt, other parts already provided fresh leaves.

Grid 2 (Figure A. 22 B) is situated in the north of Chikufwe Plain. It comprises a part of grassland, the area around the waterhole and miombo woodland adjacent to Chikufwe Plain. The waterhole still provided water and thus green and fresh plants grew around it. Contrastingly the miombo and other parts of the grasslands are either dry or burnt. The miombo rather provides few understory.

Grid 3 (Figure A. 22 C and D) is situated at Kabwe Area. It comprises small amounts of dambo and floodplain areas where the grass is either dry, burnt or moist and green. The same applies for the miombo woodland included in this grid. Some parts of the miombo here provide a very dense understory or grasslayer.

Grid 4 (Figure A. 22 E) at Fibwe Plain comprises different habitat types: grassland areas with rather long and dry grass, grassland with grased or burnt areas, moist grassland with green grass, dry miombo with few understory and moist woodland.

Grid 5 (Figure A. 22 F) near Wasa is almost entirely covered by miombo. The aspect was either burnt or freshly sprouting leaves. The understody was rather absent. Further, some areas in the north of the grid are characterised by termitaria.

Figure A. 23: Aspects of scats from different predators in Zambia: a latrine site of spotted hyena (*Crocuta crocuta*) near Kaingu Lodge (A); scats from crocodile (*Crocodylus niloticus*) (B), caracal (*Caracal caracal*) (C), serval (*Leptailurus serval*) (D), African civet (*Civettictis civetta*) (E) and white-tailed mongoose (*Ichneumia albicauda*) (F) in Kasanka NP. The adjacent scale gives cm.

Table A. 13: Ethogram: This ethogram to assess the behaviour of puku and other antelopes during this study is based on the ethogram I used to study behaviour patterns of puku in Luambe NP (RDUCH 2008).

Grazing

The animal stands with the head bowed onto the grasslayer. If the animal moves some few steps with the head still bowed down, the activity is still comprised in 'grazing'.

Browsing

The animals are standing with the head in trees or scrubs. The head of the animal or branches or leaves of the tree or scrub are moving.

Moving

Walking comprises all forms of movements exhibited by the animals indifferent if the movements are slow (walk) or fast (gallop). Jumps are included.

Vigilant behaviour

The animals show a face and a general body posture of alert staring attentively into a direction. Vigilant behaviours can also occur while the animal is standing or lying down.

Reproductive and territorial behaviours

Displaying behaviours and postures of males towards females and towards other males belong to this category, as well as agonistic interactions, as fights between males. Behaviour patterns of females that make the male continue are included but indifferent and refusing behaviours of the females are not. Mating is included.

Suckling

The category suckling includes both the female that lactates its young as well as the young itself.

Resting

While resting, the animal shows a relax posture, a relaxed face and relaxed ears. Ruminating as visible by moving jaws can occur. Resting is subdivided into three categories.

Resting (standing): Resting can occur while standing.

Resting (lying, head held up): Resting can occur while lying on the ground. Mostly the legs are folded under the body. The belly and the legs can be the contact surface to the ground. The head is raised.

Resting (lying, head on the ground): Resting can occur while lying on the ground. The legs can be folded under the body or stretched towards the side. Contact surface to the ground can be the belly and the legs or the side of the animals. The head lies on the ground.

Behaviour of comfort

The animal scratches itself with the help of teeth, hooves or horns, while standing or lying down.

Watching at the observer

The animal shows vigilant behaviour while starring at the observer

Other behaviour patterns

These are behaviours not covered by the categories mentioned above.

Out of sight

An animal was noted out of sight if it was around but only partly visible so that the behaviour could not be evaluated.

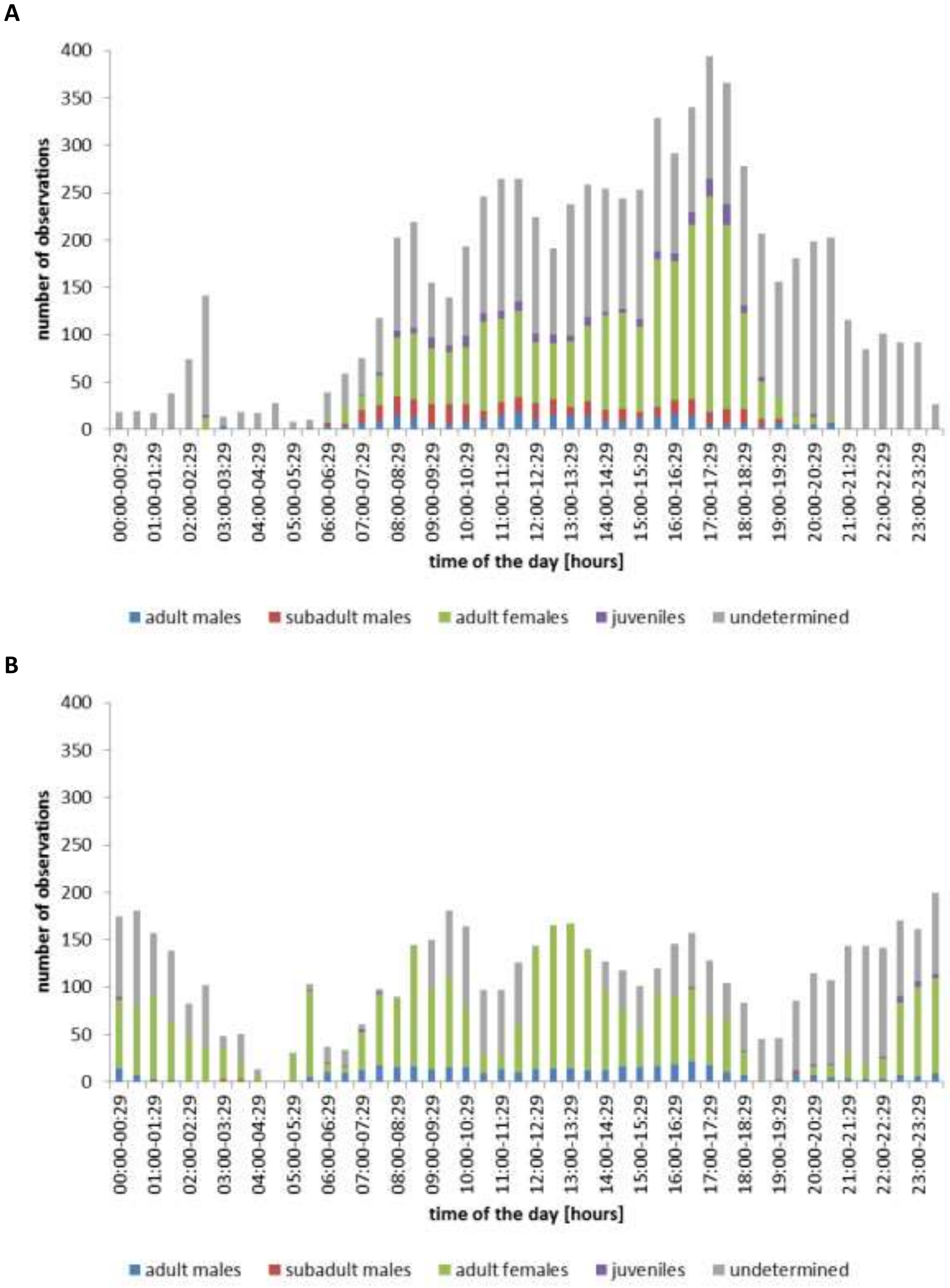
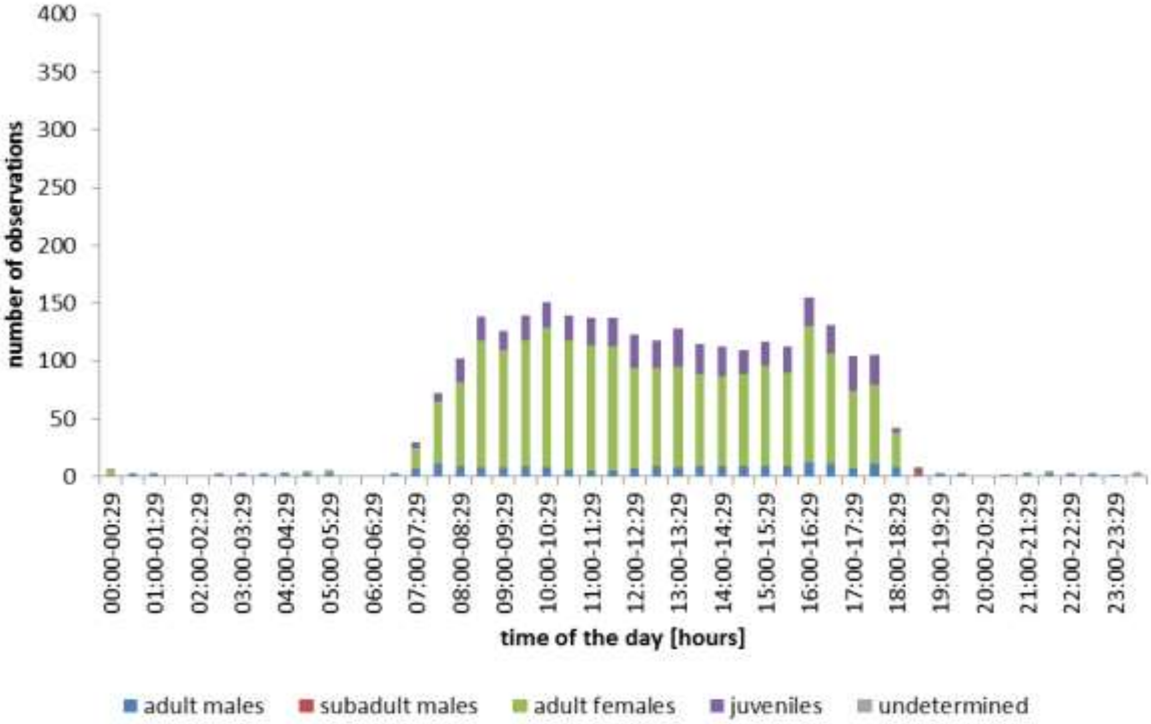


Figure A. 24: Amount of observations of puku (*Kobus vardonii*) at Kabwe Plain (Kasanka NP) during the survey for activity patterns. In cool dry season 2009 (A) und in hot dry season 2010 (B).

A



B

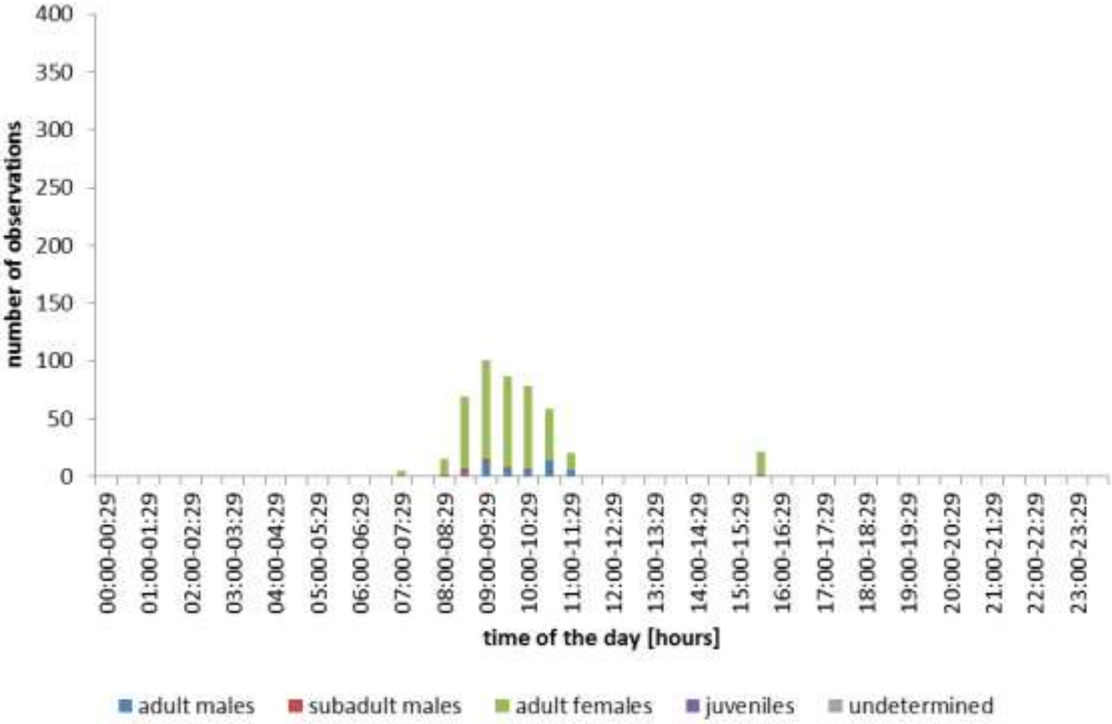


Figure A. 25: Amount of observations for puku (*Kobus vardonii*) (A) and Impala (*Aepyceros melampus*) (B) during the survey for activity patterns at Puku Pan.

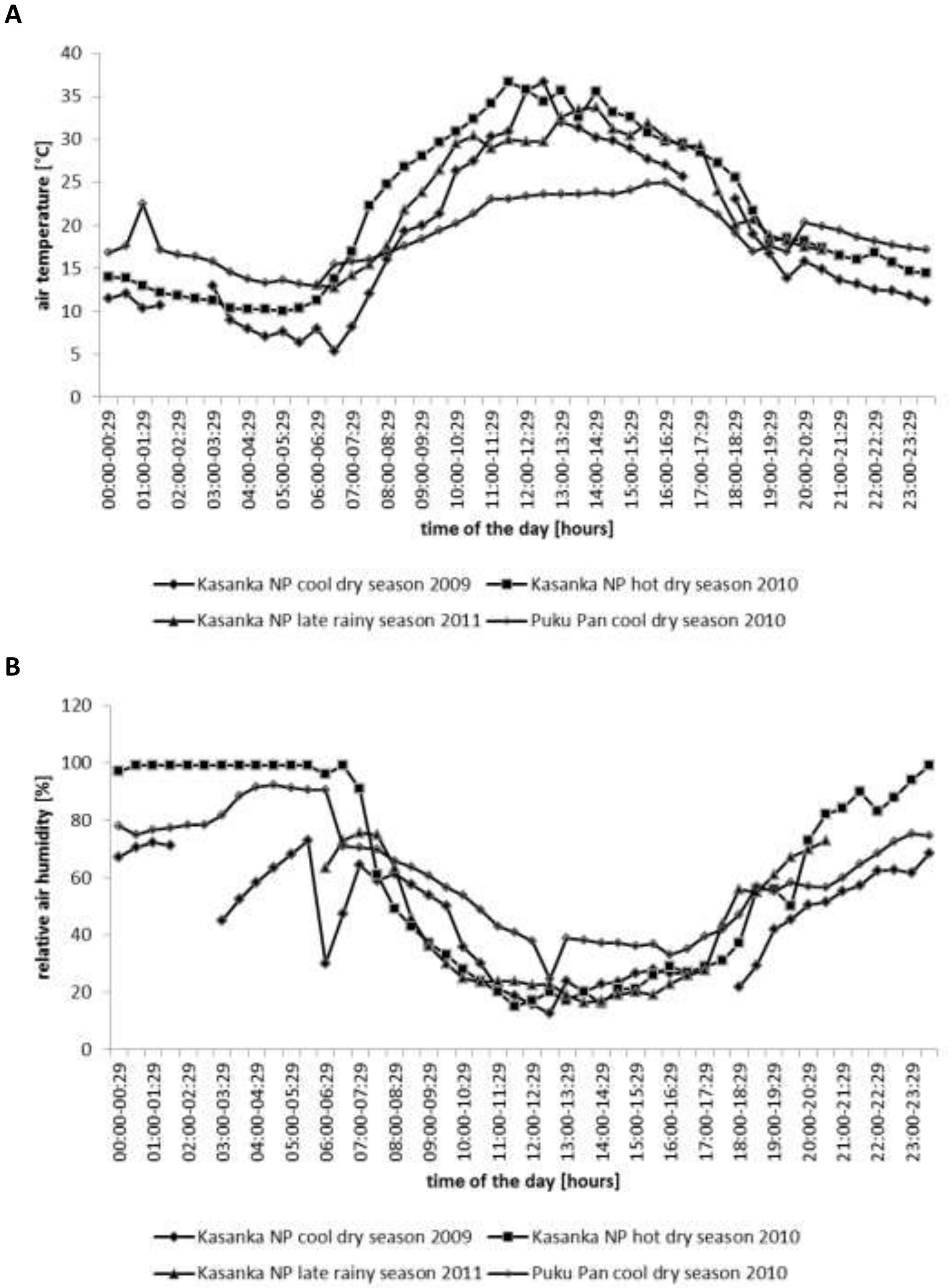


Figure A. 26: Air temperature [°C] and relative air humidity [%] during the day during the different survey for activity patterns.

Table A. 14: Quality of the behaviour sampling along the transect lines: Number of individuals encountered and those assessed for behaviours on the transect line survey and the percentage amount of animals not assessed for behaviours.

antelope species	time of the day	individuals observed	individuals assessed for behaviours	individuals not assessed for behaviours [%]
puku	7 am	213	186	20.19
	10 am	191	170	18.32
	1 pm	190	165	22.5
	4 pm	251	223	16.92
impala	7 am	300	227	35.67
	10 am	227	210	10.57
	1 pm	357	291	20.17
	4 pm	182	157	14.29