Seasonal habitat and diet partitioning between two sympatric bovid species in Pendjari Biosphere Reserve (northern Benin): waterbuck and western kob

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Received 15 January 2013. Accepted 26 August 2013

Niche theory suggests differential use of shared resources facilitates coexistence of species in a community. In this study we used the faecal stable isotope analysis with observations along transect lines perpendicular to the Pendjari River. This was to examine seasonal habitat features and diet partitioning between two sympatric bovid species waterbuck (*Kobus ellipsiprymnus*) and western kob (*Kobus kob*) in the Pendjari Biosphere Reserve. In support of niche partition hypothesis, diets of western kob and waterbuck diverged significantly along both faecal selection axes (δ^{13}C and δ^{15}N) during the resource-limited period of the dry season as opposed to wet season when there is resource abundance. Western kob and waterbuck resource partitioning does not occur only on the basis of diet segregation but also some habitat variables play an important role in the coexisting system. Findings support the niche partition hypothesis, where morphologically, ecologically and closely related sympatric species segregate at least in one of the niche dimensions to allow coexistence. The two bovid species were observed to diverge largely along distance to water source gradient. The results provided empirical evidence that habitat features acts as an additional dimension over which herbivores partition resources.

Key words: **niche overlap, habitat selection, coexistence.**

INTRODUCTION

Theoretically, two species under the resource-utilization niche concept (Schoener 2009), cannot occupy the same *n*-dimensional ecological niche without exerting strong competition on each other, since this would result in potential local extinction of one of the species. Thus, co-occurring species might tend to show differentiation in at least one of the main niche dimensions in order to avoid competition (Stewart *et al.* 2002). In African savanna ecosystems, interspecific competition is more likely to occur during the dry season when plants are dormant and forage of adequate quality becomes depleted (Arsenault & Owen-Smith 2002). Despite the acknowledgement of these coexisting African ungulate communities, few studies have gone beyond recording how differentiation in species preference to some habitat characteristics and environmental factors can interact to support the resource partitioning mechanism. Questions such as 'To what extent do coexisting sympatric large herbivores differ in their habitat and environmental resource use?' and 'how habitat selection (the use of habitat variables relative to availability) of each species is influenced by the presence of the other sympatric species?' remain unanswered. In such situations understanding habitat features and isotopic diet partitioning in coexistence mechanisms between ecologically similar herbivorous mammals will provide some valuable information in conservation management. Resource partitioning within large herbivore communities has been studied mostly in East and South African ecosystems, where their species richness is greatest (Hibert *et al.* 2010), but there is little information on the niche separation amongst wild ungulates of West Africa where past and present human pressures and conservation management together with climate conditions are quite specific (Kassa *et al.* 2007). Wildlife managers in West Africa rely on information generated from studies in the south and east African regions, which may not necessar-

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ily be applicable to the semi-arid ecosystems of West Africa with a unique assemblage of large herbivores. Interspecific interactions among sympatric ungulates with the same trophic level are of fundamental interest in that context because competition for resources is likely.

Numerous methods exist to delineate dietary patterns of wild animal populations, all with certain strengths and limitations. Stable carbon isotope ecology is a tool well suited to multispecies studies of feeding behaviour, and shifts in food web ecology in response to environmental heterogeneity across space and time. This technique is based on the fact that $^{13}C/^{12}C$ ratios in consumer tissues reflect the isotope signature of the sources from which they are derived; in African savannas, herbivore $^{13}C/^{12}C$ ratios reflect proportions of C3 (trees, shrubs, and forbs) *versus* C4 (grass) biomass intake (Cerling & Harris 1999). Experimental and field studies have shown that faecal $^{13}C/^{12}C$ ratios, despite representing only undigested plant remains, are highly consistent with diet (Sponheimer *et al.* 2003) even recording short-term shifts in the isotopic composition of available vegetation (Codron & Codron 2008). Animal faeces have a relatively short turnover time (several days) and are hence useful for reconstructing diet over subtle spatial and temporal scales. Stable nitrogen isotope ratios ($^{15}N/^{14}N$) in consumers are related to dietary protein levels, increasing upwards through food chains (Sponheimer *et al.* 2003; Robbins *et al.* 2005). Analysis of both isotopes simultaneously offers insights into more complex interactions and trophic differentiation (Codron & Codron 2008).

The waterbuck (*K. ellipsiprymnus*) and the western kob (*K. kob*) investigated in this study belong to the family Bovidae, subfamily Reduncinae. There are closely related sympatric savanna grazers, foraging not far away from water sources (Kingdon 1982). They tend to concentrate around permanent waterholes or rivers during the dry season, when most water sources have dried up, offering a unique natural opportunity for testing coexistence mechanisms. Waterbuck and western kob have similar anti-predator habitat requirements, as all of them prefer the open grassland (Fisher & Linsenmair 2002, 2006; Gutbrodt 2006; Kassa *et al.* 2007). These species are among the most abundant wild ungulate in the Pendjari Biosphere Reserve and mostly avoid the hunting zones (Sinsin *et al.* 2008). Previous observations on the habitat use by these species also revealed that they are similar in the use of habitat variables such as grass and canopy cover, slope angle and post fire regrowth (Dörgeloh 2006; Kassa *et al.* 2007; Klop & van Goethem 2008; Averbeck *et al.* 2009; Augustine 2010). With reference to the niche partition hypothesis, we predict that *K. elipsprymnus* and *K. kob* will segregate in the use of at least one of the niche dimensions (trophic and/or habitat features) in order to diminish potential competition. Thereby, the objectives of our study were: (i) to assess whether stable isotope data recorded seasonal patterns of diet shifting, (ii) to investigate seasonal patterns of microhabitat selection for both bovid species; and (iii) to examine whether diet separation along the C and/or N isotope niche axes and how differential microhabitat partitioning act in facilitating coexistence within season.

METHODS

Study area

The Pendjari Biosphere Reserve (PBR) is located in northwestern Benin (10°30′ to 11°30′N; 0°50′ to 2°00′E (Fig. 1). It was declared a Game Reserve in 1954 and upgraded to the National Park of Pendjari (NPP) in 1961. Nowadays, it comprises a strictly protected core area (named 'National Park' covering 2660 km²) and two adjacent hunting zones named 'Konkombri' and 'Pendjari', which are on the eastern and southwestern sides of the National park, respectively (together covering 1971 km²).

The PBR is limited by the foothills of the Atacora massif in the east and by the river Pendjari in the north and the west. The reserve is under a tropical climate characterized by a seven-month dry season during which game can be hunted by tourists; average annual rainfall of 1000 mm spread from end May to early October. The mean annual temperature is 27°C. During the rainy season numerous small ponds in the centre of the national park are refilled with water, in the vicinity of the large ones. During the dry season, the ponds attract a variety of animal groups, especially large mammals in search of water. The vegetation is made up of a mosaic of grasses, shrubs, trees and woodland savannas (Sokpon *et al.* 2001) which are burnt every year, earlier in the dry season to provide fresh and green pasture to herbivores that dominate the reserve.

Data collection

Fresh faecal pellets were collected during dry and wet season to generate diet profiles of water-

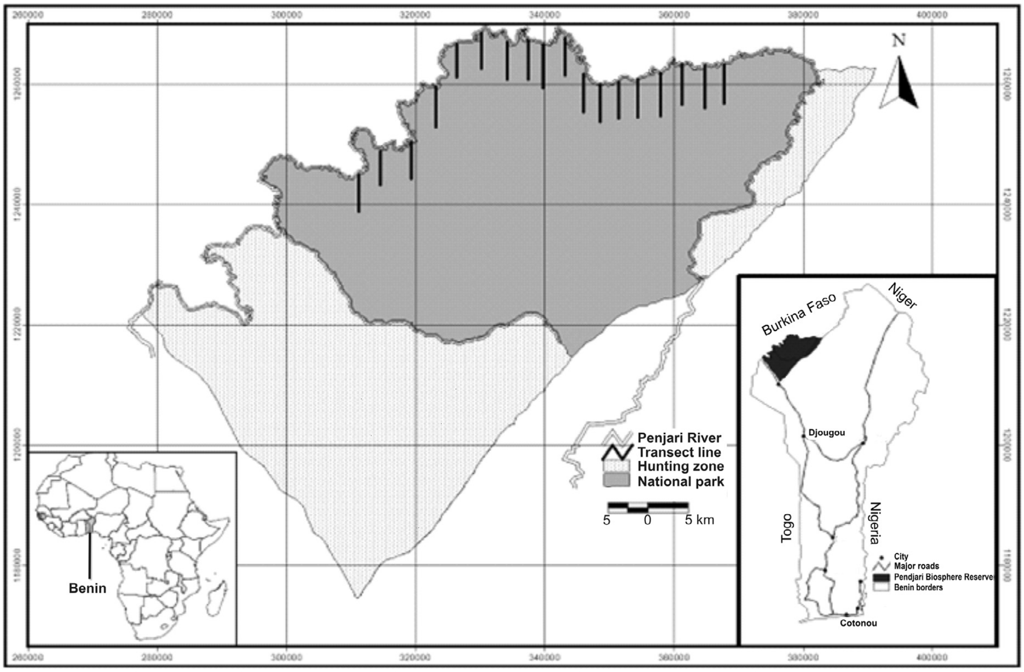

Fig. 1. Map of Pendjari Biosphere Reserve showing the line transects and the location of the reserve in Benin.

buck (*K. ellipsiprymnus*) and western kob (*K. kob*), and to assess the diet overlap between seasons. To prevent assigning pellets mistakenly to a different species than the one intended to, we collected the faecal samples from bedding sites by waiting for the animals to get up and move away. In the dry season we collected in total 16 samples for waterbuck and 20 for western kob, while in the wet season only 10 and nine samples were collected for western kob and waterbuck, respectively. To assess habitat use of western kob and waterbuck at a local scale, data were collected along line transects from January to March 2011 (dry season) and from May to July 2011 (wet season) in PBR. A total of 18 line transects, 5 km in length, were set perpendicularly to the Pendjari river (Fig. 1). All transects were walked through at 15-day intervals, each transect being sampled three times in the dry and rainy seasons. When a group of animals was sighted we recorded the species, the number of individuals, the GPS location, the type of habitat and some additional habitat variables such as: the grass cover, the canopy cover and fire within a 30 m × 30 m sampling quadrat. In that prospect a total of 136 sampling quadrats was installed along the transect line. We selected habitat variables that could potentially influence distribution of bovid species in arid and semi-arid ecosystems based on previous studies (Dörgeloh 2006; Klop & van Goethem 2008; Averbeck *et al*. 2009; Augustine 2010). Fire as a factor is used to describe whether or not the site where animals were observed had been recently burned (coded as (0) for an unburned site and (1) for burned). Grass and canopy cover were estimated visually describing the percentage of grass and canopy cover in 30 m × 30 m sampling quadrats. The species GPS location data were used to generate the distance to the closest water body using GIS. Availability of the same habitat variables were sampled along each transect at every 200 m, also within 30 m × 30 m sampling quadrats. The landscape slope was measured in degrees with a Suunto clinometer (PM-5/1520 D).

Data analysis

Dried, homogenized faeces samples were analyzed for $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios by stable light isotope ratio mass spectrometry (Codron *et al.* 2007; Codron & Codron 2008), and results expressed in the delta (δ) notation in parts per mil (‰) relative to the Vienna Pee Dee Belemnite (VPDB), and atmospheric N_2 standards, respectively. Standard deviations of repeated measurements of laboratory standards were less than 0.15‰ for $\delta^{13}C$ and 0.1‰ for $\delta^{15}N$. These analyses also provided percentage of nitrogen (%N, by weight) in each sample, an established proxy for dietary crude protein content (diet quality) in mammalian herbivores (Grant *et al*. 2000). On inspection, data for species such as buffalo are similar to values reported from Kruger National Park based on wet chemistry (Grant *et al*. 2000), implying that this method is partly comparable with traditional measures of faecal N content.

The extent of diet separation along the C and/or N isotope niche axis was determined by testing for significant differences between waterbuck and kob diet in each season. A nonparametric test, the Mann-Whitney *U*-test, was used, because the dataset did not meet the assumptions of parametric statistics (Sokal & Rohlf 1981) and sample sizes for both waterbuck and kob species. Differences in the isotope composition of western kob and waterbuck faeces are also tested using 95% confidence ellipse bands around bivariate scatter plots to separate groups of data. For assessing differences in habitat use by the three species at a local scale we first identified the most important variables in choice of habitat by each species at a local scale. Regarding the latter, generalized linear model (GLM) was performed by considering used (by all species) and unused (but available) habitats as a binary response and distance to water source, slope angle, grass cover, canopy cover and fire signals predictor variables. Subsequently, we used Akaike's information criterion for small samples (AIC) and their differences (Δ) to select the most parsimonious model with fewest variables (the lower the Δ, the more parsimonious the model) that explain most of the variation in the data. All models with AIC differences (Δ) less than two are considered useful in explaining the variability in the data according to Burnham & Anderson (1998). Subsequently, we performed discriminant function analysis (DFA) to determine whether the areas used by western kob, waterbuck and the unused but available ones could be discriminated on the basis of the most crucial variables identified. We tested for significant differences between these areas on the canonical scores of the first two functions or axes with a one-way ANOVA followed by post hoc Fisher's LSD test. Significant differences between two pair of ungulate species habitat use were also assessed by using *t*-tests for independent samples. The multivariate Hotelling's T^2 test was used to check for differences taking all the variables together and thus taking into account the relationship between them. All analyses were performed in the statistical program R (R Development Core Team 2012). The niche (habitat) overlap between the species was determined, using Pianka's index (Pianka 1986).

$$O_{jk} = \frac{\sum P_{ij} \cdot P_{ik}}{\sqrt{\sum P_{ij}^2 \cdot \sum P_{ik}^2}} \, ,$$

where O_{jk} is the measure of overlap between habitat variables j and k, and P_{ij} and P_{ik} are the proportions of habitat variables i in the habitat use of species j and k, respectively. Overlap is complete when $O_{jk} = 1$, and absent when $O_{jk} = 0$.

RESULTS

Patterns of diet variation between species and within season

The isotope stable analysis of faeces indicated a difference in diet composition between the two sympatric species (Fig. 2). We found a significant statistical difference in mean faecal δ^{13}C between the two species in dry season (Mann-Whitney *U*-test: $w = 316$, $P < 0.001$), with a higher value for western kob (–14.78‰ ± 0.94 S.D.) than that of waterbuck (–20.07‰ ± 2.04 S.D.). A difference in δ^{15}N values were found in mean faecal δ^{15}N (Mann-Whitney *U*-test: $w = 24$, $P < 0.001$). This was lower in the western kob diet (3.63‰ ± 0.93 S.D.) than that of waterbuck (5.99 ‰ ± 1.28 S.D.). No significant difference was found in wet season between the waterbuck and western kob mean faecal δ^{13}C (Mann-Whitney *U*-test: $w = 27$, $P = 0.1529$) and δ^{15}N (Mann-Whitney *U*-test: $w = 37$, $P = 0.549$), respectively. However, despite considerable interspecific overlap, δ^{13}C data for waterbuck extend across a wider range (–18.75 to –12.97‰) than those of western kob (–13.32 to –16.93‰). Western kob was shown to be constant in mean faecal δ^{13}C (Mann-Whitney *U*-test: $w = 49.5$, P-value $= 0.06$) and δ^{15}N ($W = 100.5$, $P = 0.64$) seasonally while a significant seasonal shifting along the C and/or N isotope niche axis was noticed in waterbuck (Mann-Whitney *U*-test: $w = 9$, $P = 0.0002$ and $W = 146$, $P = 0.0001$, respectively for faecal δ^{13}C and δ^{15}N).

Habitat variable predicting species distribution

In total 54 observations were made on waterbuck and 82 on western kob during the dry season. The average size of western kob groups during the

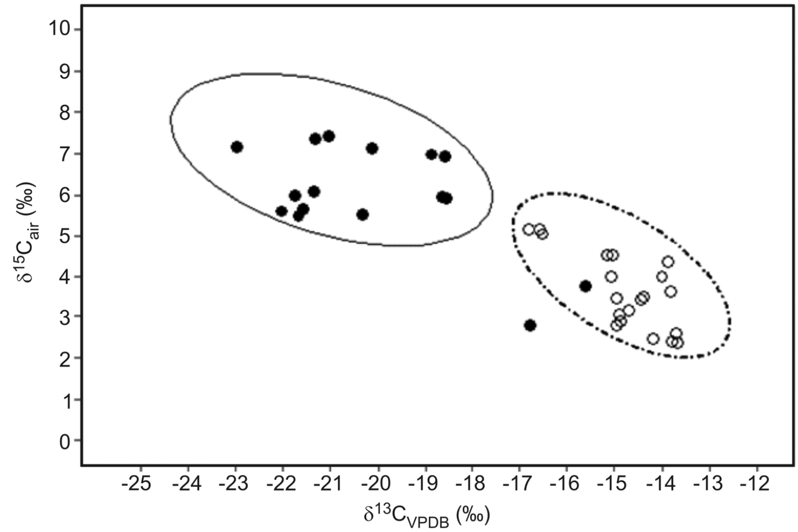

Fig. 2. Dry season stable carbon and nitrogen isotope ratios in faeces from two sympatric species from Pendjari Biosphere Reserve: *Kobus ellipsiprymnus* (●), *K. kob* (○). The ellipses show cluster separation with a coefficient of 0.95.

dry season was 27 (range 1–46), while that of waterbuck was 11 individuals (range 1–21). During the wet season we made 32 observations on waterbuck, and 51 on western kob. The average size of waterbuck groups during the wet season was 7 (range 1–13), while that of western kob was 17 individuals (range 1–38). Akaike information criterion for small sample size (AICc) indicated that although all physical variables except fire aspect contributed to explaining the variability in the habitat use data of western kob, distance to watering point is the most important variable during the dry season and grass cover in wet season, as indicated by the inclusion of these variables in the models selected for each season (the most parsimonious models highlighted in bold; Table 1), while use of waterbuck habitat is best modelled by using grass cover and distance to

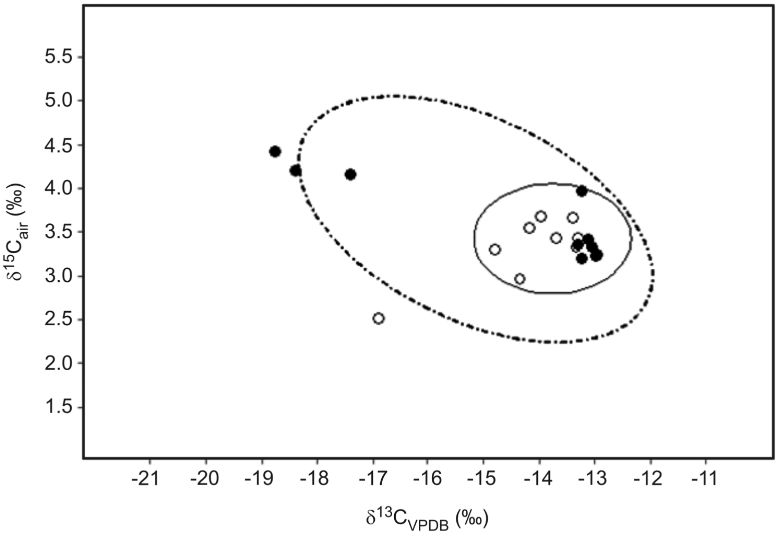

Fig. 3. Wet season stable carbon and nitrogen isotope ratios in faeces from two sympatric species from Pendjari Biosphere Reserve: *Kobus ellipsiprymnus* (●), *K. kob* (○). The ellipses show cluster separation with a coefficient of 0.95.

Table 1. Akaike's information criterion scores (AIC), their differences (Δ) and number of model parameters (*k*) for habitat models developed for seasonal habitat use by the waterbuck in Pendjari Biosphere Reserve. The values in bold are AIC differences (Δ) of less than two, which are useful in explaining the variability in the data (Burnham & Anderson 1998).

Number	Model	*k*	Dry season		Wet season	
			AIC	Δ	AIC	Δ
1	Distance	2	182.38	**0**	111.37	**0.64**
2	Grass	2	183.44	**1.06**	110.73	**0**
3	Grass + distance	3	183.45	**1.07**	112.86	2.13
4	Canopy + distance	3	184.08	**1.70**	113.36	2.63
5	Grass + distance + canopy	4	184.55	2.17	112.32	**1.59**
6	Distance + canopy + fire	4	185.10	2.72	113.69	2.96
7	Fire + distance + grass	4	185.41	3.03	114.84	4.11
8	Fire	2	185.90	3.52	113.19	2.46
9	Distance + fire	2	186.17	3.79	113.31	2.58
10	Fire + canopy + grass + distance	5	186.31	3.93	114.31	3.58
11	Canopy	2	186.34	3.96	112.49	**1.76**
12	Grass + fire	3	187.25	4.87	114.09	3.36
13	Canopy + fire	3	187.46	5.08	114.19	3.46
14	Grass + canopy	3	188.04	5.66	115.28	4.55
15	Fire + canopy + grass	4	189.11	6.73	116.08	5.35

Distance = distance to watering point (m), grass = grass cover (%), canopy = canopy cover (%).

watering point as predictors during the dry season, and grass and canopy cover during the wet season (Table 2). Fire was not found to be a significant variable in the habitat choice of either species, and hence was excluded from further analyses (DFA) on differences in habitat use by the two species.

Habitat use and partitioning

Dry season

The distance to watering point had the highest loading on root or function 1 in the habitat use during the dry season as shown by the discriminant analysis (Table 3), indicating that the loca-

Table 2. Akaike's Information Criterion scores (AIC), their differences (Δ) and number of model parameters (*k*) for habitat models developed for seasonal habitat used by the western kob in Pendjari Biosphere Reserve. The values in bold are AIC differences (Δ) of less than two, which are useful in explaining variability in the data (Burnham & Anderson 1998).

Number	Model	*k*	Dry season		Wet season	
			AIC	Δ	AIC	Δ
1	Grass	2	344.86	0	253.14	**0.25**
2	Grass + distance	3	345.23	0.37	256.32	3.43
3	Distance	2	345.25	0.39	261.42	8.53
4	Canopy + distance	3	47.45	2.59	284.54	31.65
5	Distance + fire	2	347.52	2.66	260.38	7.49
6	Fire	2	348.45	3.59	275.382	2.49
7	Distance + canopy + fire	4	354.49	9.63	297.85	44.96
8	Fire + distance + grass	4	355.27	10.41	268.94	16.05
9	Canopy	3	356.28	11.42	252.89	**0**
10	Grass + distance + canopy	4	367.12	22.26	298.57	45.68
11	Fire + canopy + grass + distance	5	368.15	23.29	289.36	36.47
12	Canopy + fire	3	369.47	24.61	259.36	6.47
13	Grass + fire	2	371.65	26.79	268.27	15.38
14	Grass + canopy	3	375.15	30.29	265.34	12.45
15	Fire + canopy + grass	4	389.56	44.7	274.05	21.16

Distance = distance to watering point (m), grass = grass cover (%), canopy = canopy cover (%).

Table 3. Standardized discriminant function coefficients for seasonal habitat use by western kob and waterbuck in the Pendjari Biosphere Reserve.

Variables	Dry season		Wet season	
	Root 1	Root 2	Root 1	Root 2
Canopy cover	0.201	0.486	–0.504	–0.513
Grass cover	–0.400	**–0.574**	–0.141	**0.780**
Distance to water	**0.750**	0.379	**–0.830**	0.481

Table 4. Mean (±S.D.) of the habitat features of areas used by the by western kob, waterbuck and those available in Pendjari Biosphere Reserve.

Variables	Waterbuck				Western kob				Available			
	Dry season (n = 54)		Wet season (n = 32)		Dry season (n = 82)		Wet season (n = 51)		Dry season (n = 68)		Wet season (n = 68)	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Canopy	37	16	35	29	40	9	19	23	19	15	33	23
Grass	57	19	53	20	43	13	61	18	44	17	54	18
Distance	168	28	953	405	374	113	863	646	624	157	624	157

Distance = distance to watering point (m), grass = grass cover (%), canopy = canopy cover (%).

tions used by the western kob differ from those used by waterbuck, and that unused but available locations could be well discriminated by distance to watering point. We found that during the dry season, western kob used habitats far from the water which were more available, whereas waterbuck occurred closer to a watering point. These differences were significant when the areas were contrasted on the basis of the canonical scores of the first two functions or axes with a one-way ANOVA (F = 34.61, d.f. =4, P < 0.05). A similar trend (t = 5.78, P = 0.003; Table 4) was found by comparing habitat use of western kob and waterbuck using a paired t-test. The same was suggested by the little overlap between the two species along a distance from water source gradient (O_{jk} = 0.098). Similarly, waterbuck used habitats significantly closer to a watering point (mean = 168 m) during the dry season, while western kob selected habitats away from watering point (mean = 374 m; t = 5.31, P = 0.023; Table 4).

Wet season

Discriminant analysis showed that distance and grass cover had the highest loadings on function 1 and function 2, respectively, during the wet season (Table 3). This suggests that the variables were important in discriminating between the three locations: western kob, waterbuck and randomly sampled resource availability sites. Figure 5 suggests that during the wet season both western kob and waterbuck use significantly higher areas than those available (F = 32.02, d.f. = 4, P < 0.001). Therefore, they did not differ in habitat use on a distance from watering point gradient during this season (t = 0.452, P = 0.652), as also indicated by the greater habitat overlap along this axis (O_{jk} = 0.885). The same trend was observed in the use of grass cover (t = 1.931, P = 0.096; O_{jk} = 0.890).

DISCUSSION

Waterbuck and western kob are taxonomically closely related, a similar size, have a similar morphology and ecological requirements (Kingdon 1982) and, in this study, live in the same geographical location (Sinsin *et al.* 2002). Based on the body size predictions of Henley & Ward (2006), one might expect them to occupy the same or comparable ecological niches. However, when niche is defined by habitat use and diet resources along the C and/or N isotope niche axes, our data suggest that Waterbuck and western kob remarkably segregate in habitat and diet only in dry season when resources become scarce. In semiarid lands, where rainfall is an unpredictable and markedly seasonal resource-shifting, coexisting herbivores are expected to develop strategies for niche differentiation more during the dry season

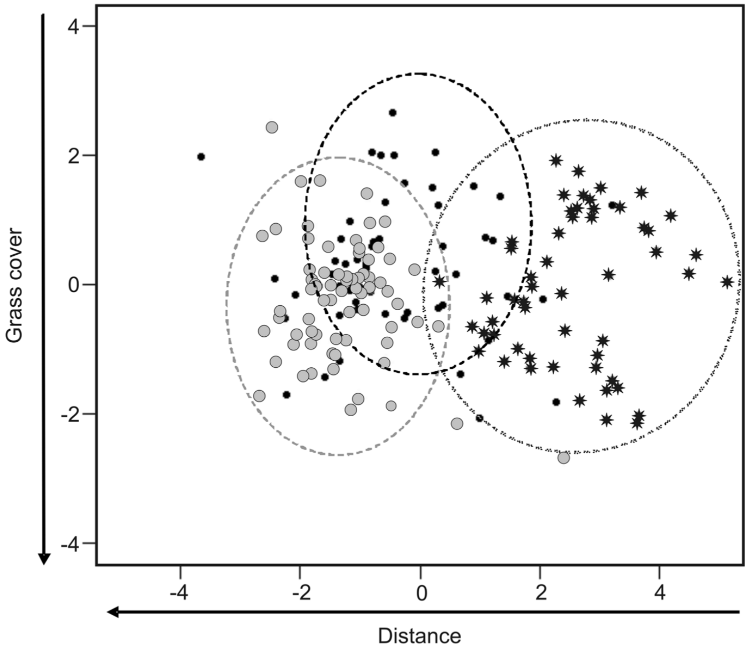

Fig. 4. Output of linear discriminant function analysis to examine whether the areas used by western kob (●), waterbuck (✳) and availability (●) during dry season could be discriminated on the basis of habitat features in the areas.

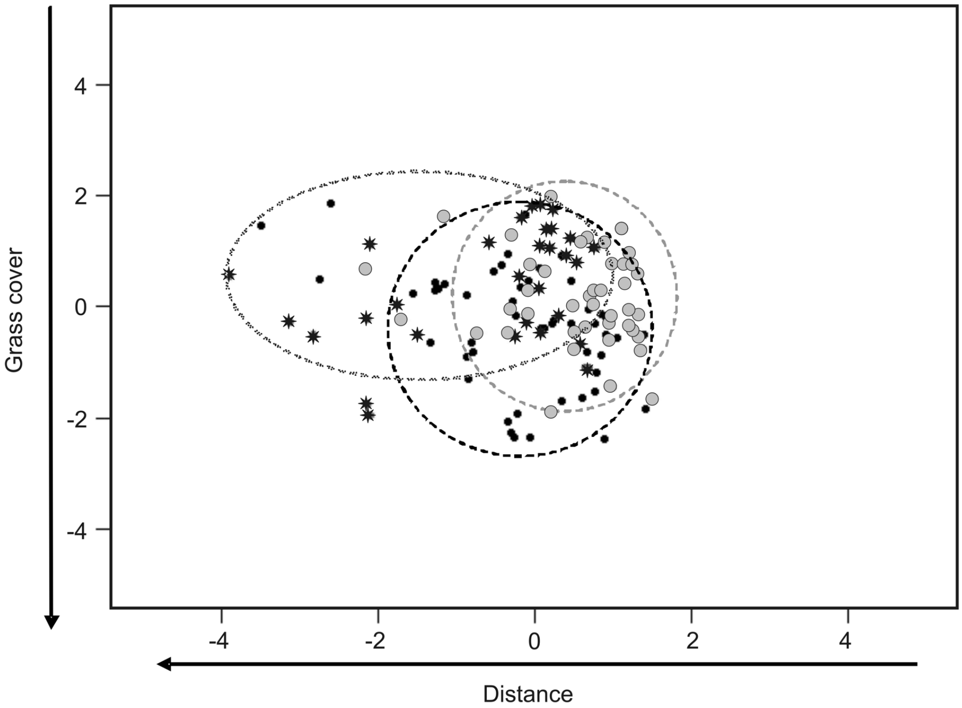

Fig. 5. Output of linear discriminant function analysis to examine whether the areas used by western kob (●), waterbuck (✳) and availability (●) during wet season could be discriminated on the basis of habitat features in the areas.

(Whitford 2002). These coexistence mechanisms were also verified in a diversity of mammal taxa, with segregation in one or more of the three main niche dimensions (diet, habitat and time) (DiBitetti *et al.* 2009), with the diet dimension being the most commonly segregated niche axis among herbivores (Stewart *et al.* 2002).

Competitive interactions are known to be stronger between morphologically similar and phylogenetically closely related sympatric species (Loveridge & Macdonald 2003; DiBitetti *et al.* 2009). Along the C and/or N isotope niche axes only waterbuck portray an ability to consume some proportion of C3 foods during the dry season as shown by the significant seasonal difference noticed in the mean faecal δ^{13}C. Switching from pure grass-based diets to include some browsing was proposed to facilitate improved diet quality when the nutritional value of available C4 grasses is low (Codron *et al.* 2008). Moreover, the seasonal difference in faecal mean of δ^{15}N is probably diet-related with waterbuck using more plants with higher δ^{15}N growing closer to water, as this species was found to select habitat closer to a watering point. We concluded that waterbuck broaden their isotope niches when resources are less abundant (dry season) to allow coexistence with the western kob. Waterbuck, are predominantly grazers (Kassa *et al.* 2007); however, a literature search showed that they can include some C3 plants in their diet, especially during the dry season when grasses become higher in structural components and lower in protein (Sponheimer *et al.* 2003; Copeland *et al.* 2008). A recent study in the Pendjari Biosphere has shown that waterbuck also took higher proportions of C3 plants in the late dry season (Kassa *et al.* 2007).

So this segregation along the isotope niche (δ^{13}C and δ^{15}N) axis experience by the western kob and waterbuck could explain the species coexisting and thereby limiting competition during the resource-limited dry season.

The relatively small sample sizes of our study might be a limitation, but the pattern of isotope niche overlap with partitioning emerging in sympatry appears quite robust, especially for the δ^{13}C data (Codron *et al.* 2011). Isotope technique is also able to detect subtle differences in diet between family groups and/or herds, even within one fairly small reserve and a small sample size (Codron & Brink 2007). Moreover Djagoun *et al.* (2013) recently found a close similarity in waterbuck and kob diet from Pendjari Biosphere Reserve and East and southern Africa studies, although one was based on the faeces representing only short-term dietary information and the other one on longer-term body tissues like hair, bones and teeth. The distribution pattern of waterbuck was predicted both in the dry and wet season by grass and canopy cover, which is in accordance with the diet preference found for this species in the PBR. The western kob distribution was predicted in dry season by the canopy cover and the distance to water; while only the distance to water source predicted this distribution during the wet season. Not surprisingly, western kob and waterbuck show a strong selection for areas close to the water source in the dry season suggesting the water-dependency of the two species and need to drink daily and forage not far away from water sources (Kingdon 1982; Estes 1991; Smitt 2011). Despite the water dependency of both species we found that the area used by western kob from differed that used by waterbuck and that unused but available locations could be well discriminated by distance to watering point (Fig. 4) at habitat level. This suggests that herbivore habitat partitioning does not occur only on the basis of the diet resource partitioning but that the segregation along habitat variable axis plays an important role in the coexisting system. They were observed to diverge largely along the distance to the water source gradient during the dry season, which is in line with our hypothesis. Such habitat partitioning, known to prevent both resource and interference competition, might have allowed co-occurrence of western kob and waterbuck at the landscape level. However, waterbuck might be at a disadvantage during the dry season, given that western kob has a higher population density in PBR (Sinsin *et al.* 2008) and versatility in the isotope niche range is one of the strategies to allow coexistence.

The largest overlap in habitat use was observed during the wet season when both western kob and waterbuck live far away from the water source due to the flooding of habitat close to the water source (Kassa *et al.* 2007). During the wet season, the habitat close to the water source often have a higher risk of flooding (Sokpon *et al.* 2001), which may force western kob and waterbuck to move to the surrounding upper areas. In contrast, during the dry season the grass is very dry and may provide little nutritious resources (Smitt 2011), which again force western kob to actively select patches retaining some humidity such as living closely to the water source. Since the dry season is the period with a severe resource limitation in the PBR due to plant senescence and limited water resource availability (Djossa *et al.* 2008), the distance from water source separation between the two species during the dry season could be related to competitive exclusion of kob from the closest areas to watering point. Heterogeneity in habitat and thus resource availability can lead to functional responses in habitat selection (Godvik *et al.* 2009), which may further account for differences for western kob and waterbuck in habitat selection. If animals require a particular resource, they may demonstrate a stronger preference for it when it is rare on the landscape. However, when that resource is abundant, its use may not increase proportionately with availability.

Although results provided strong support for differentiation between western kob and waterbuck associated with the selection by each species of particular habitat variables and range of diet, it remains unclear whether it reflected segregation due to competitive interactions; or results from mere differences in species-specific habitat preferences. Testing these alternatives would require experimental testing that was beyond the scope of this study. Further studies could help to elucidate more the mechanism underlining coexistence in ecologically similar and sympatric herbivores. The strength of these potentially asymmetric competitive interactions should be tested across seasons and types of habitat, in order to have a better understanding of the actual mechanisms promoting coexistence of these two kob species in natural landscapes.

ACKNOWLEDGMENTS

The field work of this study was funded by LOEWE-Biodiversity and Climate Research Centre (BiK-F). Analytical work was carried out in the Stable Light Isotope Laboratory in the Department of Archaeology at the University of Cape Town, supported by UCT and the South African National Research Foundation. We appreciate their dedication to support this research. We thank two anonymous reviewers for helpful comments that improved the quality of this paper. We are grateful to the local communities who participated in the research activities. Our acknowledgments also go to our field guide Djato Tchabi who helped us during the field work with bovid faecal pellet identification.

REFERENCES

ARSENAULT, R. & OWEN-SMITH, N. 2002. Facilitation versus competition in grazing herbivore assemblages. *Oikos* **97**: 313–318.

AUGUSTINE, D.J. 2010. Response of native ungulates to drought in semi-arid Kenyan rangeland. *African Journal of Ecology* **48**: 1009–1020.

AVERBECK, C., APIO, A., PLATH, M. & WRONSKI, T. 2009. Environmental parameters and anthropogenic effects predicting the spatial distribution of wild ungulates in the Akagera savannah ecosystem. *African Journal of Ecology* **47**: 756–766.

BURNHAM, K.P. & ANDERSON, D.R. 1998. *Model Selection and Inference: a Practical Information Theoretic Approach*. Springer, Berlin.

CERLING, T.E. & HARRIS, J.M. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* **120**: 347–363.

CODRON, D. & CODRON, J. 2008. Reliability of δ^{13}C and δ^{15}N in faeces for reconstructing savanna herbivore diet. *Mammalian Biology* 74: 36–48.

CODRON, D., CODRON, J., LEE-THORP, J.A., SPONHEIMER, M., DE RUITER, D.J., SEALY, J., GRANT, R. & FOURIE, N. 2007. Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology,* London **273**: 21–29.

CODRON, D. & BRINK, J.S. 2007. Trophic ecology of two savanna grazers, blue wildebeest *Connochaetes taurinus* and black wildebeest *Connochaetes gnou*. *European Journal or Wildlife Research* **53**: 90–99.

CODRON, D., HULL, J., BRINK, J.S., CODRON, J., WARD, D. & CLAUSS, M. 2011. Effect of competition on niche dynamics of syntopic grazing ungulates: contrasting the predictions of habitat selection models using stable isotope analysis. *Evolutionary Ecology Research* **13**: 217–235.

COPELAND, S.R., SPONHEIMER, M., SPINAGE, C.A., LEE-THORP, J.A. 2008. Bulk and intra-tooth enamel stable isotopes of waterbuck *Kobus ellipsiprymnus* from Queen Elizabeth National Park, Uganda. *African Journal of Ecology* **46**: 697–701.

DIBITETTI, M.S., DI BLANCO, Y.E., PEREIRA, J.A., PAVIOLO, A. & JIMENEZ, P.I. 2009. Time partitioning favours the coexistence of sympatric crab-eating fox (*Cerdocyon thous*) and pampas fox (*Lycalopex gymnocercus*). *Journal of Mammalogy* **90**: 479–490.

DJAGOUN, C.A.M.S., CODRON, D., SEALY J., MENSAH, G.A. & SINSIN, B. 2013. Stable carbon isotope analysis of the diets of West African bovids in Pendjari Biosphere Reserve, northern Benin. *South African Journal of Wildlife Research* **43**(1): 33–43.

DJOSSA, B.A., FAHR, J., WIEGAND, T., AYIHOUENOU, B.E., KALKO, E. & SINSIN, B.A. 2008. Land use impact on *Vitellaria paradoxa* c.f. Gaerten. Stand structure and distribution patterns: a comparison of Biosphere Reserve of Pendjari in Atacora district in Benin. *Agroforestry Systems* **72**: 205–220.

DÖRGELOH W.G. 2006. Habitat suitability for tsessebe *Damaliscus lunatuslunatus*. *African Journal of Ecology* **44**: 329–336.

ESTES, R.D. 1991. *The Behavior Guide to African Mammals, including Hoofed Mammals, Carnivores, Primates.*

University of California Press, Berkeley, U.S.A.

FISHER, F. & LINSENMAIR, K.E. 2002. Demography of a West African kob (*Kobus kob kob*) population. *African Journal of Ecology* **40**: 130–137.

FISHER, F. & LINSENMAIR, K.E. 2006. Changing social organization in an ungulate population subject to poaching and predation – the kob antelope (*Kobus kob kob*) in the Comoé National Park, Côte d'Ivoire. *African Journal of Ecology* **45**: 285–292.

GODVIK, I.M.R., LOE, L.E., VIK, J.O., VEIBERG, V., LANGVATN, R., MYSTERUD, A. 2009. Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology* **90**: 699–710.

GRANT, C.C., PEEL, M.J.S., ZAMBATIS, N. & VAN RYSSEN, J.B.J. 2000. Nitrogen and phosphorus concentration in faeces: an indicator of range quality as a practical adjunct to existing range evaluation methods. *African Journal of Range & Forage Science* **17**: 81–92.

GUTBRODT, B. 2006. Diet composition of wildebeest, waterbuck and reedbuck in relation to food quality in a moist savanna of Tanzania. Diploma thesis in Environmental Sciences, Swiss Federal Institute of Technology Zurich.

HENLEY, S.R. & WARD, D. 2006. An evaluation of diet quality in two desert ungulates exposed to hyperarid conditions. *African Journal of Range and Forage Science* **23**:185–190.

HIBERT, F. CALENGE, C. FRITZ, H., MAILLARD, D. BOUCHE, P., IPAVEC, A., CONVERS, A., OMBREDANE, D. & DE VISSCHER, M-N. 2010. Spatial avoidance of invading pastoral cattle by wild ungulates: insights from using point process statistics. *Biodiversity and Conservation* **19**: 2003–2024.

KASSA, B., LIBOIS, R. & SINSIN, B. 2007. Diet and food preference of the waterbuck (*Kobus ellipsiprymnus defassa*) in the Pendjari National Park, Benin. *African Journal of Ecology* **46**: 303–310.

KINGDON, J. 1982. *East African Mammals: An Atlas of Evolution in Africa*. Academic Press, New York.

KLOP, E. & VAN GOETHEM, J. 2008. Savanna fires govern community structure of ungulates in Benoue National Park, Cameroon. *Journal of Tropical Ecology* **24**: 39–47.

LOVERIDGE, A.J. & MACDONALD, D.W. 2003. Niche segregation in sympatric jackals *Canis mesomelas* and *Canis adustus*). *Journal of Zoology,* London **259**: 143–153.

PIANKA, E.R., 1986. *Ecology and Natural History of Desert Lizards*. Princeton University Press, Princeton, NJ, U.S.A.

R DEVELOPMENT CORE TEAM. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

ROBBINS, C.T., FELICETTI, L.A. & SPONHEIMER, M. 2005. The effect of dietary protein quality on nitrogen isotope discrimination in mammals and birds. *Oecologia* **144**: 534–540.

SCHOENER, T.W. 2009. Ecological niche. In: *The Princeton Guide to Ecology*, (ed.) S.A. Levis. Princeton University Press, Princeton.

SINSIN, B., SOGBOHOSSOU, E.A., NOBIME, G. & ADI, M. 2008. Dénombrement aérien de la faune dans la Réserve de Biosphère de la Pendjari: Rapport technique.–CENAGREF/Projet Pendjari CTZ/GFA Consulting, (in French).

SINSIN, B., TEHOU, A.C., DAOUDA, I. & SAIDOU, A. 2002. Abundance and species richness of larger mammals in Pendjari National Park in Benin. *Mammalia* **66**: 369–380.

SMITT, I.P.J. 2011. Resources driving landscape-scale distribution patterns of grazers in an African savanna. *Ecography* **34**: 67–74.

SOKAL, R.R. & ROHLF, F.J. 1981. *Biometry*, 2nd edn. W.H. Freeman, New York.

SOKPON, N., BIAOU, H., HOUNHYET, O., OUINSAVI, C. & BARBIER, N. 2001. Inventaire et caractérization des formations végétales du complexe national de la Pendjari, zone cynégétique de la Pendjari et de l'Atacora: région de Konkombri. Rapport. UNB/Bénin III. (In French).

SPONHEIMER, M., LEE-THORP, J.A., DE RUITER, D.J., SMITH, J.M., VAN DER MERWE, N.J., REED, K., GRANT, C.C., AYLIFFE, L.K., ROBINSON, T.F., HEIDELBERGER, C. & MARCUS, W. 2003. Diets of southern African Bovidae: stable isotope evidence. *Journal of Mammalogy* **84**, 471–479.

STEWART, K.M., BOWYER, R.T., KIE, J.G., CIMON, N.J. & JOHNSON, B.K. 2002. Temporospatial distributions of elk, mule, deer, and cattle: resource partitioning and competitive displacement. *Journal of Mammalogy* **83**: 229–244.

WHITFORD, W. 2002. *Ecology of Desert Systems*. Academic Press, Elsevier Science Imprint, London.

Responsible Editor: G.I.H. Kerley