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Comparative diet and habitat selection of puku and lechwe in northern Botswana

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Differences in resource selection (i.e., habitat selection and diet composition) may allow for coexistence of interspecific competitors. Two congeneric floodplain antelope with broadly similar habitat use are puku (*Kobus vardonii*) and lechwe (*K. leche*). In Botswana, puku are restricted to a narrow band of floodplains along the Chobe River, whereas lechwe are far more abundant, with a distribution encompassing the Chobe Riverfront, the Linyanti Swamps, Kwando River, and the Okavango Delta. We investigated factors to try to explain the contrasting distribution patterns of puku and lechwe, including seasonal diet composition and overlap, seasonal nutritional status as indicated by fecal nitrogen and phosphorus, and habitat selection. Dietary overlap ranged from 84% to 90% across seasons. *Cynodon dactylon* was the greatest contributor to the diets of both puku and lechwe, but there were differences in the relative contributions of particular grass species associated with uplands or floodplains. Fecal nitrogen and phosphorus did not differ between species and did not indicate nutritional deficiencies for either puku or lechwe. Habitat selection was broadly similar during the low-water season, but during the high-water season, puku moved from the floodplain into shrublands habitats, whereas lechwe remained on the floodplains. We hypothesize that increased predation risk during the high-water season, due to increased visual obstruction in shrublands, may limit abundance of puku in the study area.

Key words: antelope, Botswana, congener, diet selection, floodplain, habitat selection, *Kobus leche*, *Kobus vardonii*, lechwe, puku

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Differential diet and habitat selection may serve as the basis for ecological separation of sympatric herbivores and may be an important adaptation for the survival of interspecific competitors (Duncan 1975; Sinclair 1985; Murray and Illius 2000; Macandza et al. 2004). Foraging patterns, habitat selection, and distribution of herbivores are related to spatial variability in forage quality and quantity (Owen-Smith and Novellie 1982; Bryant et al. 1989; McNaughton 1990; Ben-Shahar and Coe 1992) and predation risk (Brown 1992; Fischhoff et al. 2007). Herbivores should select areas with higher forage quality and quantity, but risk of predation may result in herbivores occupying less profitable areas (Bergerud et al. 1984; Bleich et al. 1997; Hebblewhite and Merrill 2009).

The dry season is commonly considered the period of greatest nutritional stress for herbivores in African savannas (Western 1975; Sinclair 1977; Owen-Smith 1982). However, forage quality in floodplain environments may remain higher than in upland areas due to higher soil moisture. Sheppe and Osborne (1971) suggest the high-water season is the most critical period for floodplain-dwelling ungulates because available habitat becomes restricted to small areas of high ground. Hence, floodplain ungulates may face greatest food limitation during the late wet season when large portions of floodplains become inundated, rendering resources unavailable.

Two congeneric floodplain antelope that overlap in habitat use are puku (*Kobus vardonii*) and lechwe (*K. leche*). Puku and lechwe are primarily grazers (Child and Von Richter 1969; Williamson 1990; Mills and Hes 1997), have similar body size, occupy similar floodplain habitats (Rees 1978a, 1978b; Williamson 1990; Dipotso and Skarpe 2006), and therefore could be expected to have broadly similar diets and habitat needs. However, in Botswana puku are restricted to a small population occupying a narrow band of floodplains along the Chobe River in northern Botswana (Dipotso and Skarpe 2006). Lechwe are far more abundant, and their distribution encompasses the Chobe Riverfront, the Linyanti Swamps, Kwando River, and the Okavango Delta.

We investigated factors that might help to explain the contrasting distribution patterns of these 2 antelope species, including seasonal diet composition and overlap, seasonal nutritional status as indicated by fecal nitrogen and phosphorus, and habitat selection as influenced by flooding conditions. We hypothesized that diet composition would be similar throughout the year, but dietary overlap would be highest and fecal nutrient content would be lowest during the high-water season (HWS) when large portions of the floodplains become inundated. We also predicted that we would detect most differences in habitat-selection patterns during the low-water season (LWS) when floodplains were more widely available.

Materials and Methods

Study area.—The Chobe River forms the northern boundary of Chobe National Park in northeastern Botswana and the international boundary between Namibia and Botswana. The study area encompassed a 35-km stretch of river frontage from Sedudu Island in the east to Lechwe Flats in the west and was composed of 5 intensive study sites: Sedudu Island, Watercart, Puku Flats, Kabulabula, and Lechwe Flats.

Mean annual rainfall recorded in Kasane on the eastern edge of the study area is 685 mm, 95% of which falls during the wet season (October–April—Department of Meteorological Services Botswana 2009). Mean daily maximum temperature is 32°C during the wet season and 27°C in the dry season (Department of Meteorological Services Botswana 2009). River levels fluctuate throughout the year, rising from the end of November, reaching a peak during March, then subsiding toward lowest levels reached at the end of November (Ministry of Minerals, Energy and Water Resources Botswana 2009). Hence, we distinguished seasonal conditions as LWS (September to end of February) and HWS (March to end of August).

Floodplain grasslands cover the area between the Chobe River and the Kalahari sand ridge to the south (Simpson 1975). Floodplains are composed of drainage channels and small ridges that experience inundation to varying degrees during the HWS. Small depressions within the floodplains may hold water late into the dry season. *Cynodon dactylon* and *Vetiveria nigritana* dominate the floodplains with *Phragmites mauritianus*, *Paspalum scrobiculatum*, *Digitaria eriantha*, *Brachiaria* spp., and *Eragrostis* spp. being locally common.

On the sand ridge, the riparian fringe is dominated by the trees *Acacia albida*, *Combretum imberbe*, and *Diospyros mespiliformis* (Simpson 1975). Leading up the sand ridge, *Croton megalobotrys*, *Combretum mossambicense*, *Dichrostachys cinerea*, and *Capparis tomentosa* are common. Common grass species include *D. eriantha*, *Dactyloctenium giganteum*, *Panicum deustum*, *C. dactylon*, and *Brachiaria humidicola*. *Baikiaea* woodland dominates the top of the sand ridge, including *Baikiaea plurijuga*, *Guibourtia coleosperma*, and *Pterocarpus angolensis* (Simpson 1975). A more comprehensive description of the study area is available in O'Shaughnessy (2010).

Diet selection.—Data were collected from July 2007 through June 2008. Each intensive study site was divided into 4 subunits. Within each study site, subunits were surveyed consecutively until puku or lechwe were located; surveys began in a different subunit on each day of sampling. Puku and lechwe herds were located between 0600 and 1100 h using a spotting scope (10–60×) or binoculars (8 × 56). A laser range finder (Bushnell Yardage Pro 400; Bushnell, Overland Park, Kansas) was used to determine distance from the observer to the herd. Foraging sites were defined as the area where animals were observed feeding for $\geq$ 15 min and were identified by presence of tracks, droppings, and freshly grazed grass, which was determined by a lack of drying, yellowing, or browning on the cropped edge of the grass leaves. To reduce the likelihood that foraging by other herbivores would influence the assessment of forage selection by puku and lechwe, sampling was conducted immediately after focal animals had moved away. Puku and lechwe were never seen feeding in mixed groups, thus we were certain we only sampled areas grazed independently by each species. Foraging sites were considered independent if separated by at least 200 m. Throughout the study period, a total of 186 puku foraging sites, 119 lechwe foraging sites, and 586 available sites were sampled. All sampling methods complied with guidelines of the American Society of Mammalogists (Sikes et al. 2011).

At each foraging site, a quadrat (0.7 × 0.7 m) was placed over the freshly cropped grass. A further 8 quadrats were placed, 2 in each cardinal direction around the 1st quadrat, separated by 2 m. If no grazing was evident inside the quadrat but was evident close outside, the quadrat was flipped once to incorporate the grazing. If no evidence of grazing was found in 5 of 9 quadrats, an additional 4 quadrats were placed in diagonal directions from the central quadrat.

Within each quadrat, the number of freshly grazed and ungrazed grass tufts was recorded for each grass species. If a grass species (e.g., *C. dactylon*) had stolons, those stolons were considered part of the parent tuft if they were devoid of flowering structures; secondary shoots with flowering structures were considered independent plants. Some *Eragrostis* spp. could not be distinguished accurately and were classified only to genus. The proportion of leaves that were green for each grass tuft was visually estimated using the Walker 8-point scale (Walker 1976). The height (mm) of each bite on grazed portions of grass tufts was measured from the base to the lowest recognizable bite for each grass species within each quadrat. Similarly, the height of each ungrazed grass tuft was measured from the base to the tip of the tallest ungrazed leaf. The number of grazed and ungrazed tufts was summed to give the total number of grazed and ungrazed tufts of each grass species for each foraging site. Grass greenness for each grass species within the foraging site was calculated by averaging the midpoints of the greenness classes. Height of the grazed and ungrazed tufts of each grass species was averaged across the 9 quadrats for each foraging site.

Diet quality.—Fresh (< 1 day old) fecal pellets found at foraging sites were collected into paper bags. Multiple fecal samples found at a foraging site were pooled. Samples were air-dried and shaded from direct sunlight and rainfall. Fecal samples were analyzed for fecal nitrogen and phosphorus by the Agricultural Research Council Institute for Soil, Climate and Water Laboratory, in Pretoria, South Africa, using atomic absorption spectroscopy (Stowe 2003). Fecal pellets deposited unseen by observers were identified as being from puku or lechwe based on size and shape. A total of 35 puku (15 in LWS and 20 in HWS) and 30 lechwe (20 in LWS and 10 in HWS) fecal samples were collected and analyzed for nutritional status.

Habitat selection.—Our sampling regime followed protocol A, design I of Manly et al. (2002). Because we only sampled used sites during foraging periods, inferences are limited to habitat-selection patterns during foraging activity.

Eight variables were recorded at each foraging site: habitat type, shrub cover, tree cover, visual obstruction, distance to water, grass cover, grass greenness, and grass height. Habitat types were defined by predominant vegetative structure and physical features within a 25-m radius surrounding sites. Habitat type included shallow swamp (areas containing aquatic vegetation with water < 1 m deep), interface zone (area of moist soil between dry land and water), low-lying floodplain (floodplains inundated for 3–8 months per year), high-lying floodplain (floodplains inundated for < 3 months per year), grasslands (areas not inundated at any period during the year, with < 5% shrub or tree cover), shrublands (areas with predominantly woody vegetation ≤ 2 m in height), and woodlands (areas with predominantly woody vegetation > 2 m in height). Percentage basal cover of shrubs and trees was visually estimated using the Walker 8-point scale (Walker 1976). Visual obstruction was assessed with a 1-m Robel pole (Robel et al. 1970) placed 25 m from the center of the foraging site in each cardinal direction, averaging the 4 values from the cardinal points.

Grass features were evaluated within the quadrats placed within each foraging site. Percentage grass cover and grass greenness were estimated using the Walker 8-point scale (Walker 1976) at the level of the quadrat. Grass height (mm) was measured from the ground to the tip of the highest leaf of the predominant grass species. Measurements of grass cover, grass greenness, and grass height from all 9 quadrats were averaged for each foraging site. Distance to water was measured from the center quadrat to the nearest point of the Chobe River using a range finder.

Characterization of available habitat was conducted seasonally based on the water levels of the Chobe River. Habitat availability during the LWS was estimated by placing line transects in a south–north direction every 200 m across each study site. Sampling points were spaced every 200 m along each transect; the number of sampling points per transect depended on the transect length, which varied depending on the distance to the river. At each sampling point habitat features were recorded using the same methods described above.

During initial transect sampling, the location of each sampling point was recorded, using a handheld global positioning system unit (Garmin Foretrex; Garmin, Olathe, Kansas). To account for seasonal variability, transects were sampled during the last week of every month throughout the study. The number, position, and length of transects sampled each month depended on the position of impassable water. In total, 185 points were sampled along 37 transects during each month of the LWS, giving a total sample size of 370 sampling points.

During the HWS, rising water levels forced puku and lechwe off much of the floodplains and into upland habitats. Therefore, it became necessary to survey an additional 27 transects covering these areas. Transects in upland habitats were perpendicular to the main east–west park road and ran in a south–north direction from the road to the floodplain. Transects and sampling points were spaced 200 m apart. A total of 213 points were sampled during the HWS.

Statistical analysis.—To estimate seasonal diets, foraging sites were considered independent when separated by ≥ 200 m. Proportional dietary contribution of grass species at each foraging site was calculated by dividing the number of grazed tufts of each species by the total number of grazed tufts of all grass species. Dietary proportions obtained from each foraging site were averaged across foraging sites within each season to estimate the seasonal dietary contribution of each grass species for puku and lechwe.

Dietary overlap between puku and lechwe was assessed using Pianka's niche overlap formula (Pianka 1973). This index accounts for the relative proportions of grass species in the diets of puku and lechwe, and it estimates the amount of dietary overlap between the species. The index was calculated seasonally to establish changes in diet overlap over the course of the year.

Plant-based frequency of acceptance (FOA) was estimated by dividing the number of grazed tufts of a particular grass species by the total number of tufts of that species within each foraging site (Owen-Smith and Cooper 1987). Plant-based FOA values represent the likelihood of a grass species being grazed upon when it is available. The FOA value of a grass species gives an indication of preference of the species to puku and lechwe. Highly preferred grasses will be eaten on each encounter by the animal (FOA = 1), and unpalatable grasses will be avoided (FOA = 0). Seasonal plant-based FOA values were estimated by averaging the FOA values of each grass species within each season. Plant-based availabilities were calculated by dividing the number of tufts of a particular grass species by the total number of tufts of all grass species within each foraging site. Seasonal plant-based availabilities were estimated by averaging the availabilities of each grass species in each season. Because individual grass tufts within feeding sites may not be selected independently, statistical tests were not applied to these data.

Table 1.—A priori models for predicting habitat use by puku (*Kobus vardonii*) and lechwe (*K. leche*) in Chobe National Park, Botswana (July 2007–June 2008).

Grass cover
Grass height
Grass greenness
Habitat type
Shrub cover
Tree cover
Distance to water
Visual obstruction
Habitat type + Grass cover
Habitat type + Grass height
Grass height + Grass greenness
Habitat type + Grass greenness
Habitat type + Visual obstruction
Grass greenness + Visual obstruction
Grass height + Grass greenness + Grass cover
Grass height + Grass cover + Distance to water
Grass height + Grass greenness + Distance to water
Grass greenness + Shrub cover + Tree cover
Shrub cover + Tree cover + Distance to water

To determine statistical significance of grass species preference in the diets of puku and lechwe, site-based FOA values were estimated for each grass species within independent foraging sites (i.e., separated by $\geq$ 200 m). Site-based FOA was estimated for each grass species by dividing the number of foraging sites where each grass species was grazed by the total number of foraging sites in which the grass species occurred in each season. Site-based availability of each grass species was estimated by dividing the number of feeding sites where each grass species was present by the total number of feeding sites sampled in each season. Site-based FOA values represent the likelihood of a grass species being fed upon when present at a foraging site, and thus indicate the relative preference of grass species within foraging sites.

Mean fecal nitrogen and phosphorus values were compared between puku and lechwe and between seasons using 2-way analysis of variance. Nitrogen or phosphorus was the dependent variable with species and season as the factors. Significance was set at $P \leq 0.05$.

Logistic regression was used to estimate the probability of use of a site (Hosmer and Lemeshow 2000; Manly et al. 2002). Habitat type was entered as a categorical variable with 7 classes; shallow swamp was set as the reference category. Distance to water, grass height, and visual obstruction were entered as continuous variables. Grass greenness, grass cover, shrub cover, and tree cover also were entered as continuous variables. We considered 19 a priori models to establish whether use by puku and lechwe was associated with particular habitat features (Table 1). A priori models were developed to evaluate the relative roles of forage conditions (e.g., grass greenness and grass cover), predation risk (e.g., shrub cover and visual obstruction), and habitat type on habitat selection both independently and in combination.

An information-theoretic approach was used to select the most-parsimonious models using Akaike's information criterion corrected for small sample size (AIC_C—Burnham and Anderson 2002). The best models were selected using AIC_C, and models with $\Delta AIC_C < 2.0$ were considered to have equivalent support. Model uncertainty was accounted for by calculating model-averaged parameter estimates ($\pm$ *SE*) using multimodel averaging (Burnham and Anderson 2002) across all a priori models. Odds ratios and 95% confidence intervals were derived by exponentiation of the model-averaged parameter estimates.

Results

Diet selection.—Eighteen grass species were recorded in the diet of puku during the LWS, and 16 during the HWS (Table 2). Lechwe fed on 14 grass species each season. Dietary overlap between puku and lechwe was high during both the LWS (Pianka's niche overlap index = 0.841) and HWS

Table 2.—Seasonal contributions of grasses in the diets of puku (*Kobus vardonii*) and lechwe (*K. leche*) in Chobe National Park, Botswana (July 2007–June 2008). Prop. is the seasonal proportion of the diet composed of each grass species; $\bar{X}$ is the average proportion of each grass species eaten at foraging sites.

	Low-water season								High-water season							
	Puku				Lechwe				Puku				Lechwe			
	n	Prop.	$\bar{X}$	*SE*	*n*	Prop.	$\bar{X}$	*SE*	*n*	Prop.	$\bar{X}$	*SE*	*n*	Prop.	$\bar{X}$	*SE*
Acroceras macrum	21	0.07	0.66	0.10	14	0.08	0.71	0.15	21	0.09	0.61	0.10	26	0.18	0.72	0.12
Brachiaria dura	13	0.05	0.55	0.11					5	0.02	0.44	0.29				
Brachiaria humidicola	8	0.03	0.28	0.09					31	0.13	0.80	0.09				
Brachiaria nigropedata									8	0.03	0.35	0.29				
Cynodon dactylon	57	0.20	0.75	0.08	45	0.25	0.79	0.07	46	0.19	0.58	0.07	40	0.27	0.86	0.05
Chloris gayana									6	0.03	0.32	0.17		0		
Digitaria eriantha	37	0.12	0.61	0.08	18	0.10	0.59	0.10	30	0.13	0.57	0.10	10	0.07	0.23	0.07
Eragrostis spp.	36	0.13	0.43	0.08	10	0.06	0.34	0.13	27	0.11	0.48	0.12	16	0.11	0.50	0.11
Panicum deustum	9	0.03	0.27	0.12	25	0.14	0.39	0.08								
Phragmites mauritianus	18	0.06	0.74	0.13	29	0.16	0.79	0.08	13	0.05	0.60	0.14	16	0.11	0.89	0.10
Paspalum scrobiculatum	10	0.04	0.75	0.11	13	0.07	0.69	0.12					8	0.05	0.08	0.02
Vetiveria cuspidata	14	0.05	0.54	0.14	6	0.03	0.398	0.18								
Vetiveria nigritana	44	0.15	0.59	0.09	9	0.05	0.49	0.26	16	0.07	0.42	0.16	9	0.06	0.19	0.10
Other spp.	22	0.08	0.32	0.12	13	0.07	0.36	0.15	36	0.15	0.44	0.10	22	0.15	0.62	0.19

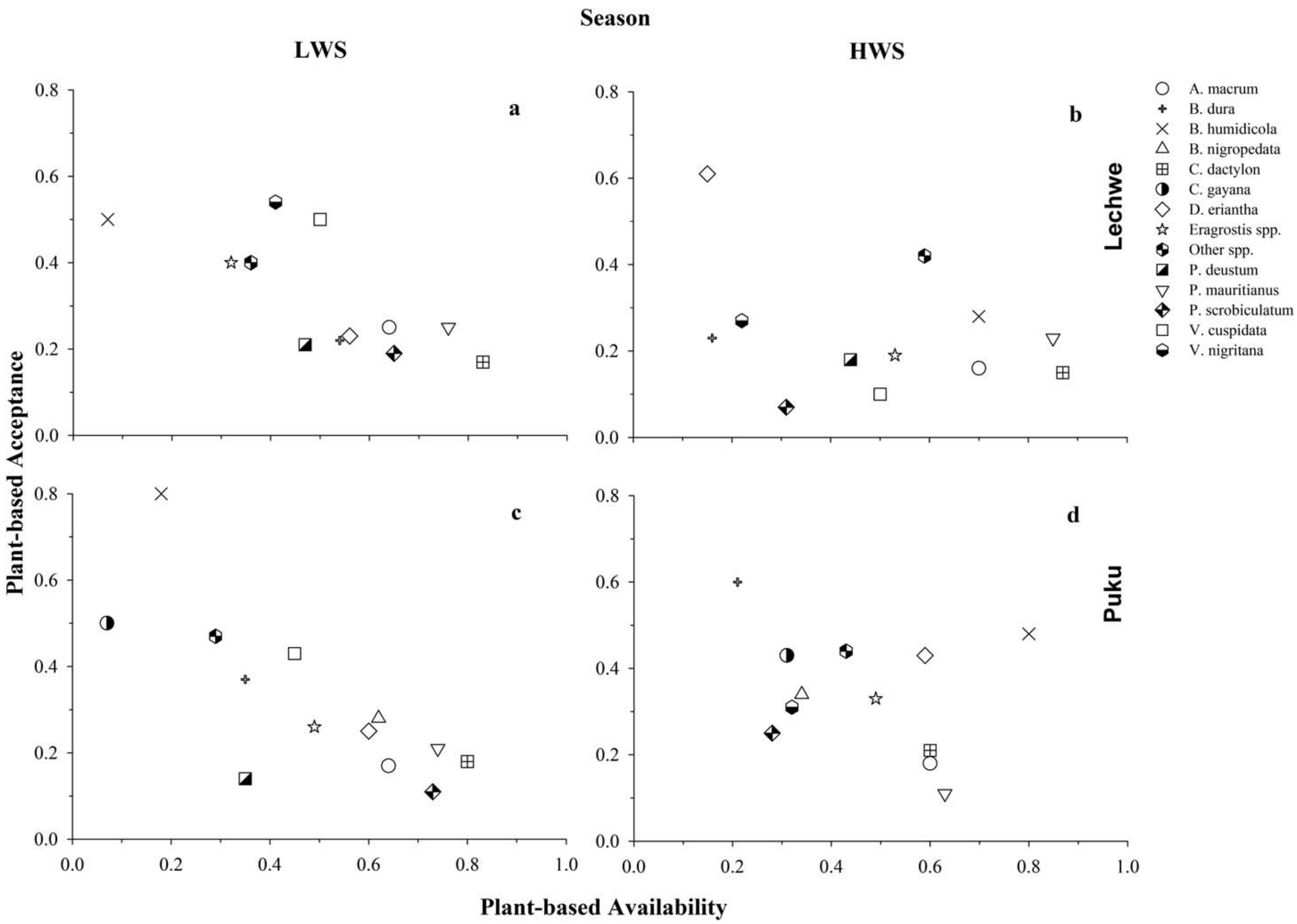

Fig. 1.—Seasonal plant-based acceptance and availabilities of grasses in the diets of puku (*Kobus vardonii*) and lechwe (*K. leche*) in Chobe National Park, Botswana. Relative frequency of acceptance values of grass species in the diets of a and b) lechwe and c and d) puku during the low-water season (LWS) and high-water season (HWS) from July 2007 to June 2008. Acceptance values represent the probability of a grass species being eaten when encountered. Plant-based acceptance values closer to 1 indicate preference of that grass species; values close to 0 indicate avoidance of that grass species.

(Pianka's niche overlap index = 0.899). During the LWS, *C. dactylon* was the greatest contributor to the diets of both puku and lechwe in both seasons (Table 2). *Brachiaria* spp. were recorded only in the diet of puku. *P. mauritianus* was more than twice as high in the diet of lechwe compared to puku, whereas the contribution of *V. nigritana* was more than 3 times higher in the diet of puku than lechwe. During the HWS, *D. eriantha* was almost twice as common in the diet of puku compared to lechwe. The contributions of *Acroceras macrum*, *Eragrostis* spp., and uncommon grass species increased substantially in the diets of lechwe during the HWS.

Plant-based FOA (Fig. 1) indicated distinctions between highly accepted grass species with FOA of ≥ 0.4, intermediately accepted species with FOA between 0.4 and 0.2, and neglected species with FOA < 0.2. Site-based FOA from both the LWS and HWS indicated that most of the available grasses were highly accepted (FOA ≥ 0.6 for puku, > 0.4 for lechwe [Fig. 2]). *C. dactylon*, which formed the majority of the diets of both species, was widely available (Figs. 1 and 2) but intermediately accepted. *V. nigritana*, *P. mauritianus*, and *A. macrum*, which were important to the seasonal diets of either puku or lechwe, also were intermediately accepted but had lower availabilities than *C. dactylon*. Grass species with the lowest availabilities tended to be those most highly accepted at both puku and lechwe foraging sites (Figs. 1 and 2).

Diet quality.—Fecal nitrogen (percent dry mass basis) did not differ between seasons for puku ($\bar{X} \pm SE$: LWS 1.61 $\pm$ 0.09, HWS 1.52 $\pm$ 0.08; $F_{1,33} = 0.637$, $P = 0.431$) or lechwe (LWS 1.69 $\pm$ 0.08, HWS 1.64 $\pm$ 0.11; $F_{1,28} = 0.148$, $P = 0.704$), nor between herbivore species within seasons ($F_{1,65} = 0.050$, $P = 0.824$). Fecal phosphorus (percent dry mass) levels for puku were significantly lower during the LWS than the HWS (LWS 0.273 $\pm$ 0.029, HWS 0.347 $\pm$ 0.025; $F_{1,33} = 4.211$, $P = 0.048$). Fecal phosphorus did not differ between the LWS and HWS seasons for lechwe (LWS 0.291 $\pm$ 0.025, HWS 0.341 $\pm$ 0.035, $F_{1,28} = 0.254$, $P = 0.618$), or between puku and lechwe within seasons ($F_{1,65} = 0.780$, $P = 0.381$).

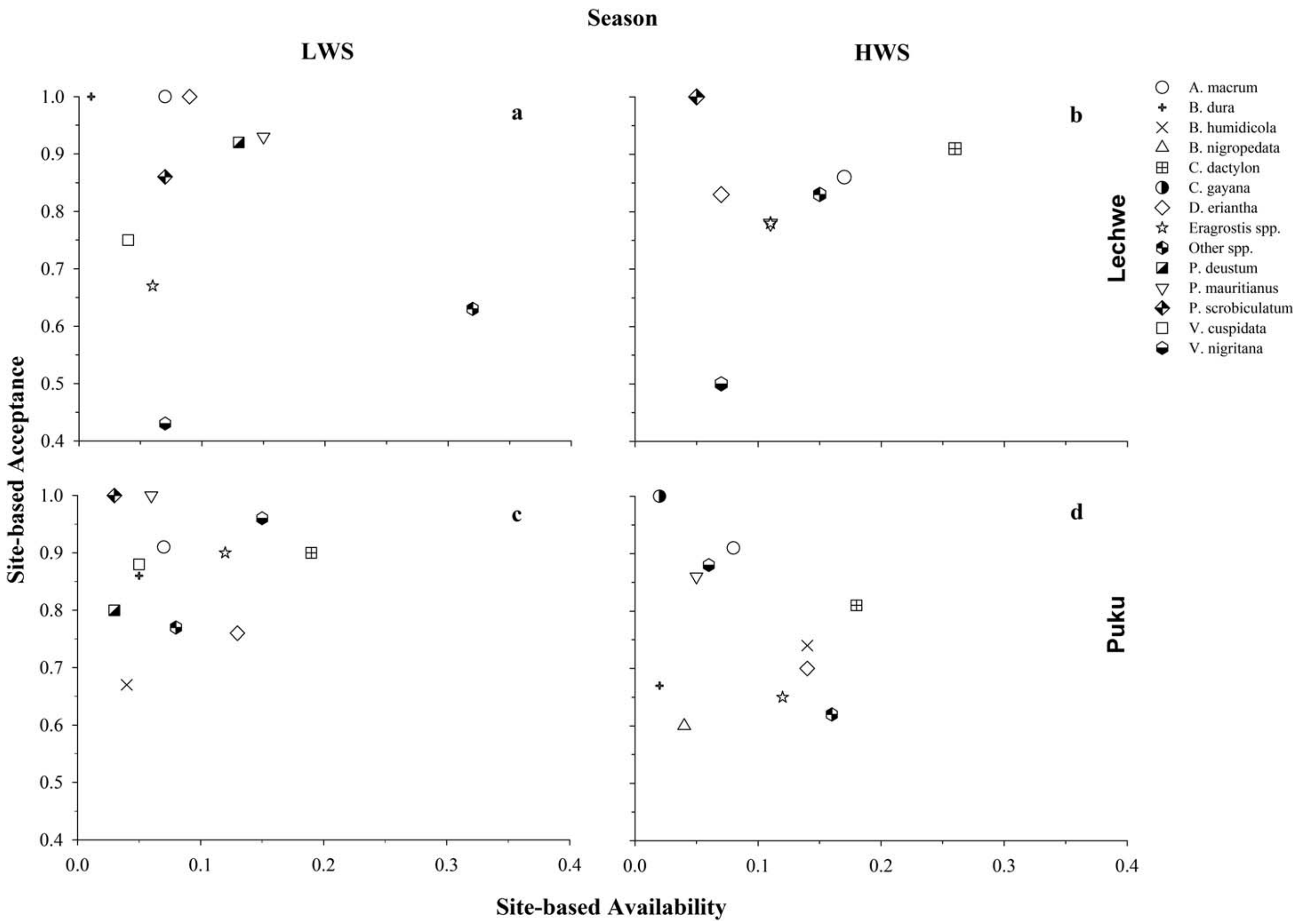

FIG. 2.—Seasonal site-based acceptance and availabilities of grasses in the diets of puku (*Kobus vardonii*) and lechwe (*K. leche*) in Chobe National Park, Botswana. Relative site-based frequency of acceptance values of grass species in the diets of a and b) lechwe and c and d) puku during the low-water season (LWS) and high-water season (HWS) from July 2007 to June 2008. Acceptance values represent the probability of a grass species being eaten when present within a foraging area. Site-based acceptance values closer to 1 indicate preference of that grass species within foraging sites; values close to 0 indicate avoidance of that grass species within foraging sites.

Habitat selection.—During the LWS, grass height, greenness, and cover were the most important variables predicting habitat selection by puku (Table 3). Puku were much more likely to use the interface zone and grassland habitats than shallow swamp, with the odds of use decreasing with increases in grass height and grass greenness, and increasing with grass cover (Table 4). Habitat type and grass cover were in the highest ranking model predicting habitat selection by lechwe during the LWS (Table 3). Similar to puku, lechwe were more likely to use the interface zone and grassland habitats than shallow swamp, with the odds of use increasing with increasing grass cover (Table 4).

During the HWS, grass height, cover, and distance to water were in the most-supported model predicting habitat selection by puku (Table 3). The odds of use by puku was highest in interface zone, high-lying floodplain, grassland, and shrubland habitats with dense swards of short grasses (Table 4). The odds of puku selecting a site were higher in areas farther from water during the HWS; lechwe were more likely to use areas with higher grass greenness and less likely to use areas with higher levels of visual obstruction (Table 4). Contrary to the results for puku, the probability of lechwe using shrublands was significantly lower (Table 4).

In both seasons lechwe foraged in areas that were closer to water and had lower levels of visual obstruction and shrub cover, but had higher levels of grass cover and grass greenness compared to sites used by puku and available sites (Table 5). During the LWS, lechwe fed in areas with shorter grass than those used by puku and at available sites, but during the HWS grass height at lechwe sites was taller than at sites used by puku but lower than generally available (Table 5).

Across seasons, puku consistently fed in areas with shorter grasses than generally available (Table 5). Grass cover was higher at puku foraging sites than generally available during the LWS but not the HWS, whereas distance to water and

Table 3.—Five highest ranking a priori models for probability of use by puku (*Kobus vardonii*) and lechwe (*K. leche*) relative to environmental characteristics in Chobe National Park, Botswana (July 2007–June 2008). Maximized log likelihoods, number of parameters (k), Akaike's information criterion adjusted for small sample size (AIC_C), ΔAIC_C, and Akaike weights are given. LWS = low-water season; HWS = high-water season.

	Model	Log likelihood	*k*	AIC_C	ΔAIC_C	Weight
Puku						
LWS	Grass height + Grass greenness + Grass cover	322.14	4	330.28	0.00	0.989
	Habitat type + Grass cover	327.06	6	339.37	9.08	0.011
	Grass cover	345.46	2	349.50	19.22	0.000
	Grass height + Grass cover + Distance to water	342.31	4	350.45	20.17	0.000
	Grass height	358.44	2	362.48	32.20	0.000
HWS	Grass height + Grass cover + Distance to water	131.37	4	139.66	0.00	0.976
	Grass height + Grass greenness + Distance to water	138.77	4	147.06	7.40	0.024
	Habitat type + Grass cover	149.29	7	164.13	24.46	0.000
	Habitat type + Grass greenness	154.52	7	169.36	29.69	0.000
	Habitat type + Grass height	154.53	7	169.37	29.70	0.000
Lechwe						
LWS	Habitat type + Grass cover	241.71	6	254.03	0.00	1.000
	Habitat type + Grass height	263.94	6	276.26	22.23	0.000
	Grass height + Grass greenness + Grass cover	271.11	4	279.26	25.23	0.000
	Habitat type + Visual obstruction	273.82	6	286.14	32.11	0.000
	Grass height + Grass cover + Distance to water	280.59	4	288.74	34.71	0.000
HWS	Grass greenness + Visual obstruction	46.20	3	52.49	0.00	0.780
	Grass height + Grass greenness	50.51	3	56.80	4.31	0.090
	Grass height + Grass greenness + Grass cover	48.46	4	56.95	4.46	0.084
	Grass height + Grass greenness + Distance to water	49.86	4	58.35	5.86	0.042
	Visual obstruction	60.40	2	64.54	12.05	0.002

shrub and tree cover were less than available during the LWS but not the HWS (Table 5).

Discussion

Our findings showed quite substantial overlap in diet and habitat use between puku and lechwe. Dietary overlap was highest during the HWS when the availability of floodplains was most constricted. Nevertheless, *Brachiaria* spp. made a substantial contribution to the diet of puku, although not eaten by lechwe, whereas the contribution of *D. eriantha* to the diet of puku was twice that of lechwe in the HWS. Both of these grass species are more typically found in upland savannas than in floodplains. On the other hand, *A. macrum* and *P. mauritianus*, species typical of wetlands, contributed more to the diet of lechwe than puku. Correspondingly, although lechwe remained in floodplains during the HWS, puku moved into shrubland habitats. Use of shrubland habitats during the HWS distinguishes the Chobe puku from other populations that have been studied (De Vos 1965; Dowsett 1966; Child and Von Richter 1969; Rees 1978a, 1978b; Rosser 1992; Mills and Hes 1997).

Although the dry season is generally the most nutritionally limiting period for herbivores in African savannas (Western 1975; Sinclair 1977; Owen-Smith 1982), we found little or no seasonal difference in fecal nutritional indicators for our 2 floodplain-inhabiting antelope. Although elevated phosphorus levels in puku feces during the HWS are likely due to consumption of upland grasses, fecal nitrogen and phosphorus concentrations in puku and lechwe remained above the critical thresholds suggested for large ungulates (Grant et al. 1995; Stowe 2003).

Niche partitioning results from species-specific differences in foraging strategies, habitat use, and spatial heterogeneity in forage distribution, forage quality, and predation risk (Owen-Smith and Novellie 1982; McNaughton 1990; Ben-Shahar and Coe 1992; Brown 1992; Fischhoff et al. 2007). High overlap in diet and habitat use indicates the potential for competition when resources are limited relative to animal abundance. However, sympatric herbivores may show distinct foraging strategies resulting from morphological and physiological characteristics (Hofmann and Stewart 1972; Gordon and Illius 1988; Hofmann 1989; Wegge et al. 2006). The main niche distinction that we observed was the tendency of puku to move to upland shrublands during the HWS when habitat availability was most restricted on the floodplains, whereas lechwe stayed in the remaining floodplain habitat. Nevertheless, this difference may not be sufficient to avoid competition (Rosenzweig 1981; Wegge et al. 2006).

Assuming habitat selection is an outcome of fitness maximization (Rosenzweig 1981; Morris 2003), we suggest that the results reported here may have arisen due to 3 possible mechanisms. First, during the HWS, lechwe may have outcompeted puku within floodplain habitats, thereby pushing puku into shrublands. Lechwe are slightly larger in body size compared to puku (Kingdon 1982) and were numerically superior in the Chobe region (R. O'Shaugnessy, in litt.). Higher densities of western kob (*Kobus kob*), a sister species to puku, give them a competitive advantage over waterbuck (*K. ellipsiprymnus*) in Pendjari Biosphere Reserve in Benin (Sinsin

TABLE 4.—Model-averaged logistic regression coefficient estimates, standard errors, odds ratios, and 95% confidence intervals for odds ratios for variables included in the best approximating models for the probability of use by puku (*Kobus vardonii*) and lechwe (*K. leche*) relative to environmental characteristics in Chobe National Park, Botswana (July 2007–June 2008). β-estimates of habitat classes reflect probability of use compared to shallow swamp. *CL* = confidence limit; LWS = low-water season; HWS = high-water season.

	Variable	β	*SE*	Odds ratio	95% confidence limits for odds ratio	
					Lower *CL*	Upper *CL*
Puku						
LWS	Grass height	−0.002	0.001	0.998	0.996	1.000
	Grass greenness	−0.066	0.015	0.936	0.909	0.964
	Grass cover	0.037	0.008	1.038	1.022	1.054
	Interface zone	3.154	1.718	23.428	2.332	235.303
	Low-lying floodplain	1.718	1.065	5.573	0.689	45.036
	High-lying floodplain	2.068	1.064	7.907	0.981	63.761
	Grasslands	3.109	1.134	22.393	2.425	206.721
HWS	Grass height	−0.004	0.001	0.996	0.994	0.998
	Grass greenness	−0.018	0.012	0.982	0.959	1.006
	Grass cover	0.056	0.012	1.058	1.033	1.083
	Distance to water	0.019	0.005	1.019	1.009	1.029
	Interface zone	2.803	1.22	16.499	1.517	179.441
	Low-lying floodplain	2.168	1.390	8.739	0.573	133.304
	High-lying floodplain	2.587	1.171	13.293	1.339	131.923
	Grassland	3.266	1.292	26.209	2.082	329.908
	Shrubland	3.036	1.203	20.827	1.971	220.101
Lechwe						
LWS	Grass cover	0.054	0.010	1.055	1.035	1.076
	Interface zone	2.017	0.685	7.516	1.963	28.777
	Low-lying floodplain	−1.087	0.509	0.337	0.124	0.915
	High-lying floodplain	−1.161	0.030	0.313	0.106	0.922
	Grassland	1.425	0.635	4.158	1.198	14.434
HWS	Grass greenness	0.130	0.039	1.139	1.056	1.228
	Visual obstruction	−0.065	0.022	0.937	0.898	0.978
	Interface zone	1.479	1.182	4.389	0.433	44.525
	Low-lying floodplain	0.401	1.055	1.493	0.189	11.816
	High-lying floodplain	0.354	0.868	1.423	0.259	7.809
	Grassland	−0.927	0.899	0.396	0.068	2.307
	Shrubland	−2.632	0.707	0.072	0.018	0.288

TABLE 5.—Mean and 95% confidence limits for habitat characteristics at foraging sites used by puku (*Kobus vardonii*) and lechwe (*K. leche*) available sites during the low-water and high-water seasons in Chobe National Park, Botswana (July 2007–June 2008). *LCL* = lower 95% confidence limit; *UCL* = upper 95% confidence limit.

	Puku			Lechwe			Available		
	$\bar{X}$	*LCL*	*UCL*	$\bar{X}$	*LCL*	*UCL*	$\bar{X}$	*LCL*	*UCL*
Low-water season									
Distance to water (m)	150.3	100.9	199.6	84.8	56.2	113.4	167.7	149.9	185.3
Grass height (mm)	197.7	169.6	225.8	138.6	117.0	160.1	248.1	223.9	272.4
Grass cover (%)	68.6	64.5	72.6	76.2	71.8	80.6	57.5	54.9	60.0
Grass greenness (%)	71.1	68.8	73.4	74.7	72.5	76.8	74.3	72.8	75.8
Visual obstruction (%)	10.9	8.3	13.5	5.9	3.3	8.7	11.0	9.3	12.8
Shrub cover (%)	0.1	−0.04	0.3	0.02	−0.02	0.7	0.6	0.2	0.9
Tree cover (%)	0.0	—	—	0.0	—	—	0.1	0.02	0.2
High-water season									
Distance to water (m)	154.0	103.6	204.4	16.1	8.4	23.9	86.1	71.3	101.0
Grass height (mm)	236.7	206.0	267.5	251.9	208.1	295.8	488.3	442.9	533.6
Grass cover (%)	46.5	40.4	52.5	72.6	64.5	80.6	53.8	49.7	58.0
Grass greenness (%)	61.6	56.7	66.6	80.9	78.3	83.6	77.2	74.9	79.5
Visual obstruction (%)	37.3	30.9	43.6	10.6	6.9	14.4	46.3	42.5	50.1
Shrub cover (%)	22.8	18.1	27.6	0.0	—	—	12.9	9.8	16.0
Tree cover (%)	3.3	1.8	4.7	0.0	—	—	1.8	1.1	2.5

et al. 2008; Djagoun et al. 2013). High densities of lechwe within floodplains could restrict space and resources available to puku during the HWS, forcing them to move onto uplands.

Second, lechwe often flee into shallow water to escape predators (Rees 1978a, 1978b; Williamson 1990). Reduced predation risk due to lower levels of visual obstruction and close proximity of escape terrain in floodplains may have outweighed negative consequences associated with reduced habitat availability during the HWS. The use of the floodplains by other ungulates also is greatly reduced during the HWS, decreasing interspecific competition from zebra (*Equus quagga*), buffalo (*Syncerus caffer*), and impala (*Aepyceros melampus*), while also decreasing prey concentrations that attract predators (Sheppe and Osborne 1971; Omphile and Powell 2002; de Boer et al. 2010; Valeix et al. 2010).

Third, puku may have actively sought shrubland habitats during the HWS because they are better adapted than lechwe to use upland habitats. Puku in other parts of their range, including the population in the Kilombero Valley, Tanzania, are known to move to the boundary between the floodplains and Miombo woodlands during the HWS (Jenkins et al. 2002). However, along the Chobe River there was an abrupt transition from the floodplain associated with an alluvial terrace, meaning that the extent of drier but still open regions on the floodplain was greatly restricted.

Valeix et al. (2009) found that several ungulate species showed a strong preference for open habitat types with increased visibility in the presence of lions (*Panthera leo*). Personal observations and reports from safari guides suggested that puku experienced higher levels of predation during the HWS compared to the LWS. We found 6 puku carcasses in shrubland habitat during the HWS, compared to 1 carcass found on floodplains during the LWS. The current puku population in Chobe National Park is estimated to be around 125–145 individuals (Dipotso and Skarpe 2006). The lack of nutritional deficiencies reflected in fecal nutrient levels indicates that puku were not subjected to lower-quality foraging habitats within shrublands. Hence, predation during the HWS seems to be the main factor limiting the growth and dispersal of the small puku population in Chobe National Park. Coincidentally, evidence from populations in Zambia (De Vos 1965; Dowsett 1966; Rosser 1992) shows that puku avoid habitats with increased levels of visual obstruction and predation risk and notably these populations number in the thousands. Hence, our findings suggest that niche distinctions between puku and lechwe in Chobe National Park arise mainly in their capacity to remain in floodplain habitats during the HWS and thereby maintain greatest security from predation.

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