



Original investigation

Population characteristics and coexistence of puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) in and around Kafue National Park, Zambia

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ABSTRACT

Sympatric occurrence of puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) characterises large parts of the protected areas in Zambia. The present study assessed traits of the populations as well as spatial and dietary overlap of both antelopes in Kafue National Park and adjacent Game Management Areas in western Zambia. Data were collected via distance sampling along line transects (population and distribution) and via microhistological analyses of dung (diet). Hunting activities might result in fewer males in both antelopes in the Game-Management areas. During the cool dry season there was considerable spatial overlap between puku and impala. However, puku are more abundant in grassland areas, while impala reach highest population densities in intermediate habitats. The diet of puku was characterised by high amounts of grasses during both the cool dry season and the late rainy season. Impala shifted from browsing during the cool dry season to a more grazing diet during the rainy season. This study found niche partitioning via habitat and diet as a key to understand the coexistence of these antelopes and improves our knowledge of Zambian Wildlife.

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Introduction

Herbivore assemblage can result in competition or facilitation. Two bovid species may be competitive if they exhibit a great degree of similarity in resource use at least during periods of forage scarcity (Bagchi et al., 2003). There is evidence for facilitation via the stimulation of the regrowth of grasses during the wet season. Facilitation and competition are suggested to alternate between seasons (Arsenault and Owen-Smith, 2002). With the beginning of the dry season, the ungulates are assumed to retreat to ‘food-refuges’ in order to reduce competition (Sinclair, 1983). Competition for food resources in African bovids is suggested as an important key to understanding their sympatric occurrence and bovid radiation in Africa (Estes, 1991; Sinclair, 1983). By adapting their size, their feeding apparatus, their digestive system and their dispersion patterns, bovids are able to specialise more narrowly and efficiently than other ungulates (Estes, 1991). The underlying processes of the supply and exploitation of resources are poorly understood (Murray and Illuis, 2000). A series of studies has attempted to find explanations for the observed resource partitioning in ungulates: body size does not generally explain the feeding type. As there are small and large browsers (suni, *Neotragus moschatus*), versus

greater kudu, *Tragelaphus strepsiceros*), so there are small and large grazers (oribi, *Ourebia ourebi*, versus African buffalo, *Syncerus caffer*) (Hofmann, 1989). Bovids can be classified into feeding types based on selectivity (Jarman, 1974). These feeding types in turn are associated to body size, group size and also anti-predator behaviour (Jarman, 1974; Brashares et al., 2000). Bovids are characterised by anatomical differences, which are assumed to reflect the proportions of C3 browse and C4 grass in the diet. These differences correlate with the degree of feeding selectivity with regard to short-, medium- and tall grass grazing (Codron et al., 2008). It is the utilisation of specific parts or the specific growth stages of plants that might differ between bovid species (Murray and Brown, 1993) and which ultimately leads to resource partitioning. Arsenault and Owen-Smith (2008) found that the scaling of mouth width relative to body size was able to explain coexistence. Mouth width affects the ability to select the food. Whereas the narrow-mouthed topi (*Damaliscus lunatus*) is able to feed selectively, going for bite quality, the wide-mouthed wildebeest (*Connochaetes taurinus*) goes for bite quantity (Murray and Illuis, 2000). By doing so, both species modify the vegetation in such a way that it is not suitable for the respective other one (Murray and Illuis, 2000). Interspecific competition and habitat choice are connected. In order to avoid interspecific competition animals obtain their food from different habitats (Sinclair, 1983). On the other hand species that overlap in habitat make use of different food sources (Schoener, 1974).

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The co-occurrence of two antelopes, puku (*Kobus vardonii* Livingstone, 1857; Bovidae, Reduncini) and impala (*Aepyceros melampus* Lichtenstein, 1812; Bovidae, Aepycerotini), is typical for large parts of protected areas in Zambia. Sympatric occurrence of both antelopes is found in Kafue National Park (KNP) and the Luangwa Valley, in western and eastern Zambia (Ansell, 1978). In contrast to the aforementioned concepts, both antelopes are similar in body aspects: puku weight between 48–91 kg reaching 77–83 cm in shoulder height. Impala have a body mass of 40–80 kg and have a shoulder height of 75–95 cm (Kingdon, 1997). Also their mouth width appears equally narrow (V. Rduch, pers. obs.). However, according to general classifications, they differ in diet. The puku is classified as an obligate grazer characterised by a proportion of 93% monocots and 7% dicots in their food (Gagnon and Chew, 2000). The diet of impala – a browser-grazer – is intermediate, with monocots and dicots making up 45% each complemented by an amount 10% fruits, but these amounts are variable (Gagnon and Chew, 2000).

This study improves our understanding of the sympatric occurrence of these antelopes in Zambia and thereby contributes to their protection. Generally, Zambian wildlife is poorly studied compared to other African countries. To understand these animals' population characteristics, their autecology is as important as their synecology. First, we need to study the populations in and around KNP with respect to their distribution and structure as a basis for effective conservation, and for an assessment of possible competition between the species. Second, we need to study their diets and evaluate the dietary overlap. Dietary analyses from Zambia have not been conducted; apart from observations of the use of vegetation communities by puku (Rosser, 1992).

Results from inside and outside KNP are not expected to differ considering the similar natural environment but they might be influenced by differences according to the status of protection. Differences in habitat choice between the two species might reduce their competition. The puku is known to inhabit perennial moist grasslands (Jenkins, 2013), whereas the impala prefers light woodlands (Fritz and Bourgarel, 2013). Coexistence of both antelopes is favoured by resource partitioning during a least some periods of the year. During times of competition, when species retreat into the 'food-refuge', diet breadth should be smaller and less overlapping than during times of high food abundance. Presumably, the impala is the crucial element to allow for coexistence, as it is able to switch from graze to browse (Kleynhans et al., 2011) and therefore limiting the competition with puku.

Material and methods

Study area

KNP is the largest national park of Zambia and covers 22,480 km². It is situated in western Zambia (Fig. 1A) and surrounded by Game Management Areas (GMA). In contrast to national parks, both non-consumptive and consumptive use of the resources are permitted in GMA which includes unrestricted entrance and residence as well as controlled hunting (Nyirenda et al., 2008; Leonard, 2005). The Kafue River passes through KNP in the north and borders KNP in the southern parts forming alluvial floodplains (Mkanda and Chansa, 2011). Extensive miombo woodlands characterise the region. Miombo woodlands cover 3 million km² in southern central Africa (Shorrocks, 2007) and 50% of Zambia's surface (Leonard, 2005). The canopy is light and 15–20 m high while the ground layer comprises grasses and herbs (Leonard, 2005). Dambos are characteristic grasslands associated with miombo woodlands, where they form shallow drainage lines (Ansell, 1978). The combination of precipitation and temperatures results in 3 dis-

tinct seasons: a warm rainy season (November–April), a cool dry season (May–August) and a hot dry season (September–November) (Leonard, 2005).

Data were collected in two study areas representing only parts of KNP and surrounding GMA (Fig. 1B): in Mumbwa GMA and Namwala GMA (26°58'43E–26°4'21E, 15°11'27S–15°20'2S) (Fig. 1C) and in the northern part of KNP (26°22'27E–26°25'35E, 14°39'5S–14°41'60S) (Fig. 1D). Both areas touch Kafue River and are situated on its eastern bank.

Data collection on line transects

Distance sampling was carried out from a car to examine the populations and their distribution. Stretches of unsurfaced road tracks were used as line transects, leading through different habitats with various orientations towards the Kafue River (Fig. 1C and D). The transects were driven at four preset times of the day. Data collection took place in the cool dry season (CDS) in 2010 (GMA: 13-Jul. to 22-Aug.; KNP: 29-Aug. to 3-Sep.). The antelopes were recorded regardless of how far they were detected from the transect line. Data collected included group size, radial distance, sighting angle and habitat. Adult and subadult males (fully-grown with horns, lyre-shaped in adult males), females (fully-grown, without horns), juveniles and neonates (not fully-grown with a shoulder height lower than belly of full-grown animals in neonates) were differentiated. During data collection puku were mostly calm in contrast to the nervous impala which complicated determination of sex and age classes. Binoculars (Steiner, SkyHawk 10 × 42) were used, distances were measured (Carl Zeiss, Victory 8 × 26 T* PRF) and angles were determined with a compass, rounded to 10°.

Analyses of population densities, population characteristics and habitat use

Estimations of population densities were conducted using the software Distance 6.0 release 2 (Thomas et al., 2009). I counteracted changes in detection probability in the patchy environment by using multiple-covariates distance sampling (MCDS) (Marques et al., 2007). Covariates of habitat types were assigned to all observations: (1) grasslands (open, short grasslands), (2) intermediate habitat (scrubs, open woodland, light scrubland, edge of woodlands) and (3) woodland (dense woodland, miombo, thicket). The estimations were based on sightings of only puku or impala. Right-truncation was applied. This procedure excluded those observations that were furthest away from the transect lines. Modelling of the data becomes easier and the precision of the estimation improves (Buckland et al., 2001). For this analysis 1–10% of the sightings were excluded. Post-stratification was used here, a stratification of the data after they have been collected and examined (Buckland et al., 2001). The aim was getting density estimations in each habitat type as well as along each transect line. Encounter rate was estimated for each habitat or each transect. In order to estimate the cluster size, i.e. the group size, the simple average of the clusters observed was used. For the population estimation along the transect lines all data were combined, but the data from each habitat were considered separately. The estimation of detection probability was performed for all data combined. For more details on the analyses see Rduch (2014). No extrapolation of the total population size for puku or impala in KNP was attempted, since it would not be reliable given that only a fraction of KNP was covered by the study area.

Differences in group sizes were checked for significance using the Mann–Whitney-*U*-test (*U*-test). The relationship between the number of puku and impala in mixed groups was analysed with

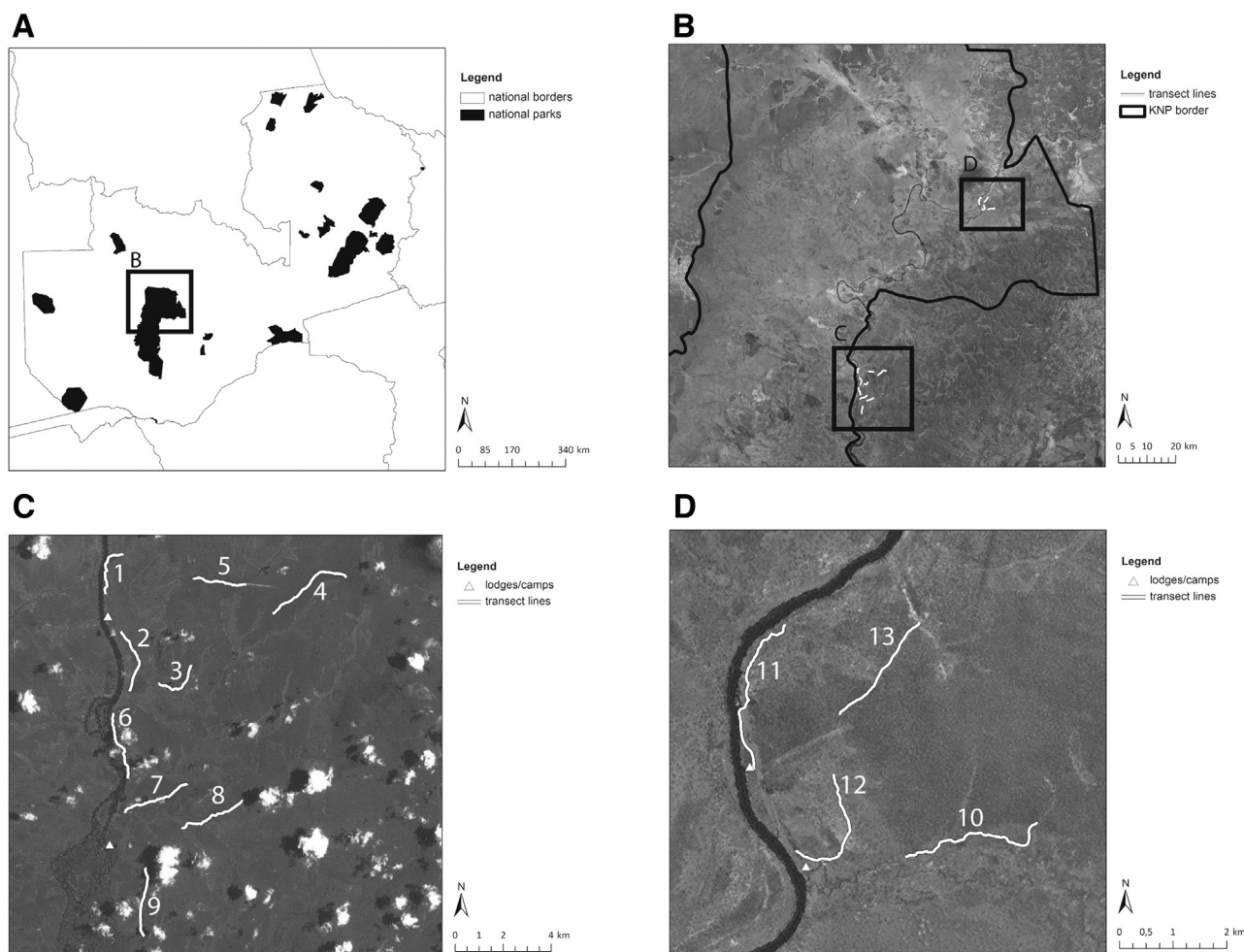


Fig. 1. Location of Kafue National Park in Zambia (A), the study areas (B), situation of the transect lines in the Game Mangement Areas (C) and in Kafue National Park (D). Maps created with ESRI ArcMap 10.0.

Spearman's rank correlation. All statistical tests were performed using SPSS 13.0 statistical software (SPSS Inc. Chicago, Illinois, USA).

Dung collection and preparation

Microhistological analyses of dung – a non-invasive and cheap method – were performed to assess the diets. Plant epidermises are very robust and 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; Bartholott and Marthens, 1979).

Dung from both species was collected during the CDS throughout the study areas in the GMA (10 July–27 August 2010) and in KNP (27–6 September 2010). During the LRS the study area within KNP could not be accessed at all and the collection of dung in the GMA (5 May–7 May 2011) focussed on the area around PukuPan Lodge (for puku) and on the main access road (for impala) because of inundations. Collected dung was 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. It was feasible to differentiate between dung from male and female puku as animals were observed while defecating. Only dung of adult puku was taken. This approach was impossible for impala as they fled quiet rapidly when being approached to close and stopped too far away to allow a safe collection of dung. Thus, dung was collected from middens used by this species (Stuart and Stuart, 2000). Attention

was paid to take the freshest dung characterised by a green colour and moist consistency.

The procedure for dung preparation generally followed methods presented by Hooimeijer et al. (2005), Gutbrodt (2006), Suter et al. (2004) and de Jong et al. (1995). From each dry dung 5–7 g were ground, mixed with water, boiled for 70 min, soaked over night, processed in a household blender and transferred into 70% alcohol.

Under a microscope (Olympus BX41) at 200 times magnification, 100 fragments were examined for each sample. Only fragments with at least 4 visible epidermal cells were considered. Fragments were categorised according to their origin from monocots, cells arranged in rows, and dicots, cells arranged in a scattered, non-linear way. As fragmentation may differ between species during digestion (Holchek et al., 1982), counts of fragments are invalid as grasses may break into fragments differing in size (Stewart, 1967). Instead following Stewart (1967), the proportion of different grasses in the sample was estimated. The area of the fragments was measured in relative units via the scale in the microscope ocular.

Reference collection of grasses

In order to obtain a more detailed determination of the monocot fragments up to genus/species, I established a reference collection of the epidermal cell patterns from fresh grass occurring in the study areas (conf. Rduch, 2014). The microscopic images of the reference collection were compared with the fragments in

question. However, it is possible that some grass species were overlooked during the collection of grasses. The genera *Hyparrhenia* and *Andropogon* had to be lumped, even though *Andropogon* was not detected in the study areas (conf. Rduch, 2014). Both closely related species exhibit a very similar epidermal structure (see Bartholott and Marthens, 1979).

Analyses of diet characteristics and dietary overlap

The following analyses were carried out based on the proportions of the different plant taxa in the diets. While in monocots the proportion of each genus/species is included, dicots are considered as a whole. The diet breadth was calculated for each dung sample: first, it was calculated as Levins Index whose values increase with decreasing niche breadth (Colwell and Futuyma, 1971). Second, a standardised form B_{standard} was calculated. Here values range between 0, minimum diet breadth, and 1, maximum diet breadth (Phillips et al., 2007). Based on B_{standard} , differences in diet breadth were tested. The one-way ANOVA was used. The Kruskal–Wallis-test (KW-test) was used instead of the ANOVA, if the variables showed significant results in Levene's test of homogeneity of variance. Overlap of diets was calculated using the Pianka index (Pianka, 1974), one of the most widely used indices. It reaches values between 0, which means no overlap, and 1, which means total overlap of the compared diets. The mean values of the plant proportions from all dung samples from one region, season or sex (as given in Table 4) constitute the basis for the calculation of the Pianka Index. A Principal Component Analysis (PCA) was carried out to check for differences of the diets between species and between seasons. Here each dung sample was considered separately. The grass species *Cyperus*, *Hemarthria*, *Loudetia*, *Melinis*, *Oryza*, *Phragmites*, *Pogonarthria*, *Pennisetum*, *Setaria* and *Tristachya* were excluded as they were only represented in small amounts in the diets (conf. Table 4). During the LRS 2011, only two dung samples of male puku were found. These were excluded from the statistical evaluation of the data. Statistics and graphs were performed with SPSS 13.0 statistical software (SPSS Inc. Chicago, Illinois, USA).

Results

Data basis during distance sampling

A number of 146 sightings of puku and 102 sightings of impala was made. These sightings comprised 854 individuals of puku and 1129 individuals of impala.

Group sizes

Group sizes of puku ranged from 1 to 37 individuals (mean 5.83; SE 0.48). Groups of impala were larger including 1–75 individuals (mean 11.07; SE 1.42). There were no differences in group sizes between the different study areas for each antelope (puku: U -test: $Z = -0.140$, $p = 0.888$, $N = 145$; impala: U -test: $Z = -0.497$, $p = 0.619$, $N = 102$). The difference in group sizes was significant between species generally (U -test: $Z = -2.895$, $p = 0.004$, $N = 247$) and when considering the study areas separately (group sizes of puku vs. impala: in KNP: U -test: $Z = -2.046$, $p = 0.041$, $N = 134$; in GMA: U -test: $Z = -2.070$, $p = 0.038$, $N = 113$).

Group composition

Single adult males were common in both species (Table 1). Puku had more single females, groups of females and of breeding groups (groups comprising one male, one or more females and juveniles). Noticeable is the number of observations of 'other

groups' in impala which included males, females and juveniles in different numbers. In both species, there were more females than males (Table 1) and sex ratio was more pronounced in the GMAs. Juveniles were far less frequent in impala than in puku (Table 1). Two neonate puku were observed in the GMAs. Mixed groups of puku and impala were observed on 22 occasions, especially in areas where both species reached high densities. Mixed groups included 2–71 animals comprising 1–20 puku and 1–67 impala. There was no correlation between the number of puku and impala (Spearman's rank correlation: $r = -0.013$, $p = 0.955$, $N = 22$).

Estimations of population densities

Puku reached highest local population densities (110.64 animals/km², 100.58 animals/km²) along transects situated near the Kafue River (Table 2) characterised by a mixture of floodplain, burnt areas and riverine thickets. Along these transect lines, impala can also reach very high densities (60.84 animals/km², 108.91 animals/km²). Transect lines remote from Kafue River, but providing grassland areas had lower densities of puku (13.38 animals/km², 18.74 animals/km²); but impala densities were higher (32.61 animals/km², 68.84 animals/km²). Along transect lines near the Kafue River, but characterised mainly by thickets and scrublands puku were less abundant (21.41 animals/km²) than impala (32.61 animals/km²). Concerning habitat types, the density of puku was highest in grasslands (14.66 animals/km²), whereas impala were most abundant in intermediate habitats (18.06 animals/km²) (Table 3). Both species were least abundant in woodlands.

Dietary composition

In puku, the amount of monocots was very high, above 97%, throughout sexes, regions and seasons. Eleven grass taxa were found in the study areas (Table 4). While some grasses were consumed in high amounts (*Panicum* spp., *Hyparrhenia/Andropogon*-grasses, *Sporobolus* spp. and *Brachiaria* sp.), others were only observed on a few occasions. Sexes differed in the proportions of different grasses in their diets. But also the diets in the two study areas differed in the proportions of grass species. Differences are reflected by the results of the Pianka index (Table 5) and the PCA (Fig. 3). The impala's diet relied on browse during the CDS in both study areas, but on grazing during the LDS (Table 4). *Hyparrhenia/Andropogon*-grasses were very frequent followed by *Panicum* spp., *Sporobolus* spp., *Digitaria* sp. and *Brachiaria* sp.

Diet breadths

Generally, the diet breadths for both species were narrow, as values of B_{standard} rarely reached 0.30 (Table 4, Fig. 2). Impala had a narrower diet than puku. During the CDS, the diet breadths of puku in both GMA and in KNP were similar (one-way ANOVA: $df = 1$, F -value = 0.949, $p = 0.342$, $N = 22$) just as in impala (one-way ANOVA: $df = 1$, F -value = 3.565, $p = 0.88$, $N = 12$). Differences between species were significant for both GMAs (one-way ANOVA: $df = 2$, F -value = 18.544, $p < 0.001$, $N = 17$) and for KNP (KW-test: $df = 2$, $p = 0.031$, $N = 17$). During the LRS, the diet of puku females were narrower, those of impala were broader compared to the CDS (one-way ANOVA: $df = 1$, F -value = 5.967, $p = 0.035$, $N = 12$).

Dietary overlap

During the CDS, high values of the Pianka index mark a high intra-specific overlap between puku females and males (Table 5). Interspecific-overlap between puku and impala was low during the CDS but increased during the LRS. The plots resulting from the PCA

Table 1
Social organisation of puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) in Kafue National Park (KNP) and the Game Management Area (GMA) during the cool dry season 2010. Single individuals or groups of subadult males or juveniles were not observed.

	Puku <i>Kobus vardonii</i>		Impala <i>Aepyceros melampus</i>	
	KNP	GMA	KNP	GMA
Number of observations	78	67	56	46
Group composition [% of all observations]				
Males				
Single adult male	20.83	25.45	17.39	25.00
2 or more adult males	9.72	0	23.91	13.89
Adult and subadult males (2 or more)	4.17	1.82	0	2.78
1 adult male and 1 or more juv	5.56	1.82	0	0
Females				
Single adult female	2.78	5.45	0	2.78
Single adult female + 1 juv	1.39	0	0	0
1 adult female and 2 or more juv	2.78	1.82	0	0
2 or more females (+juv)	13.89	34.55	13.04	8.33
Pairs				
Pair: adult male + adult females	5.56	0	0	0
Pair: adult male + adult females + juv	0	1.82	0	0
Breeding groups				
1 adult male and 2 or more females +juv	26.39	23.64	17.39	19.44
Others				
Other group compositions	6.94	3.64	28.26	27.78
Amount of all groups not to be classified	7.69	17.91	17.86	21.74
Population structure				
Ratio				
Females: all males	1.52	4.12	2.01	3.38
Females: adult males	1.36	6.35	2.31	3.83
Females: juveniles and neonates	5.24	3.31	0.03	0.05
Amount of unclassified individuals [% from all observed individuals]	2.29	10.47	12.07	29.65

Table 2
Local estimated population densities of puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) along the transect lines during the cool dry season 2010. Numbers of the lines refer to Fig. 1. D%CV (% coefficient of variation of D) is 10.85 for puku and 16.06 for impala. E(S) (expected cluster size [animals]) is 6.10 for puku and 11.02 for impala, E(S) %CV (% coefficient of variation of expected cluster size) is 8.54 for puku and 12.79 for impala, ER %CV (% coefficient of variation of ER) is 0 for both. These values apply through all lines.

No. of transect	Main habitats	Puku (<i>Kobus vardonii</i>)		Impala (<i>Aepyceros melampus</i>)	
		D	ER	D	ER
Transect lines in the Game Management Area					
1	Grasslands, riverine thickets, burnt areas	110.64	13.33	60.84	5.42
2	Open woodland, thickets, scrubland	17.17	2.07	30.98	2.76
3	Miombo, small grassland areas	30.17	3.64	10.21	0.91
4	Miombo	0	0	2.87	0.26
5	Miombo	0	0	4.88	0.43
6	Thickets, scrublands	21.41	2.58	32.61	2.90
7	Miombo, one patch of grassland	8.03	0.97	3.62	0.32
8	Grassland, open woodlands	13.38	1.61	32.61	2.90
9	Miombo	0	0	7.49	0.67
Transect lines in Kafue National Park					
10	Grassland (mostly burnt)	18.74	2.26	68.84	6.13
11	Grasslands, riverine thickets, burnt areas	100.58	12.12	108.91	9.70
12	Grasslands, open woodlands	60.64	7.31	8.64	0.77
13	Miombo	6.92	0.83	9.36	0.83

Abbreviations: D = estimate of population density [animals/km²]; ER = encounter rate [number of observed objects/total length of transect lines].

Table 3
Estimated population densities of puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) in different habitat types during the cool dry season 2010 combined for both study areas.

	Habitat type	D	D %CV	E(S)	E(S) %CV	ER	ER %CV
Puku <i>Kobus vardonii</i>	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
Impala <i>Aepyceros melampus</i>	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

Abbreviations: D: estimate of population density [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.

(Fig. 3, Table 6) are similar for the GMA and KNP for the CDS. Diets of impala were different from those of the puku due to low values of component 1 resulting from the high percentage of dicots. The

diets of puku males and females overlapped in the two regions. During the LRS, the situation changed. Particularly impala shifted their diet.

Table 4
Diet composition and diet characteristics of puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) in Kafue National Park (KNP) and the Game Management Area (GMA) during 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.

Antelope species	Puku (<i>Kobus vardonii</i>)												Impala (<i>Aepyceros melampus</i>)					
	KNP				GMA				KNP				GMA					
	2010				2011				2011				2010		2011			
	Cool dry season				Cool dry season				Late rainy season				Cool dry season		Late rainy season			
Sex	Females		Males		Females		Males		Females		Males		Unknown		Unknown		Unknown	
	%	SE	%	SE	%	SE	%	SE	%	SE	%	SE	%	SE	%	SE	%	SE
Dicots	1.57	0.67	2.11	1.00	2.49	0.73	2.35	0.87	0.86	0.43	0		67.60	4.22	76.04	4.55	17.07	1.66
Total monocots	98.10	0.61	97.65	1.03	97.27	0.68	97.17	1.11	98.99	0.56	100.00	0.00	32.24	4.25	23.57	4.72	82.44	1.78
<i>Brachiaria</i> sp.	0.93	0.50	6.48	2.07	5.44	1.80	3.55	1.69	8.03	2.89	13.12	0.94	0.98	0.98	0.20	0.20	3.38	1.26
<i>Cynodon</i> sp.	0.53	0.37	1.19	0.84	0.46	0.36	0		0		0.82	0.82	0		0		0.97	0.68
<i>Digitaria</i> sp.	1.02	0.48	1.73	0.95	0.53	0.34	1.03	0.65	2.12	1.25	2.81	2.81	0.19	0.12	0		3.66	1.73
<i>Eragrostis</i> spp.	6.28	2.34	4.35	1.19	4.30	2.39	7.39	3.31	3.65	1.57	1.68	0.88	0.27	0.27	1.03	0.49	1.23	0.79
<i>Hemarthria altissima</i>	0		0		0		0		0		0		0		0		0	
<i>Hyparrhenia/Anthropogon</i> spp.	9.83	2.82	21.30	3.43	17.10	2.21	20.85	1.14	11.70	2.40	1.70	0.78	6.79	2.87	3.33	1.71	28.57	4.58
<i>Loudetia</i> sp.	0		0		0.23	0.23	0		0		0		0		0		0	
<i>Melinis nerviglumis</i>	0		0		0		0		0		0		0		0		0	
<i>Oryza</i> sp.	0		0		0		0		0		0		0		0		0	
<i>Panicum</i> spp.	14.67	3.19	21.54	6.12	32.36	2.59	29.05	6.06	45.22	3.76	40.35	25.55	9.56	2.19	7.48	2.80	20.73	5.06
<i>Pennisetum</i> sp.	0		0		0		0		0		0		0		0		0	
<i>Phragmites australis</i>	0.28	0.28	0		0		0		0		0		0		0		0	
<i>Pogonarthria</i> sp.	1.22	0.79	0		0.57	0.57	0		0		0		0		0.85	0.85	0	
<i>Setaria</i> spp.	0		0		0		0		0		0.57	0.57	0		0		0	
<i>Sporobolus</i> spp.	28.11	9.12	17.15	3.22	5.53	2.70	8.33	5.43	6.09	2.22	0.76	0.76	6.84	2.96	1.52	0.61	4.05	2.32
<i>Tristachya</i> sp.	0		0		0		0		0		0		0		0		0	
<i>Cyperus papyrus</i>	0		0		0		0		0		0		0		0		0	
Undetermined monocots	35.22	3.25	23.91	1.73	30.75	3.61	26.97	1.90	22.19	2.41	38.18	19.88	7.62	2.01	9.15	1.84	19.84	4.35
Undetermined plant-fragment	0.33	0.33	0.24	0.17	0.25	0.16	0.48	0.48	0.14	0.14	0		0.15	0.10	0.39	0.25	0.50	0.17
Mean number of food items per sample (food items are grass species and dicots as a whole)	7.00	0.32	6.50	0.56	6.50	0.56	5.80	0.37	0.21	0.52	6.00	2.00	4.17	0.40	4.50	0.22	6.17	0.48
Diet breadth (Levin's index)	3.20	0.59	3.78	0.39	3.19	0.28	3.09	0.27	2.55	0.21	2.84	1.37	1.79	0.13	1.43	0.13	3.66	0.40
Diet breadth (B_{standard})	0.13	0.03	0.16	0.02	0.13	0.02	0.12	0.02	0.09	0.01	0.11	0.08	0.05	0.01	0.03	0.01	0.16	0.02
Number of dung samples	5	0	6	0	6	0	5	0	6	0	2	0	6	0	6	0	6	0
Number of fragments	500	0	600	0	600	0	500	0	600	0	200	0	600	0	600	0	600	0

Table 5

The dietary overlap between puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) in Kafue National Park (KNP) and in the Game Management Area (GMAs) at different times of the year. The degree of overlap/similarity is higher when the Pianka Index value is closer to 1.0. Regular: overlap during the cool dry season 2010, Italics: overlap during the late rainy season 2011, shaded in grey: intraspecific comparison between the cool dry season and the late rainy season, –: no dung samples available for evaluation. *: overlap between male puku during the late rainy season and other groups was not assessed due to the low number of samples.

		Puku (<i>Kobus vardonii</i>)				Impala (<i>Aepyceros melampus</i>)	
		Females—GMA	Males—GMA	Females—KNP	Males—KNP	GMA	KNP
Puku (<i>Kobus vardonii</i>)	Females—GMA	0.97	0.98	0.65	0.90	0.17	0.25
	Males—GMA	*	0.79	0.72	0.94	0.17	0.25
	Females—KNP	–	–	–	0.82	0.12	0.22
	Males—KNP	–	–	–	–	0.15	0.25
Impala (<i>Aepyceros melampus</i>)	GMA	<i>0.71</i>	*	–	–	0.51	0.99
	KNP	–	–	–	–	–	–

Table 6

Rotated component matrix as given in SPSS 13.0. and total variance explained by the component. Highest absolute values of the components are bold.

Amount of plant group in %	Component	
	1	2
Dicotyl plants	–0.834	–0.359
<i>Brachiaria</i> sp.	0.683	
<i>Cynodon</i> sp.		0.825
<i>Digitaria</i> sp.	0.229	0.656
<i>Eragrostis</i> ssp.	0.559	–0.218
<i>Hyparrhenia/Andropogon</i> grasses	0.506	0.364
<i>Panicum</i> ssp.	0.746	–0.296
<i>Sporobolus</i> ssp.	–0.173	0.538
% of variance explained (rotation sum of squared loadings)	29.667	22.473

Discussion

Group sizes

Group sizes are related to population densities, especially when the antelopes live in non-permanent groups (Wirtz and Lörcher, 1983). Impala groups recorded tend to be larger than those of puku which might be related to the high density of impala in intermediate habitats. In Kasanka National Park, situated in the north of the central province of Zambia, the population density of puku reached more than 36 animals/km² in grassland areas (Rduch, 2015). This population density is more than twice compared to the population density of 14.66 animals/km² in grasslands KNP estimated by this study. Further, the mean group size of puku in Kasanka National Park during the cool dry season was 10.47 animals which is twice as big than in and around KNP during this study. This again shows the interrelation between group size and population density. However, differences in group sizes between puku and impala observed here might also be due to differences social organisation, ecology or predation pressure.

Group composition and seasonality

Social organisation of impala during the rut consists of well-defined groups: territorial adult males, bachelor groups and breeding herds. These groups often merge when not in rut (Fritz and Bourgairel, 2013). The high amount of 'other group compositions' in impala in the present study is considerable and reflects these merged groups. This leads to the conclusion that our line transect survey during July to September does not cover the rut but probably indicates a period of transition (see also below). Puku males defend resource based territories which are defended year round (Rosser, 1989, 1992). The number of male groups was low in the GMA. Male groups were more present in KNP, in numbers comparable to other studies (Dipotso and Skarpe, 2006; de Vos and Dowset, 1964). Single males, probably owners of territories, are generally very common (conf. Dipotso and Skarpe, 2006; Child and

von Richter, 1969; de Vos and Dowset, 1964). In KNP single males were rare, but probably merged into the more frequent breeding groups that made out 26.39% of the observed groups. Female groups, accompanied or not by young puku or an adult male, were very common. In the GMA this was the most frequent group composition of puku representing 41.82% of the observations.

Sex ratios of puku and impala are biased towards females (e.g. Child and von Richter, 1969; Dipotso and Skarpe, 2006; de Vos and Dowset, 1964; Dasmann and Mossman, 1962; Jarman and Jarman, 1973). However, in both antelopes there were even fewer males in the GMA than in KNP pointing back to the low numbers of male groups in puku. Low numbers of males might be a result of (trophy) hunting permitted in the GMAs.

Most of the puku in Luangwa Valley are born from January to May during the rainy season, but births can take place year-round (Rosser, 1989). This may also be the case with the puku in KNP and the GMA: only two neonates were observed. Juvenile puku were seen in greater numbers indicating a period of birth nearer to the time of data collection. In contrast to puku, impala are seasonal breeders. A short breeding period from October to November is reported for Luangwa Valley (Ansell, 1960). This seems also to apply for KNP: young impala were rarely seen during the dry season but neonate impala were seen in November (V. Rduch, pers. obs.). Based on a gestation period of 27–28 weeks (Fritz and Bourgairel, 2013) the rut of impala might take place around April.

Since both species occur in high densities at the same places the formation of mixed groups by coincidence is likely—also reflected by the variable number of both species within these groups. However, interspecific association can facilitate grazing and reduce predation risk (McNaughton, 1988).

Habitat use

The observed use of grasslands including floodplains or dambos by puku agrees with several studies (de Vos and Dowset, 1964; Jenkins et al., 2002; Dipotso and Skarpe, 2006; Child and von Richter, 1969; O'shaughnessy et al., 2014; Rduch, 2015). Impala

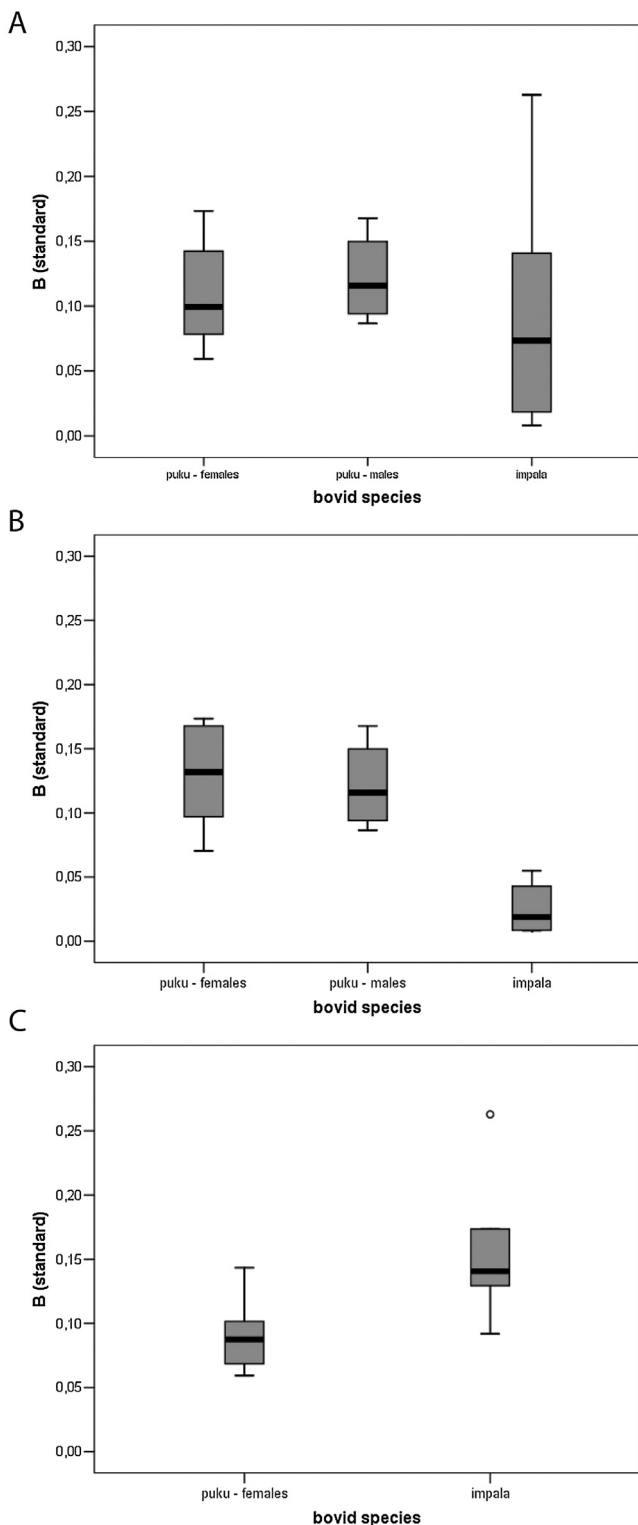


Fig. 2. Boxplots showing the diet breadth (B_{standard}) of puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) during the cool dry season 2010 in Kafue National Park (A) and in the Game Management Area (B) and during the late rainy season 2011 in the Game Management Area (C).

use grasslands after a bushfire. They are attracted by newly sprouting grasses (Wronski, 2003) and in this case they appear also in grasslands remote from the Kafue River where no or only few puku occur. However, at low densities puku occurred in patches of grass-

lands within woodlands not too far away from rivers, as previously reported (de Vos and Dowset, 1964).

Intermediate habitats, open woodlands, and the edge of woodlands, are perfect habitat for impala as reflected by their high density in these areas (Estes, 1991). They represent good feeding grounds, especially for browse, their important food during the dry season (Dunham, 1980; this study).

Impala used woodlands slightly more than puku, probably due to their browsing activities. Woodlands were only marginally used by puku. The use of miombo woodlands by puku should be studied in more detail. During the CDS, puku generally did not occur in miombo woodlands far from their main habitats. However, during the wet season habitat switches to the miombo were observed in Tanzania (Jenkins et al., 2002). Unfortunately, due to bad road conditions during the LRS, although planned, another data collection along the transects was impossible.

Diets

This is the first time that the diet of puku was evaluated in the miombo ecoregion. The puku could be confirmed as a grazing antelope feeding almost exclusively on monocots during the course of this study. *Hyparrhenia/Andropogon*-grasses are typical grasses of the miombo woodlands (Frost, 1996), not previously known to be part of the puku's diet, but consumed in high amounts here. In contrast to other studies (O'shaughnessey et al., 2014; Child and von Richter, 1969; Rosser, 1992) the amounts of *Eragrostis*, *Cynodon* and *Digitaria* in the puku's diet were small, whereas the amount of *Sporobolus* was high. Dietary differences between males and females might be, among others, a result of territorial behaviour that delimits the range of the feeding sites: females can find good feeding places across male territories, while territorial males are confined to their territories (Rosser, 1992). The diet of non-territorial males might further differ from territorial males and females. Future dung analyses taking into account male territorial status might provide interesting insights into the autecology of puku. Proportions of grass species utilised by puku differ between the two study areas, which is most visible for *Hyparrhenia/Anthropogon* spp., *Panicum* spp. and *Sporobolus* spp. This speaks against extended roaming activities in puku but probably indicates an opportunistic choice of grasses.

Impala are known as browser-grazer intermediates (Gagnon and Chew, 2000) with variable amounts of both monocots and dicots in their diet. The amounts vary between seasons (Fritz and Bourgarel 2013) and sex (van Rooyen and Skinner, 1989; Sponheimer et al., 2003). During the dry season they prefer fresh grasses growing after bushfires (Wronski, 2003) but also rely on browse as shown by this study. This shift to dicots is related to better food quality (van Rooyen, 1992; Dunham, 1980). The main grass genera in the impala's diet in this study were: *Panicum*, *Hyparrhenia/Andopogon* and *Sporobolus*. During the LRS the grasses *Digitaria* and *Brachiaria* complete this list. *Pogonarthria* and *Melinis*, although in small amounts only, were for the first time recorded as food plants of impala. Unlike in Krueger National Park, South Africa, (Sponheimer et al., 2003) impala showed a similar diet in the two study areas in and around KNP due to the similar environment. Impala roam to a much higher degree than puku (Rduch, 2014), which might compensate small-scale differences in available food plants.

Puku and impala showed relatively narrow dietary niches: they feed on few species of grasses indicating that grazing antelopes are quite choosy. Ignoring the exact species composition of browse, impala seem to confirm the idea of the classical idea of 'food-refuge' during the dry season (Sinclair, 1983). They reduce competition with puku during this time of the year. In contrast, puku showed their largest diet breadth in the CDS which seems uncommon. This

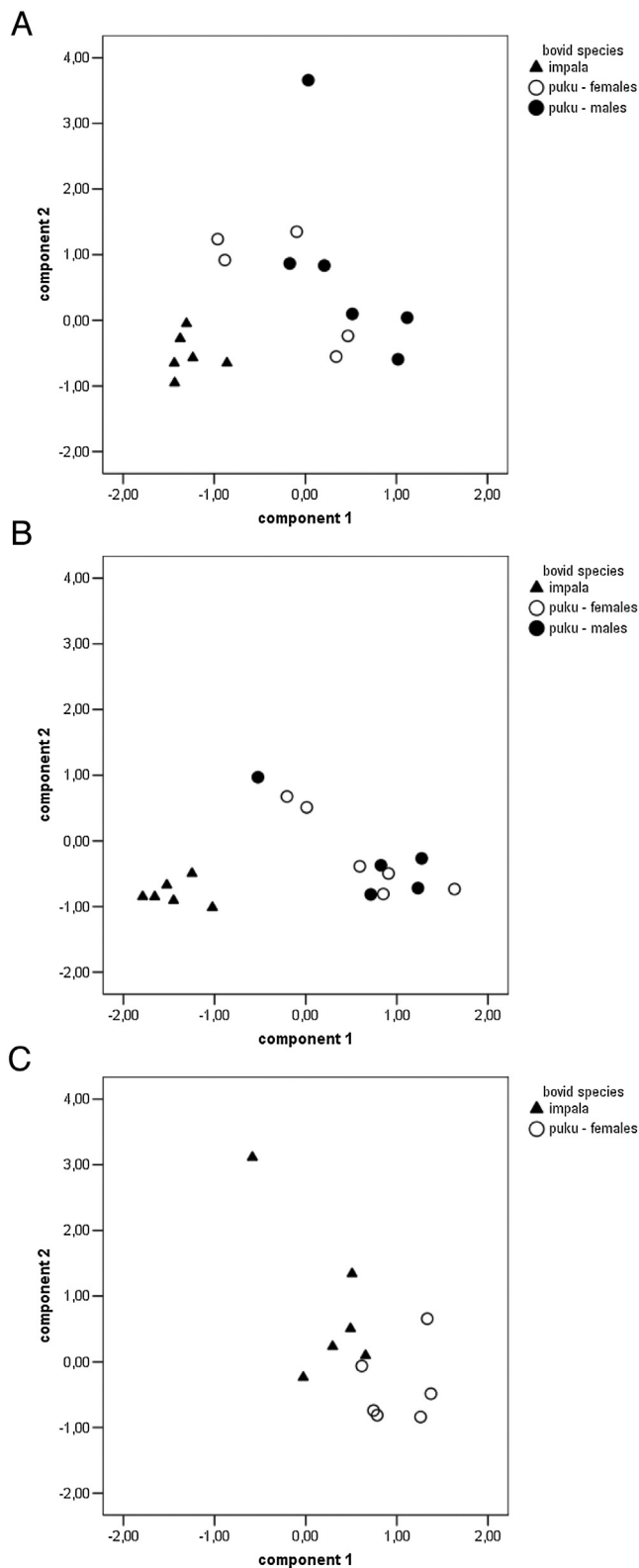


Fig. 3. Scatterplots based on the results of the PCA showing the dietary overlap between puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) during the cool dry season 2010 in Kafue National Park (A) and the Game Management Area (B) and during the late rainy 2011 season in the Game Management Area (C).

raises the question if inundated areas during and after the rains restrict the puku's food choice. More observations throughout the course of a year are needed to confirm this.

Niche overlap

A large overlap in habitat use, as observed for puku and impala during the CDS in an around KNP, could well be a sign of a non-problematic coexistence between individuals of two species (de Boer and Prins, 1990). And indeed during this time of the year, they use different food resources. The Pianka index values were low in both KNP and GMAs and the results of the PCA for diets in the sub-regions showed impala and puku well-separated from each other. This was different in the LRS: Pianka index values increase between puku and impala. This degree of higher dietary overlap was underlined by the results of the PCA. However, a slight overlap still exists during the CDS. Regarding grass species, puku and impala overlap especially concerning *Panicum* spp., which maintains its nutritive value during the dry season (Jungius, 1971). Overlap in *Hyparrhenia/Andropogon*-grasses might be due to the abundance of this plant group in the study areas. The middens of impala are used mainly by (territorial) males (Stuart and Stuart, 2000). Males are reported to have fewer amounts of dicots in their diet than females (van Rooyen and Skinner, 1989; Sponheimer et al., 2003). If this is true for the study region the actual dietary overlap between puku and impala might be even less marked. The methods used for this study did not allow differentiating between growth stage or different parts of the plants taken, nor is it possible to assess the nutritional value of the ingested food plants, which all probably affects plant choice.

Autecological needs of both species seem to be the driver for the spatial overlap during the CDS. Impala need to drink during the dry season (Jarman and Sinclair, 1979), which makes them to stay around perennial water sources. Puku meet their dietary requirements in grasslands near water. The factors that cause puku to neglect grasslands remote from the river require further studies. Data collection during and after the rains were impossible during this study. Additional studies should provide year-round information on the area of occurrence of these antelopes.

Conclusion

Puku and impala make up only a fraction of the bovid community in Zambia. Other antelopes seem less abundant, but might be more numerous than revealed by line transect sampling e.g. bushbuck (*Tragelaphus scriptus*) or bush duiker (*Sylvicapra grimmia*) (Rduch, 2014). It is very possible that they exhibit a certain dietary overlap with puku, e.g. waterbuck (*Kobus ellipsiprymnus*), or impala, e.g. bushbuck (*T. scriptus*) (Gagnon and Chew, 2000). Further, other members of the ecosystem also compete with bovines or restrict the available resources including invertebrates (Sinclair, 1979) or elephants (Fritz et al., 2002).

This study is one of few that investigated the underexplored but magnificent Zambian wildlife. Focussing on the autecology of puku and impala and their synecology in Zambia, it provided important information for conservations purpose and for a better understanding of the ecosystem. It gave actual information on populations and revealed slight differences in population structure between KNP and GMA for both species—a possible impact of hunting in the GMA. Puku and impala overlap spatially during the CDS, and overlap along the transect lines seems considerable. At a closer look, puku are more abundant in grasslands while impala reach higher densities in woody areas. In contrast to spatial overlap, dietary overlap between puku and impala, was low during the CDS. Each species appears to occupy a separate food niche. As opposed to this, the two antelope species showed an increased dietary overlap during the LRS, when food seems abundant and when impala switched its diet.

This study shall only be a first step. Information on puku and impala distribution and ecology during and shortly after the rainy

season is equally important and should be the subject of future research. Resource partitioning during specific times of the year may be one factor that explains the high numbers and the sympatric occurrence of these two co-existing antelope species that is characteristic for KNP and other protected areas of Zambia.

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