Diet and food preference of the waterbuck (*Kobus ellipsiprymnus defassa*) in the Pendjari National Park, Benin

Barthélémy Kassa[1,2*], Roland Libois[2] and Brice Sinsin[1]

[1]*Laboratoire d'Ecologie Appliquée, FSA, UAC, 01 BP 526 Catonou, Bénin and* [2]*Unité de Recherches Zoogéographiques, Bât. B22, Bvd du Rectorat, ULg, 4000, Sart Tilman (Liège), Belgium*

Abstract

This study investigated composition and selectivity in diet for waterbuck in the Pendjari National Park in north-western Benin, through the use of micrographic analysis of faecal samples. Three plant species (*Panicum anabaptistum, Echinochloa stagnina* and *Andropogon gayanus*) were regularly consumed all year round. Meanwhile, three other species (i.e., *Hyparrhenia involucrata, Acroceras amplectens* and *Oryza barthii*) are mostly found in its diet during the beginning of the rainy season. During the dry season, long life grasses (>40%) and tree forage (about 35%) were the most dominant life form in the diet. On the contrary at the beginning of the rainy season, annual species (> 50%) were dominant. In conclusion, the waterbuck has a grazer regime when plant species are abundant and a mixed diet during the dry season. Waterbuck's food niche breath, defined by Hespenheide [*Ecology and Evolution of communities*. Harvard Univ. Press, 1975], was lower than 1, implying this antelope does not eat all food categories in a proportional way. Shannon diversity index showed that the diet was more diversified during the rainy season and less diversified at the end of the dry season. Based on [*Ecology*, **64** (1983), 1297] diet selectivity index, waterbuck exerted a positive selection on the major graminaceous species.

Key words: Bénin, food, Pendjari Park, selectivity, waterbuck

Résumé

Une étude a été réalisée sur le régime et la sélectivité alimentaire du waterbuck dans le Parc National de la Pendjari au Nord-Ouest Bénin à partir d'une analyse micrographique des échantillons de crottes. Trois espèces végétales *(Panicum anabaptistum, Echinochloa stagnina* et *Andropogon gayanus*) sont particulièrement consommées en toutes saisons. La consommation d'espèces annuelles comme *Hyparrhenia involucrata, Acroceras amplectens* et *Oryza barthii,* est observée en saison humide. Durant la saison sèche, l'alimentation du waterbuck est un régime mixte de graminées vivaces (> 40%) et de fourrage ligneux (environ 35%), alors que pendant la saison des pluies ce sont les herbacées annuelle (> 50%) qui dominent. Le waterbuck est donc un animal paîsseur en période d'abondance alimentaire. La largeur de la niche alimentaire du waterbuck est inférieure à l'unité. Donc, le waterbuck ne consomme pas toutes ces catégories alimentaires dans les mêmes proportions. L'indice de diversité de Shannon indique que le régime alimentaire du waterbuck est plus diversifié en saison humide qu'en fin de saison sèche. Les valeurs de l'indice de sélectivité alimentaire de Chesson (1983), indiquent que le waterbuck exerce une sélection positive sur la plupart des graminées consommées.

*Correspondence: E-mail: kbarthimy@yahoo.fr

Introduction

The Pendjari Biosphere reserve in the Republic of Benin is one of the most important and better preserved natural areas in West Africa (Bousquet, 1992; Delvingt, Heymans & Sinsin, 1989; Lamarque, 2004). Many authors were involved in the study of its fauna, mainly birds (Green & Sayer, 1979) and mammals (PNUD/FAO, 1981; Delvingt, 1987; Sinsin *et al.*, 2001, 2002, 2004), pointing out its high number of species, its diversity and scientific interest. However, in the past few years, Sinsin *et al.* (2001, 2002, 2004) and di Silvestre, Sinsin & Daouda (2003) have noticed a progressive reduction in the waterbuck

population (*Kobus ellipsiprymnus defassa*), from 3000 individuals in 1976 to 120 in 2004.

Despite important conservation measures (against poaching) recently implemented by the National Centre for the Fauna Reserves Management, the demographic condition of this antelope remains a subject of great concern (MAEP, 2004).

The quality and availability of food resources is undoubtedly one of the constraints to the population dynamics of ungulates (Sinclair, 1977; Boyce, 1992; Mwangi & Western, 1998). In African savannah ecosystems, the mortality induced either by food shortage or by a significant decrease in food quality can even exceed the deaths caused by the various predators (Sinclair, 1977; Bousquet, 1984).

This study aimed at gathering information on the diet of the waterbuck during the dry season, i.e., during a period of severe reduction of food availability and quality (Fournier, 1987, 1994). Hopefully, information about the grazed species and the antelope's diet selectivity will help to understand and prevent the above-mentioned decline.

Fig 1 Study area location (National Park of Pendjari)

Study area

The Pendjari biosphere reserve (National Park–PNP) is located in the dry Sudanese region of Benin, at the boundary with Burkina-Faso (in the north-western part of the country). It covers an area of 4711.4 km^2, extending from 10°30′ to 11°30′N and from 0°50′ to 2°00E (Fig. 1).

Mean monthly temperature varies from 19°C during the cold dry season (end of October to mid February) to 34°C during the hot dry season (mid February to mid May). At this time, the temperature rises to 43°C during the day. The rainy season runs from mid May to mid October when the wind regime changes from the 'harmattan' (cold and dry northern wind) to the maritime trade-winds. The mean yearly rainfall is around 1100 mm. The monthly average relative humidity varies between 25% and 85%.

The PNP is limited by the foothills of the Atacora massif in the East and by the river Pendjari in the North and the West. Large hills (hills of Buem) and floodplains are also present. Therefore, during the rainy season, nearly 60% of its area is covered with water.

Under the pressure of the 'Harmattan winds' the Park gradually dries up from the end of the rainy season in October, with a peak in February and March. Meanwhile there are points of large ponds near the river (Tiabiga, Fogou, Mondri, Diwouni and Yangouali) or in the centre of the park (Bali). During the dry season, the ponds attract a variety of animal population, especially large mammals in search for water.

The vegetation cover of the PNP is made up of a mosaic of grasses, shrubs, trees and woodland savannas which are burnt every year. In the floodplains, *Mitragyna inermis, Panicum anabaptistum, Schyzachirum rupestre, Andropogon canaliculatus, Vetiveria nigritana, Andropogon* spp. and *Hyparrhenia* spp. are the most dominant. In drier areas, the main grass species found belong to the *Andropogon* and *Hyparrhenia,* whereas in wetter areas species such as *V. nigritana, P. anabaptistum, S. rupestre, A. canaliculatus* are found.

Methods

Material

Waterbuck dropping samples were collected every month (40 samples per month), except in March and in May, from January to July 2004, covering three climatic periods: the cold-dry season (January–February), the hot-dry season (April) and the rain season at its beginning (June–July). Simultaneously, a reference collection of plant species likely to be eaten by waterbucks was made: green parts of

grasses, leaves of trees, bark fragments were collected in the forest, identified to species, air dried and then finely chopped (mixer with 250 μ meshes).

Droppings sample and referential plant species were conditioned in the lab for 30 min and at 90°C into a mixture of 225 ml water, 525 ml acetic, 21 g trichloracetic and 51 ml nitric acids. After two centrifugation runs (2000 rpm, during 10 min), the acids are removed and the sample is stored in denaturized alcohol.

The identification of plant fragments in droppings is based on the observation of epidermal features which can discriminate between the different species (Norris & Bukovac, 1968; Stewart & Stewart, 1971; Maizeret, Boutin & Sempéré, 1986).

At the beginning of this study on waterbuck droppings, reference elements were prepared by mounting a small drop of the alcoholic suspension on a microscopic slide and taking photographs of the cytological structures characterizing each species (Metcalfe & Chalk, 1950; Metcalfe, 1960).

The samples of waterbuck droppings were prepared in the same way, and three different slides were prepared for each dropping.

The slides were screened and the different fragments identified by comparison with the photographs of the reference collection. All the fragments were counted and the relative occurrence of each plant species calculated. A few pieces were discarded as they did not show any interesting features. No consideration was given to thick fragments as their opacity hinders observation.

Data analysis

All the slides prepared from droppings of a particular month were pooled in a monthly sample. For every month, the Shannon diversity index ($H' = -\sum p_i.\log_2(p_i)$: Shannon, 1948) and the Food Niche Breadth (FNB = $((\sum {p_i}^2)^{-1}-1)/(n-1)$: Hespenheide, 1975) were evaluated (n = number of species in the diet; P_i = relative number of fragments of the i^{th} species). FNB varies from 0 when a single food category appears to be dominant to 1 when all the food categories are equally represented in the diet.

Monthly frequency distributions were compared using a *G*-test (Sokal & Rohlf, 1995). Food selectivity was also studied, computing the Chesson (1983) S_i index, comparing the ratio of a food category in the diet (R_i) with its ratio in the habitat (P_i) using the following formula, where n is the total number of species in the diet:

$$S_i = \frac{R_i/P_i}{\sum_{i=1}^{n} R_i/P_i}$$

S_i varies between 0 and 1 and there is a preference (selectivity) when $S_i > 1/n$ or an avoidance when $S_i < 1/n$.

To test the statistical significance of the differences between S_i and 1/n, 1000 S_i values were computed for each food category by a bootstrap procedure (Manly, 1990; Efron & Tibshirani, 1993). The average S_i obtained was then compared with the 1/n value using Student's *t*-test (Palm, 2002).

P_i ratios were obtained from Gbédjinon (2003) and Kassa (2003).

Results

To check the accuracy of the results, a graphic test was done to show the progress of potential food species as the screening of the slides goes on (Fig. 2). From this graph, the relative frequencies of occurrences are nearly stable after the examination of 60–65 slides. Such a graph was drawn for each month and the analysis continued until the frequencies became stable. The results as presented in this study should therefore be considered as representative of the diet of the waterbuck in the study area.

In PNP, 27 plant categories were identified in the diet of the waterbuck (Table 1). The study period revealed that three species (*Panicum anabaptistum, Echinochloa stagnina* and *Andropogon gayanus*) are commonly eaten by the waterbuck whereas the consumption of the other species occurs at specific periods:

- *Vetiveria nigritana* and, to a lesser extent, *Cyperus quadrangularis* and *Acacia sieberiana* are important throughout the dry season. Although the relative occurrence of the two latter species decreased through the time.
- *Grewia mollis, S. rupestre* and *A. canaliculatus* are eaten only during the cold-dry season and in low proportions.
- At the end of the hot-dry season *Pteleopsis suberosa, Cymbopogon giganteus* and *Terminalia avicennioides* are eaten, but their importance remains rather marginal.
- During the rainy season, *Hyparrhenia involucrata, Acroceras amplectens, Oryza barthii, Tephrosia bracteolata, Brachiaria jubata, Diheteropogon amplectens* and some other species of minor importance appeared and replaced nearly all the food categories eaten during the dry season.

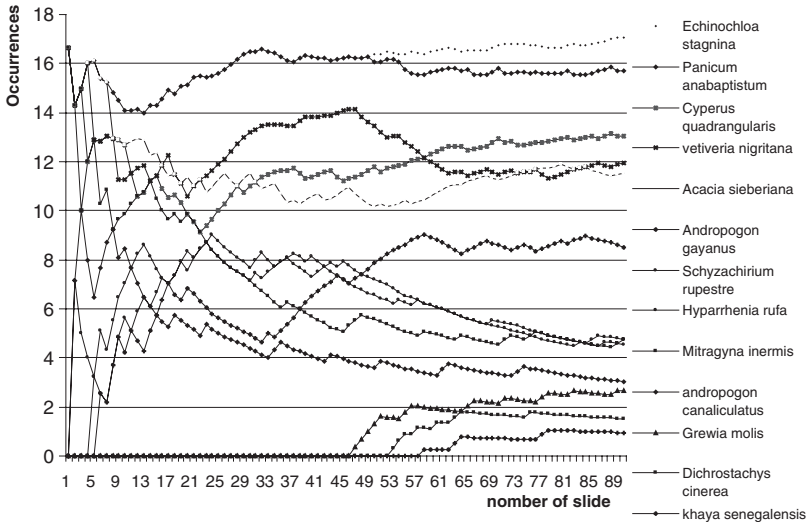

Fig 2 Evolution of the proportions of the different food categories of January

Table 1 List and diet category occurrences

TB	Species	January	February	April	June	July
He	*Panicum anabaptistum*	0.25	0.083	0.029	0.064	0.05
Ge	*Echinochloa stagnina*	0.25	0.117	0.036	0.04	0.06
He	*Andropogon gayanus*	0.083	0.354	0.505	0.188	0.123
Ph	*Acacia sieberiana*	0.08	0.057	0.0182	0	0
Ph	*Mitragyna inermis*	0.02	0.005	0.037	0	0
He	*Vetiveria nigritana*	0.13	0.205	0.158	0	0
Ge	*Cyperus quadrangularis*	0.08	0.065	0.035	0	0
Ph	*Grewia molis*	0.025	0.05	0	0	0
He	*Schizachyrium rupestre*	0.023	0.05	0	0	0
He	*Andropogon canaliculatus*	0.012	0.006	0	0	0
Ph	*Khaya senegalensis*	0.007	0	0.005	0	0
He	*Hyparrhenia rufa*	0.019	0	0	0	0
Ph	*Dichrostachys cinerea*	0.011	0	0	0	0
Ge	*Cissus gracilis*	0	0.008	0	0	0
Ph	*Pteleopsis suberosa*	0	0	0.026	0	0
He	*Cymbopogon giganteus*	0	0	0.07	0	0
Ph	*Terminalia avicennioides*	0	0	0.035	0	0
Th	*Hyparrhenia involucrata*	0	0	0	0.29	0.213
Th	*Acroceras amplectens*	0	0	0	0.192	0.175
Th	*Oryza barthii*	0	0	0	0.139	0.12
Th	*Commelina* sp.	0	0	0	0.022	0.02
Th	*Tephrosia bracteolata*	0	0	0	0.064	0.115
He	*Brachiaria jubata*	0	0	0	0.04	0.05
He	*Diheteropogon amplectens*	0	0	0	0.01	0.045
Th	*Rottboellia cochinchinensis*	0	0	0	0.002	0.005
Th	*Andropogon fastigiatus*	0	0	0	0	0.011
Ch	*Melochia corchorifolia*	0	0	0	0	0.002

TB (Biological type); Th (Therophyte); He (Hemicryptophyte); Ch (Chamephyte); Ge (Geophyte); Ph (Phanerophyte).

These seasonal differences are highly significant ($G = 14{,}767.85$; $P < 0.001$). In January and February, only four grasses (*E. stagnina, Panicum anabaptismum, V. nigritana* and *A. gayanus*) make up the bulk of the waterbuck's diet. In January, a tree (*A. sieberiana*) is significantly included in the diet as well as *C. quadrangularis*. In April, the diet is largely dominated by *A. gayanus* alone, the only most frequent perennial grass to be found in June and July. During the rainy season, the waterbucks eat mostly three annual grasses *(H. involucrata, A. amplectens* and *O. barthii*) and a leguminous plant (*T. bracteolata*). Likewise certain trees such as *Khaya senegalensis, T. avicennioides, Mitragyna inermis* are of marginal importance in the diet.

In conclusion, during the dry season, the major part of the diet is made up of perennial (hemicryptophytes) and geophyte species with more than 50 and 10–30% of the occurrences respectively. After the first rain, notwithstanding the important part (30%) still taken by the hemicryptophytes, the situation changes completely as annual species (therophytes) represented more than 60% of the diet. These annual species are mostly grasses. Trees and chamephytes appeared only during the dry season, as a minor but significant part of the diet.

Food niche breadth and Shannon diversity index vary accordingly, decreasing from January to Apri1 and then increasing to a maximum value in July. For January, February, April, June and July, the food niche breadth values are 0.42, 0.39, 0.21, 0.4 and 0.55 respectively. For the same period, Shannon diversity index's value is 2.96, 2.72, 2.5, 2.98 and 3.15 bits respectively. This indicates a rather monotonous diet at the end of the dry season on the one hand, and a more diversified diet after the first rain on the other hand.

Selectivity indexes are presented in Fig. 3. The zero corresponds to the inverse of the number of food categories (1/n). Therefore, the positive values indicate a food preference, whereas the negative ones show food avoidance. Confidence intervals (95%) are also shown to allow the detection of significant deviation from the null hypothesis (no selectivity).

In January, waterbuck clearly preferred *E. stagnina* and, to a lesser extent, *A. sieberiana, Panicum anabaptistum* and *C. quadrangularis*, whereas other species were avoided. *V. nigritana* and *Dicrostachys cinerea* are consumed in the same proportion as they occur in the bush. In February, waterbuck preference is *A. gayanus, Panicum anabaptistum, V. nigritana* and *E. stagnina*, while *A. canaliculatus, Mitragyna inermis* and *Cissus gracilis* were avoided.

Andropogon gayanus and *V. nigritana* were still preferred in April whereas other available species (e.g. *E. stagnina, C. quadrangularis*) were equally selected and eaten. At the beginning of and during the rainy season, the antelopes dietary preferences considerably change, as they grazed preferentially annual grasses and forbs such as *O. barthii, H. involucrata, A. amplectens and T. bracteolata.*

Discussion

Several authors have shown that it is important to assess the quantity and quality of the most and the least eaten plant species making up the bulk of an herbivore's diet (Cavender & Hansen, 1970; Laitat, 1982; Maizeret *et al.*, 1986; Maillard & Picard, 1987; Ego, Mbuvi & Kibet, 2003). The present results are therefore probably not exhaustive but the dietary importance of the possible 'missing categories' is certainly insignificant, at least in a quantitative point of view.

During this study, 27 plant species were found in the faeces of the waterbuck. A comparable figure (26 species) was reported by Herbert (1972) in South Africa (Sabi-Sand natural reserve). Nevertheless, in the W National Park (Republic of Benin), i.e. in the same phytogeographical conditions, Ayegnon (2004) found only thirteen species. However, his samples were exclusively collected in February and are therefore very close to the figure (eleven species in February) found in this study. It clearly appears that the number of species found in the waterbuck's diet each month does not vary significantly, i.e., between eleven and thirteen. *Pennicetum pedicelatum, H. involucrata, E. stagnina, V. nigritana* and *A. gayanus* are the common species found in the waterbuck diet in the W National Park (Ayegnon, 2004).

The samples collected concerned three different periods. the first 2 months relate to the onset of the dry season. The second period starts from April which is the most critical month as most grasses and forbs faded and only available as straw. The third period starts with the rain in June and July when, the vegetation recovers. The diet of the waterbuck changes according to those environmental conditions: its species composition varies as well as its diversity.

During the dry season, when conditions are at the worst, the antelopes mainly feed on a few species whereas in the rainy season, the diet is more diversified. In other areas, similar observations were made about the waterbuck's diet (Child & Richter, 1969; Herbert, 1972) and also about the

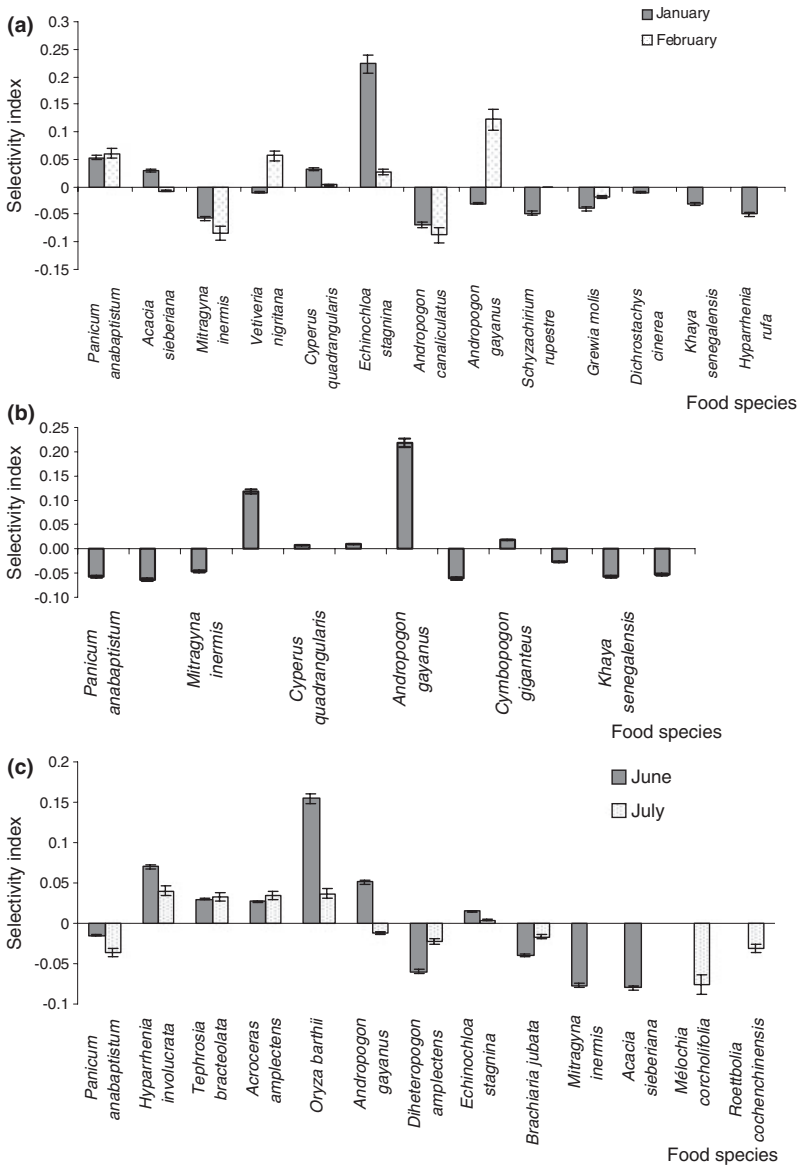

Fig 3 (a) Chesson's selectivity index calculated for food species of January and February. (b) Chesson's selectivity index calculated for food of April (c) Chesson's selectivity index calculated for food species of June and July

diet of other large herbivores: the black rhino, *Diceros bicornis* (Waweru, 1985; Muya, 1993; Muya & Oguge, 2000), lesser kudu *(Tragelaphus imberbis*) (Owen-Smith, 1994), eland (*Taurotragus oryx)* (Watson & Owen-Smith, 2000), hartebeest *(Alcelaphus buselaphus*), and wildebeest (*Connochaetes taurinus*) in Kenya (Ego *et al.*, 2003). As demonstrated on the buffalo (*Syncerus caffer*) and the wildebeest in the Serengeti National Park, the dry season is a period of severe food shortage and of a sharp reduction in food quality (e.g., low protein content). When shortages persist, as was the case in the 1960s in the Serengeti, the consequences for the herbivores might be very severe (Sinclair, 1977).

Most of the grass species positively selected by the waterbuck in all seasons have relatively high protein content. *Panicum anabaptistum, A. gayanus* and *E. stagnina* are the most interesting from this point of view during the most critical times of the dry season (Kassa & Gnagnon, 2006). At the same time, *V. nigritana* with its high level of digestible cellulose (i.e., energy content) is particularly appreciated by the antelope. In the Kenyan savannahs of the Nakuru N.P., Mwangi & Western (1998) have noticed

starvation often leading to death of the waterbuck, compared with the buffalo or to the impala when the food quality is dropping.

Of course, the diet composition is highly dependant on vegetation phenology. Some species are eaten and preferred in special circumstances. Several grasses appear to be selected during more than one period all over the study area: *E. stagnina* and *Panicum anabaptistum* during the cold dry season and *A. gayanus* from February to June. The only phanerophyte which is positively selected is *A. sieberiana.* Because the waterbuck is a grazer, this could be viewed as exceptional. However, this preference is observed in January while the tree is in fructification, and the nice flowers' smell attracts the baboons and a number of herbivores (Baumer, 1995). For the waterbuck, green husks left by the baboons under the trees are a valuable sweet food. *Vetiveria nigritana* is selected from February i.e. just when young stems sprout after fires events. Annual grasses *(O. barthii, A. amplectens, H. involucrata*) are only eaten after the first rains, when they become available again.

During the rainy season when food is abundant, several herbivores become more selective (Muya & Oguge, 2000; Ego *et al.*, 2003), their choice being particularly guided by a higher protein content (Sinclair, 1977; Gartlan *et al.*, 1980; Holechek, Martin & Pieper, 1982) and this may explain why the waterbuck prefers the hard stems of *A. gayanus* to the young soft sprouts of annual grasses.

Food choice by animals also depends on vegetation condition (Fournier, 1994; Kassa, 1998). In Nazinga ranch, Ouédraogo (2005) noted that fire and rain are the most important factors affecting the diet composition of waterbuck. In Pendjari National Park, Gbédjinon (2003) found that perennial grasses (e.g. *V. nigritana, A. gayanus* and *Panicum anabaptistum*) are widely browsed by herbivores after fire. This is certainly related to the abundance of the straw at the end of the wet season.

References

Ayegnon, D.T.D. (2004) *Ecologie alimentaire de quelques grands herbivores du Parc du W, et leur rôle dans la dissémination des herbacés: le cobe de Buffon (Kobus kob) le redunca (Redunca redunca), le code Defassa (Kobus defassa)*. Mémoire DEA, FLASH/UAC, Abomey-Calavi, Bénin.

Baumer, M. (1995) *Arbres, arbustes et arbrisseaux nourriciers en Afrique occidentale*. Enda-Editions, Dakar, Sénégal.

Bousquet, B. (1984) *Méthodes et résultats des inventaires des grands mammifères en vue de leur gestion rationnelle en Haute Volta*. Thèse de doctorat, Université de Languedoc, France.

Bousquet, B. (1992) *Guide des Parcs Nationaux d'Afrique. Afrique du Nord et Afrique de l'Ouest*. Delachaux et Niestlé, Paris.

Boyce, M.S. (1992) Wolf recovery for Yellourstone National Park: a simulation model. In: *Wildlife 2001* (Eds D. R. McCultlough and R. A. Barrett). Elsevier Science. Publishers LTD, London, USA.

Cavender, R.B. & Hansen, R.M. (1970) *The Microscope Method Used for Herbivore Diet Estimates and Botanical Analysis of Litter and Mulch at Pawnee Site*. Grassl. Biome, Us Int Biol. Prog. Techn. Report no. 18, New York.

Chesson, J. (1983) The estimation and analysis of preference and its relationship to foraging model. *Ecology* **64,** 1297–1304.

Child, G. & Richter, W.V. (1969) Observation on ecology and behaviour of lechwe, puku and waterbuck along the Chobe River, Botswana. *Z. f. Säugetierkunde* **34,** 275–295.

Delvingt, W. (1987) *Rapport sur l'évaluation des populations de grands mammifères dans le Parc National et la zone Cynégétique de la Pendjari*. PAPN/DFRN/MDR, Cotonou, Bénin.

Delvingt, W., Heymans, J.-C. & Sinsin, B. (1989) *Guide du Parc National de la Pendjari*. CECA-CEE-CEEA, DFRN/MDR, Cotonou, Bénin.

di Silvestre, I., Sinsin, B. & Daouda, I. (2003) *Mission sur les grands et moyens mammifères menacés dans les parcs nationaux et zones cynégétigues du Bénin*. MAEP/CENAGREF/AGRECO, Cotonou, Bénin.

Efron, B. & Tibshirani, R.J. (1993) *An Introduction to the Bootstrap*. Chapman and Hall, New York.

Ego, W.K., Mbuvi, D.M. & Kibet, P.F.K. (2003) Dietary composition of wilbdebeest (*Connochaetes taurinus*), kongoni (*Alcephalus buselaphus)* and cattle (*Bos indicus)*, grazing on a common ranch in south-central Kenya. *Afr. J. Ecol.* **41,** 83–92.

Fournier, A. (1987) Cycle saisonnier de la phytomasse et de la production herbacée dans les savanes soudaniennes de Nazinga (*Burkina faso*). Comparaison avec d'autres savanes ouest africaines. *Bull. Ecol.* **18,** 409–430.

Fournier, A. (1994) Cycle saisonnier et production nette de la matière végétale herbacée en savanes soudaniennes pâturées. Les jachères de la région de Bondoukuy (Burkina Faso). *Ecologie* **25,** 173–188.

Gartlan, J.S., Mckey, D.B., Waterman, P.G. & Struhsaker, T.T. (1980) A comparative study of the phytochemistry of two African rain-forests. *Biochem. Sys. Ecol.* **8,** 401–422.

Gbédjinon, R.A. (2003) *Etude comparative de l'effet des brûlis dans l'aménagement des aires protégées: périmétre des mares Fogou et Diwouni dans la Réserve de Biosphère de la Pendjari*. Mémo. DTI. EPAC/UAC, Abomey-Calavi, Bénin.

Green, A. A. & Sayer, J.A. (1979) *Développement des Parcs Nationaux du Bénin Plan directeur du Parc National de la Pendjari; FAO/DP/BEN/77/011*. Rapport Technique 1, Rome.

Herbert, H.J. (1972) The population dynamics of the waterbuck *Kobus ellipsiprymnus* (Ogilby, 1833) in the Sabi-Sand wildtuin. *Mammalia depicta*, Allemagne, Berlin.

Hespenheide, H.A. (1975) Prey characteristics and predator niche width. In: *Ecology and Evolution of Communities* (Eds M. L. Cody and J. M. Diamond). Harvard Univ. Press, London.

HOLECHEK, L.H., MARTIN, V. & PIEPER, R.D. (1982) Botanical composition determination of range herbivore diets : a review. *J. rang. Manag* **35,** 600–608.

KASSA, B. (1998) *Problématique de l'aménagement écologique pour la conservation des ressources fauniques dans le Parc National du W au Bénin : Périmètre de Kérémou*. Th. Ing. Agro, FSA/UNB, Abomey-Calavi, Bénin.

KASSA, B. (2003) *Evaluation du pâturage exploité par le waterbuck et le cob de Buffon autour des pleines d'inondation de la Pendjari*. LAE/FSA/UAC, Cotonou, Bénin.

KASSA, B. & GNAGNON, I. (2006). *Structure et composition de l'habitat du waterbuck dans le Parc, National de la Pendjari*. Rapport de stage de fin de cycle. EPAC/UAC, Abomey-Calavi, Bénin.

LAITAT, E. (1982) *Méthodologies spécifiques de détermination du régime alimentaire d'ongulés sauvages*. Mémorie, Faculté des Sciences Agronomiques de Gembioux, Belgique.

LAMARQUE, F. (2004) *Les grands mammifères du complexe WAP*. ECOPAS, Ouagadougou, Burkina Faso, 101p.

MAEP (2004) *Rapport d'évaluatian du Projet Pendjari*. Rapport Technique. GTZ-DPNP/CENAGREF, Cotonou, Bénin.

MAILLARD, D. & PICARD, J.F. (1987) Le régime alimentaire automnal et hivemal du chevreuil (*Capreolus capreolus*) dans une hêtraie calcicole, déterminé par l'analyse des contenus stomacaux. *Gibier faune sauvage* **4,** 1–30.

MAIZERET, C., BOUTIN, J.M. & SEMPÉRÉ, A. (1986) Intérêt de la méthode micrographique d'analyse des fèces pour l'étude du régime alimentaire du chevreuil (*Capreolus capreolus*). *Gibier faune sauvage* **3,** 159–183.

MANLY, B.F.J. (1990) On the statistical analysis of niche overlap data. *Can. J. Zool.* **68,** 1420–1422.

METCALFE, C.R. (1960) *Anatomy of the Monocotyledons*, Vol I *Graminee*. Oxford at the Clarendon press, USA.

METCALFE, C.R. & CHALK, L. (1950) *Anatamy of the dicotyledons*. Vol. I et II. Oxford at the Clarendon press, USA.

MUYA, S.M. (1993) *Nairobi National Park black rhino food plant herbarium report*. Unpublished Technical Report. Rhino Conservation Programme, Kenya wildlife service, Nairobi.

MUYA, S.M. & OGUGE, N.O. (2000) Effects of browse availability and quality on black rhino *(Diceros bicornis michaeli*). *Afr. J. Ecol.* **38,** 62–71.

MWANGI, E.M. & WESTERN, D. (1998) Fluctuations in food supply in an insularised and heavily grazed savannah ecosystem in Kenya. *Afr. J. Ecol.* **36,** 207–212.

NORRIS, C. & BUKOVAC, F. (1968) Structure of the pear leaf cuticle with special reference to cuticular penetration. *Am. J. Bot* **55,** 975–983.

OUÉDRAOGO, M. (2005) *Régulation de la dynamique des populations de buffles (Syncerus caffer Sparrman) et de waterbucks (Kobus ellipsiprymnus Ogilby) et moyens de gestion à mettre en oeuvre pour préserver l'équilibre des communautés végétales dans le ranch de Nazinga (Burkina Faso)*. Thèse de Doctorat; Faculté universitaire des Sciences Agronomiques de Gembloux, Belgique.

OWEN-SMITH, N. (1994) Foraging responses of Kudus to seasonal changes in food resources: elasticity in constraints. *Ecology* **75,** 1050–1062.

PALM, R. (2002) Utilisation du bootstrap pour les problèmes statistiques liés à l'estimation des paramètres. *Biotechnologie, agronomie, société et environnement* **6,** 143–153.

PNUD/FAO, (1981) *Développement des Parcs Nationaux. Bénin. Les mammifères du Parc National de la Pendjari*. PNUD/FAO, Rome, Italy.

SHANNON, C.E. (1948) A mathematical theory of communication. *Bell System Tech. J.* **27,** 379–423.

SINCLAIR, A.R.E. (1977) *The African Buffalo. A Study of Resource Limitation of Population*. University of Chicago Press, Chicago.

SINSIN, B., KASSA, B., TIOMOKO, D., ASSOGBADJO, A. & SOGBOHOSOU, E. (2001) *Dénombrement aérien des grands mammifères dans la Réserve de Biosphère de la Pendjari (Rapport technique)*. CENAGREF–GTZ/MDR, Cotonou, Bénin.

SINSIN, B., TÈHOU, A.C., DAOUDA, I. & SAÏDOU, A. (2002) Abundance and species richness of large mammals in Pendjari National Park in Benin. *Mammalia* **66,** 369–380.

SINSIN, B., KASSA, B., TIOMOKO, D. & TÈHOU, A. (2004). *Dénombrement aérien de la faune sauvage dans la Réserve de Biosphère de la Pendjari*. Rapport Technique GTZ-Pendjari, CENAGREF/MAEP, Cotonou, Bénin.

SOKAL, R.R. & ROHLF, F.J. (1995) *Statistical Tables*, 3rd edn. W. H. Freeman, NewYork.

STEWART, D.R.M. & STEWART, J. (1971) Comparative food preferences of five east African ungulates at different seasons. In: *The Scientific Management of Animal and Plant Communities for Conservation* (Eds E. DUFFY and A. S. WATT). Blackwell Scientific publication, Oxford, UK.

WATSON, L.H. & OWEN-SMITH, N. (2000) Diet composition and habitat selection of eland in semi-arid shrubland. *Afr. J. Ecol.* **38,** 130–137.

WATSON, L.H. & OWEN-SMITH, N. (2002) Phenological influences on the utilisation of woody plants by eland in semi-arid shrubland. *Afr. J. Ecol.* **40,** 65–75.

WAWERU, F.K.J. (1985) *Populatron status, ranging patterns and feeding strategies of the black rhinoceros (Diceros bicomis* L.), Nairobi National Park. Msc thesis, University of Nairobi, Kenya.

(Manuscript accepted 2 July 2007)

doi: 10.1111/j.1365-2028.2007.00827.x