

Spatial and Seasonal Variation of Major Cation and Selected Trace Metal Ion Concentrations in the Okavango-Maunachira-Khwai Channels of the Okavango Delta

By Wellington R.L. Masamba and Andrew Muzila¹

Abstract

The concentration of the metal ions Na, K, Ca, Mg, Zn, Cu, Mn, Co, Fe, Cr, Ni, and Pb were determined in water samples of the Okavango Delta's panhandle - Maunachira-Khwai water system during periods of high (June 2004) and low (November 2004) water flow. The concentrations of Na (1.67 to 12.77 mg/L), K (1.37 to 5.80 mg/L), Ca (2.46 to 6.98 mg/L) and Mg (0.69 to 2.83 mg/L) increased with distance from Mohembo indicating concentration of these metal ions by evaporation. Cu (up to 0.028 mg/l), Co (up to 0.053 mg /L), Fe (0.010 to 0.60 mg/L), Ni (up to 0.052mg/L), Mn (up to 0.044 mg/L) and Pb (0.017 to 0.28 mg/L) generally decreased in concentration with increase in distance from Mohembo, indicating that the Delta acts as a filter for these ions. Zn (0.049 to 0.101 mg/L) had lower concentrations at Mohembo than the other sampling sites, indicating solubilisation of previously deposited metals ions, or presence of Zn within the Delta. Chromium was not detected except at Seronga (0.026 mg/L) during periods of high water flow

Introduction

The sustainability of the Okavango Delta depends primarily on the quantity and quality of water that comes in from its catchment in Angola and Namibia. However, very few water quality studies have been carried out on the Okavango Delta, presumably because the Okavango basin is considered to have little industrial, agricultural or other human developments that could lead to pollution. Major ion chemistry of the lower Boro River showed that the waters could be characterised as calcium-sodium-bicarbonate, with moderate alkalinity and moderate to high amounts of silica (Sawula and Martins, 1991). The metal ions determined in this study were Ca, Mg, Na and K. In another study, dissolved trace metals in the Boro River were found to have concentrations in the sub- $\mu\text{g/l}$ level for transitional metals except Fe, Mn and Zn (Sawula *et al*, 1990). A water monitoring programme of the Okavango Delta reported, among other water quality parameters, the mean concentrations of Ca, Mg, K, Fe, Mn and Al (Cronberg *et al*, 1995). Water samples from areas around the Upper Panhandle, Lower Panhandle, North-Western Moremi Game Reserve and South East of Chief's Island were analysed for Ca, Mg, Na, K, Fe and Mn as part of a rapid biological assessment of the aquatic ecosystems of the Okavango Delta (Ashton *et al*, 2003). In most of these studies, analysis was done for only a few metal ions, and the emphasis was on the Jao/Boro River system (Warmeant, 1997). It is however known that, generally, there is a gradient of increasing concentration towards the outlet as well as the edges of the Delta.

Metal contamination of aquatic ecosystems is important because some metals are toxic to plants and/or animals. For example, Pb and Cr (as Cr^{6+} compounds) are toxic to humans. Lead can cause several unwanted effects, such as disruption of the biosynthesis of haemoglobin

¹ Authors: Harry Oppenheimer Okavango Research Centre, University of Botswana, Private Bag 285, Maun.Tel: 267 6861833. Email: wmasamba@orc.ub.bw

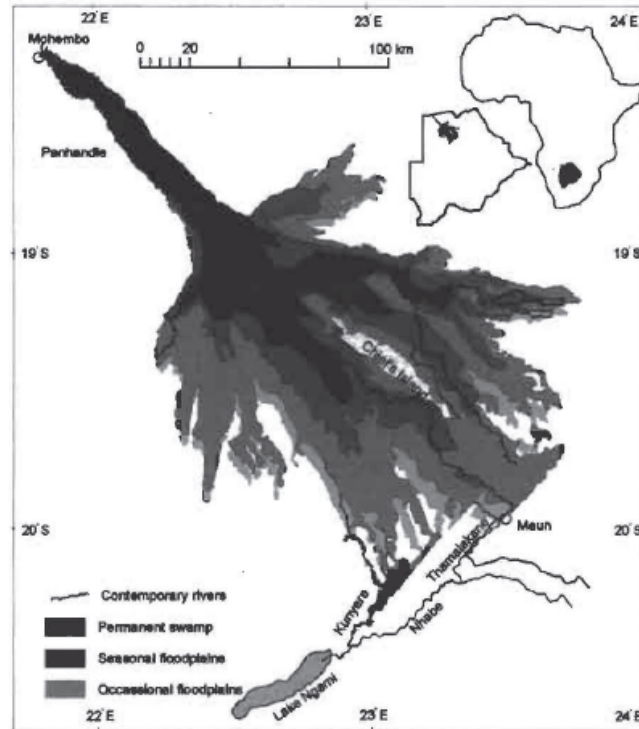


Figure 1. Map of the Okavango Delta showing Sampling locations.

and anaemia, a rise in blood pressure, kidney damage, miscarriage and abortion, disruption of the nervous system, brain damage, reduced fertility of men through sperm damage, diminished learning abilities of children, behavioural disruption of children, impulsive behaviour and hyperactivity (Patnaik, 1999). Many Cr^{6+} compounds are carcinogenic (Patnaik, 1999).

Further it is recommended that water used for crop irrigation have no more than the following maximum concentrations in mg/L (assuming a 10000 m³ water per hectare per year consumption) Al (5.0), Cd (0.01), Co (0.05), Cr (0.10), Cu (0.20), Fe (5.0), Mn (0.20), Ni (0.20), Pb (5.0) and Zn (2.0) (Csuros and Csuros, 2002; Manaham, 2000). Other problems arise from presence of metals in water, including the staining of fixtures (iron and manganese) and consumption of too much soap (calcium and magnesium). Studies of metal contaminants are also important because metals are persistent as they cannot be degraded further (Cunningham *et al*, 1998). The potential for the introduction of metals into water exists from landfills, detergents, sewage, agriculture and the transport sector (e.g. boats) within the catchment area (Ashton *et al*, 2003).

The Okavango Delta is a tourist attraction centre and is very rich in biodiversity. Increases in developmental activities in the Delta and its catchment area, such as agriculture and tourism, as well as the cessation of hostilities in Angola, indicate that there is potential for an increase in concentrations of toxic constituents in the Delta. Baseline studies are needed in order to assess future impacts.

Study Area

This study focused on the distribution and concentration of major cations (Na, K, Ca and Mg) and trace metal ions (Co, Cr, Cu, Fe, Mn, Ni, Pb and Zn), in water samples along the Okavango-Maunachira-Khwai river channel in the northeastern portion of the Okavango Delta (Figure 1).

This river channel was chosen because very few studies on water quality have been conducted in this area.

Eight sites were selected along the main channel as follows: Mohembo (Site 1), Sepopa (Site 2), Seronga (Site 3), near the Nqoga/Jao junction (Site 4), near the Maunachira/Mboroga blockage (Site 5), in Xakanaxa lagoon (Site 6), near the Department of Water Affairs camp in Xakanaxa (Site 7), and near Khwai bridge (Site 8). The grid references of the sampling sites are given in Table 1.

Table 1. Sampling sites and their coordinates.

Site	Site Description	Distance From Mohembo (km)	Coordinates
1	Mohembo	0	E 021° 47.107' S 18° 15.327'
2	Sepopa	85	E 022° 11.937' S 18° 44.706'
3	Seronga	115	E 022° 25.133' S 18° 51.911'
4	Near Nqoga/Jao Junction	140	E 022° 34.590' S 18° 59.263'
5	Near the Maunachira/ Mboroga blockage	185	E 022° 52.824' S 19° 04.031'
6	Xakanaxa lagoon	250	E 023° 25.902' S 19° 11.144'
7	Xakanaxa, near Water affairs camp	265	E 023° 21.161' S 19° 07.565'
8	Near Khwai Bridge	300	E 023° 44.862' S 19° 10.091'

Materials and Methods

Grab water samples were collected in triplicates from the middle of the channel at each sampling site into 300 mL polyethylene bottles, previously rinsed in nitric acid and deionised water. The bottles were rinsed three times with the sample before sample collection. For the determination of dissolved metals, the samples were filtered through a 0.45- μ m membrane filter and preserved in nitric acid, kept in a cooler box under ice until reaching the laboratory, where they were refrigerated at 4°C (Csuros and Csuros, 2002; Clesceri *et al*, 1998).

The preserved water samples were analysed for the dissolved metals with a Sherwood Flame photometer (Sherwood, United Kingdom) for Na and K. and a Varian Spectra AA220 flame atomic absorption spectrometer (FAAS) with a Varian SPS5 auto sampler (Varian, Australia). The operator's manuals for the instruments were used for operation of the instruments, and standard procedures were followed (Clesceri *et al*, 1998).

Results and Discussions

Sodium, Potassium, Calcium and Magnesium

Figures 2 and 3 show the concentrations of sodium, potassium, calcium and magnesium. For these metal ions, the concentration of each ion more or less stayed constant for the first 185 km and then increased. The increase in concentration for Na and K was greater than that for Ca and Mg. In the panhandle (up to 185 km from Mohembo, Site 1), Ca is the predominant ion, followed by Na, K and Mg in that order. This relationship changes such that 300 km from Site 1 Na predominates, followed by K, Ca and Mg. These results show that for these ions, increases in concentration due to evaporation is higher than reduction in concentration due to ion removal by chemical sedimentation. This observation is easy to understand for sodium and potassium, which form soluble compounds with most anions and do not therefore easily deposit from the water. Calcium and magnesium form insoluble salts such as CaCO_3 , MgCO_3 and CaSO_4 , which would result in some removal from water systems; thus we find Ca and Mg, which predominates in the panhandle, having lower concentrations than Na and K at Khwai. There was little variation in the concentrations of these ions between the two sampling periods except for Ca, which was higher in November (low water level) than in June (high water level). Sawula and Martins (1991) reported increases in concentrations of Na, K, Mg and Ca from Seronga to the junction of the Boro and Thamalakane Rivers.

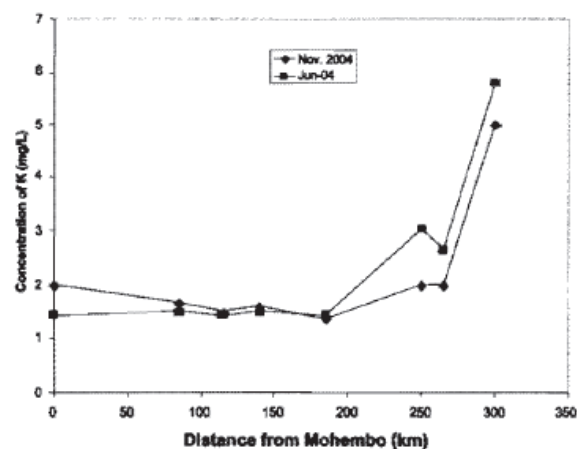
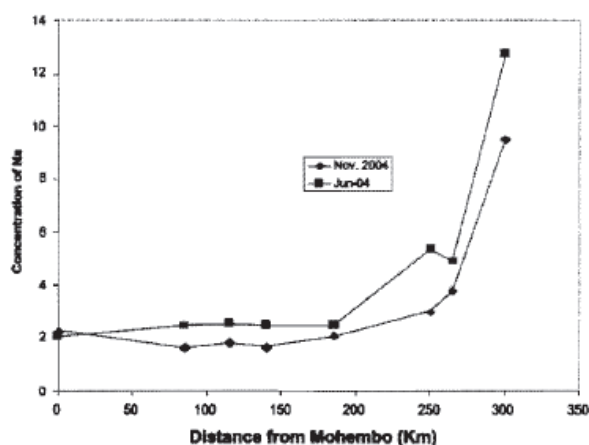


Figure 2. Concentrations of Na (A) and K (B) with respect to distance from Mohembo and high floods (June) and low floods (November).

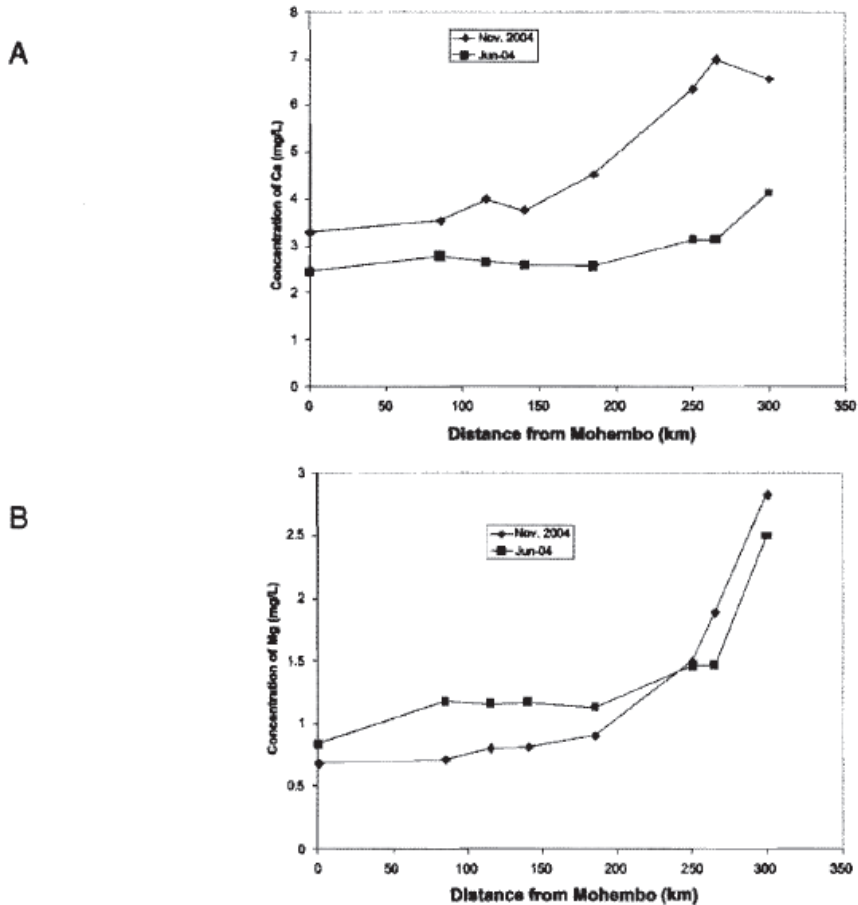


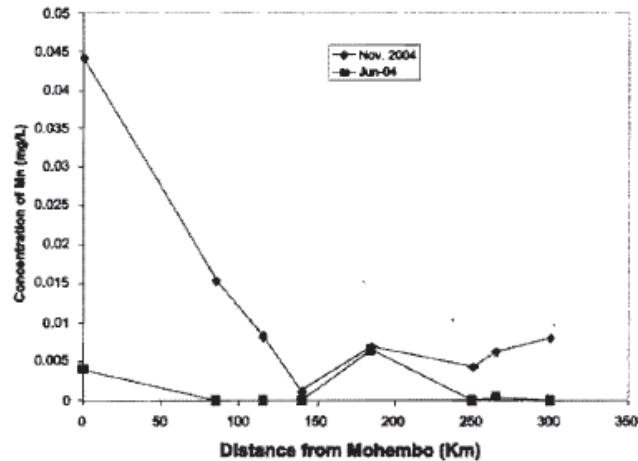
Figure 3. Concentrations of Ca (A) and Mg (B) with respect to distance from Mohembo and high floods (June) and low floods (November).

Lead and Manganese

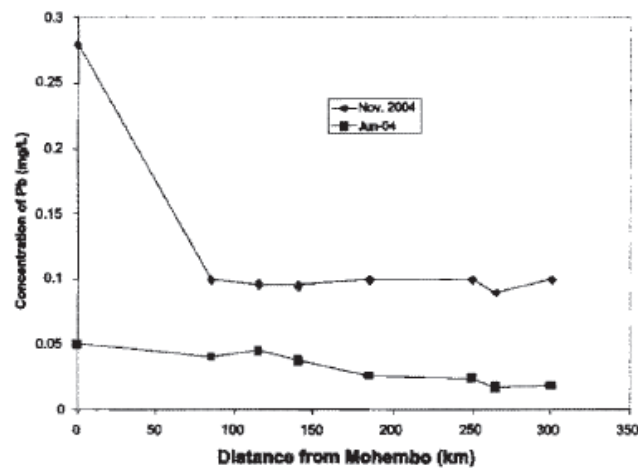
There is a general decrease in concentrations for Pb and Mn from Site 1 to Site 8 (Figure 4) indicating that for these heavy metals, deposition predominates over evaporation effects and the Delta acts as a filter. The decrease in concentration was by a factor of about 3 for lead: from 0.045 mg/L at Site 1 to 0.017 at Site 7 in June, and from 0.28 at Site 1 to 0.09 at Site 7 in November. The concentrations were higher in November due to evaporative concentration. Manganese showed a similar pattern, except that there is a local maximum 185 km from Site 1. This area does not have human activities; hence the Mn at this site, manifest in both June and November, should arise from natural sources. For Mn, seasonal differences were important only for the first 115 km, where the November samples had higher concentrations.

Iron, Nickel, Cobalt and Copper

Iron shows a different pattern between the two sampling months, in that in June there was a steady decrease of concentration from Site 1 to Site 8, but in November the concentration of iron at Site 1 was the lowest, increasing to Site 3 and then decreasing (Figure 5). It would appear that precipitation of iron occurs during periods of high floods, and dissolution of precipitated/sedimented iron during the period of low water floods. It should also be noted that the iron concentrations were higher in November at all sampling points except Site 1. There is a



A



B

Figure 4. Concentrations of Mn (A) and Pb (B) with respect to distance from Mohembo and high floods (June) and low floods (November).

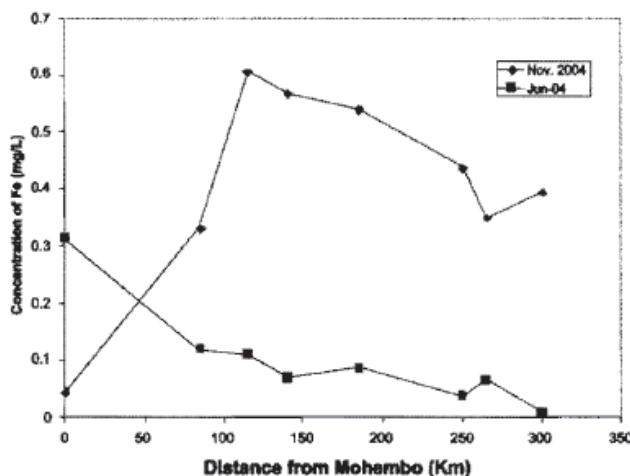
98% decrease in the concentration, from 0.31 mg/L at Site 1 to 0.01 mg/L at Site 8, for the June sampling, but there was only a 30 % decrease in November.

In November, the concentration of nickel decreased from 0.041 at Site 1 to 0.017 mg/L at Site 8, with a local maximum 115 km from Site 1 (Figure 5). A similar trend was observed in June, except that the concentrations at Sites 1 and 2 were much lower than in November. The highest concentrations of nickel, for June and November, were at Site 3, indicating either anthropogenic activity or natural presence of nickel at this site.

In June, cobalt concentrations decreased from 0.023 at Site 1 to 0.018 mg/L at Site 8 (Figure 6), corresponding to a 22 % decrease in the concentration. Except for the initial increase from Site 1 to Site 2, the cobalt concentration for November was more or less constant at around 0.05 mg/l. It would appear that during periods of high flow, the Delta acts as a sink for cobalt, whereas during periods of low flow the cobalt is solubilised.

The concentration of Cu was very low in both the June and November samples. There is a general decrease in the concentration of copper as the distance from Site 1 increases for the June and November samples, except that for the November samples, a value of 0.03 mg/L, which was higher than the other values, was determined at Site 8.

A



B

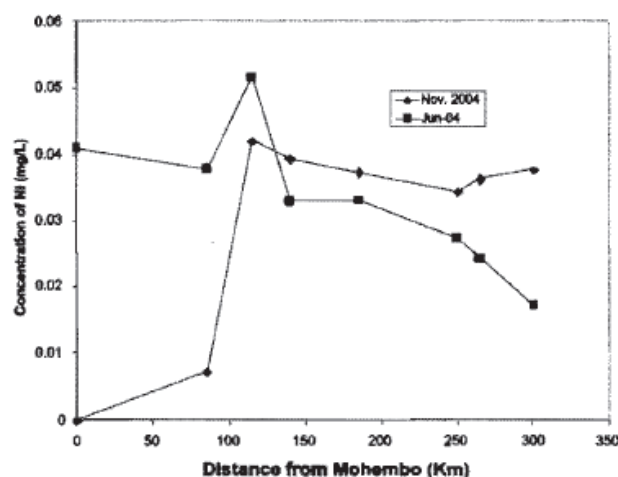


Figure 5. Concentrations of Fe (A) and Ni (B) with respect to distance from Mohembo and high floods (June) and low floods (November).

Cr

For both the June and November samples, chromium was below the instrument detection limit in all samples, except at Site 2 (June samples) where the concentration was 0.025 mg/l.

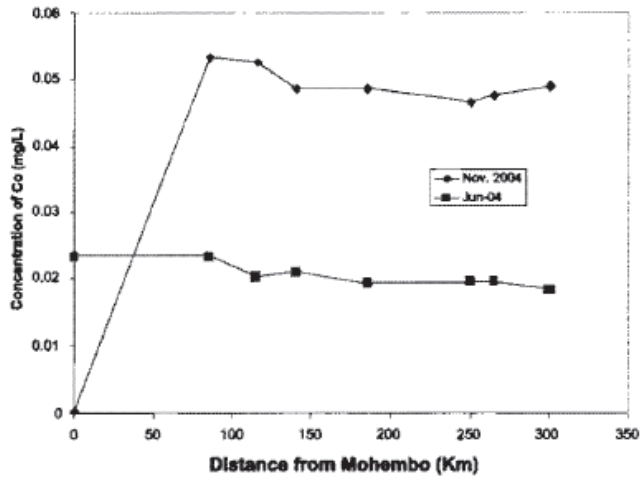
Zn

The concentration of zinc generally increases from Site 1 to Site 8, indicating that either previously deposited zinc was solubilised and/or that evaporative effects, similar to those for Na, K, Ca and Mg, are more pronounced than deposition effects (Figure 7).

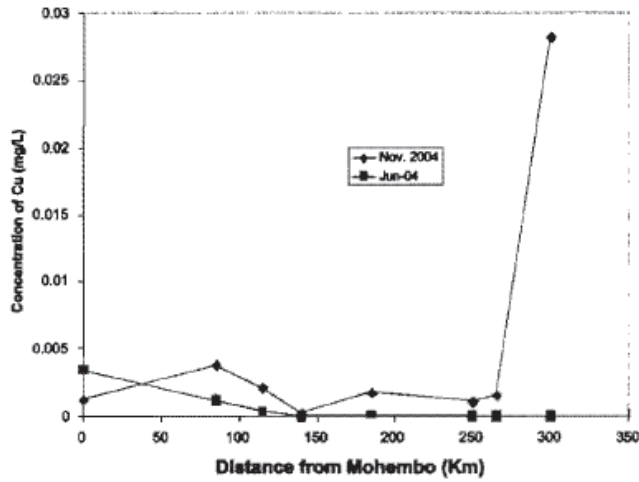
Comparison of Results with Previous Work and with Drinking Water Standards

Comparison of the results of this study and studies by others indicate that the concentrations of these metal ions are variable but, with the exception of Cronberg *et al* (1995) and Ashton *et al* (2003), they are much lower for the Boro Channel compared to the Munachira Channel.

The concentrations of the major ions Ca, Mg, Na and K are all well below the Botswana Drinking Water Specifications (Botswana Bureau of Standards, 2000), but the concentrations of Zn, Ni and Pb were higher than this specification in some cases.



A



B

Figure 6. Concentrations of Co (A) and Cu (B) with respect to distance from Mohembo and high floods (June) and low floods (November).

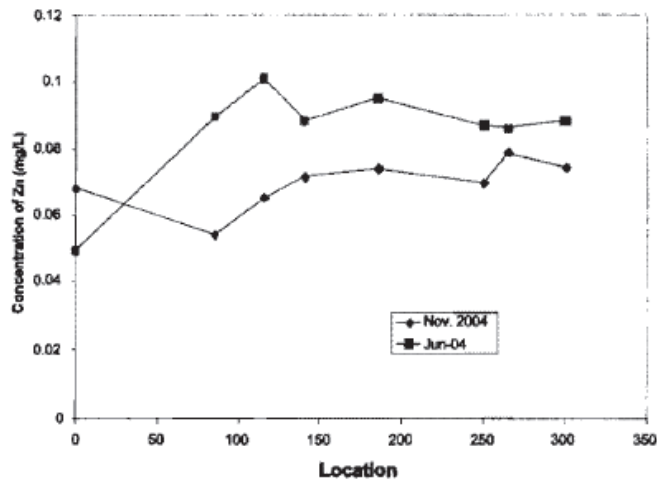


Figure 7. Concentrations of Zn with respect to distance from Mohembo and high floods (June) and low floods (November).

Conclusions

This study has shown that there are different types of behaviour for metal ions studied. The concentrations of Na, K, Ca, Mg and Zn increased as the distance from Site 1 increased, indicating that for these, evaporation predominates over sedimentation. The concentrations of Fe, Co, Ni, Pb, Cu and Mn decreased with distance from Mohebo, indicating that for these elements the Delta acts as a filter - deposition supersedes evaporation effects. For Cu and Mn, sharp increases in concentration at localised points may indicate local introduction of these ions either from natural origins or from anthropogenic sources, and may require further investigation. Cr was not detected in any samples except at one location. Most of the concentrations are below the Botswana Drinking Water Standards except in some cases those for Zn, Ni and Pb. Generally, the results for November samples were higher than those for June samples.

Acknowledgements

We would like to express our appreciation to the following people who made this study possible: academic staff at the Harry Oppenheimer Okavango Research Centre (HOORC), especially Mr O.T. Thakadu and Dr B. Ngwenya. Mr I. Mosie and Mr B. Mogojwa were of assistance during field work, and Mr Letshwenyo and Ms Kupe helped with laboratory work. Special thanks to the Department of Water Affairs for offering their motor boats for sampling. This work was funded by the University of Botswana's Harry Oppenheimer Okavango Research Centre's Winter Course.

References

- Ashton, J.P., Asunder, H., Hart, R., Prince-Nengu, J., Botshelo, O., Lekhuru, M., Mehlomakulu, M., Tylol, I. (2003) Water quality of the Okavango Delta, Botswana; In: Alonso, E. L. and Nordin, L. (Eds.) *RAP Bulletin of Biological Assessment*, 27, p. 38. Washington: Conservation International.
- Botswana Bureau of Standards 2000. Drinking Water Specifications. Gaborone.
- Cronberg, G., Gieske, A., Prince, N.J., Sternstrom, I.M. (1995) Hydrobiological studies of the Okavango Delta and Kwando/Linyanti, Chobe River, Botswana; Surface water quality analysis. *Botswana Notes and Records*, 27, 151-226.
- Csuros, M. and Csuros, C. (2002) Environmental sampling and Analysis for metals, pp. 73, 204-207. Florida: CRC Press LLC.
- Cunningham, W.P., Cooper, T.H., Gorham, E., Hepworth, T.M. (1998) *Environmental Encyclopedia*, 2nd ed. New York: Gale.
- Clesceri, L.S., Greenberg, A.E. and Eaton, A.D. (1998) *Standard methods for the examination of waste water*. Washington D.C.: American Public Health Association.
- Manahan, S.E. (2000) *Environmental Chemistry*, 7th Ed. Florida: Lewis Publishers.
- Patnail, P. (1999) *A comprehensive guide to the hazardous properties of chemical substances*, 2nd Ed. New York: Wiley.
- Sawula, G., Martins, E. (1991) Major ion chemistry of the lower Boro River, Okavango Delta, Botswana, *Fresh Water Biology*, 26, 481-493.
- Sawula, G., Martin, E., Nengu, J., Themner, K. (1990) Notes on trace metals in the Boro River, Okavango Delta. *Botswana Notes and Records*, 24, 135-149.
- Warmeant, P. (1997) Review of water chemistry and water quality in the Okavango Delta. Report prepared for: Permanent Okavango Basin Commission. Unpublished.

Habitat Utilization by Impala (*Aepyceros melampus*) in the Okavango Delta

By C.M. Bonyongo, University of Botswana, Harry Oppenheimer Okavango Research Centre, Cbonyongo@orc.ub.bw

Abstract

This paper presents preliminary results from a long-term study on the ecology of large herbivores in the Okavango Delta. The paper evaluates habitat selection and utilization by impala (*Aepyceros melampus*) at the various habitat scales. Impala, the most abundant and widely distributed mammal species in the Delta, showed seasonality in habitat use and habitat selection. In all seasons impala used mixed open woodlands more than any other habitat type. Open grasslands and upper floodplains are also key habitats for impala. As a mixed feeder, impala are able to use a wide range of habitats.

Introduction

The Okavango Delta in northwestern Botswana supports a wide diversity of wildlife, with the largest populations found in the Moremi Game Reserve and a number of adjacent controlled hunting areas (CHAs). In the Delta, seasonal flooding causes shrinking and expanding of the grazing resources when floods come and when floods recede. It is therefore likely that seasonal habitat fragmentation caused by seasonal flooding and seasonal changes in forage quantity and quality have profound impacts on the seasonal patterns of habitat utilization by various wildlife species.

Impala (*Aepyceros melampus*) are the most common and most abundant herbivore species throughout the Okavango Delta. Bonyongo (2004) estimated 104,000 impala in Moremi Game Reserve together with NG31 - NG34. Despite their high population and wide distribution, little is known about impala's seasonal patterns of habitat selection and utilization within the highly heterogeneous and dynamic Okavango Delta habitats. Terminology can be confusing. Habitat refers to a distinctive set of physical environmental factors that a species uses for its survival and reproduction (Thain & Hickman, 2000; Allaby, 2003). Habitat use implies occupation of a habitat without any connotation of preference or that habitat is used 'for something'. Habitat selection implies choice among those habitats available, and individuals may search for certain habitats for specific behaviours (e.g. breeding, feeding and resting). Habitat preference implies choice of one habitat over others without regard to its availability (Morrison *et al.*, 1998).

Ever since the conception of ecology as a subject, studies of habitat selection and habitat use by different forms of wildlife have attracted considerable attention, with more studies emerging in recent years (Kaunda *et al.*, 2002). In studies of habitat use and habitat selection, it is essential to define the scale being investigated because habitats are heterogeneous and often composed of many different components. Previous studies suggest that ungulates (e.g. Johnson, 1980; Bell, 1982; Rolstad *et al.*, 2000; George & Zack, 2001; Matson, 2003) select habitat at a broad scale, at a micro-habitat scale within their home ranges and finally at an individual plant species scale.

When assessing habitat selection, most attention is usually paid to the independent role

of a single resource, in particular food (Myterud, 1998; Laus-Huge, 1999). According to classical foraging theory and habitat selection, a forager must continue to exploit a patch until the harvest rate in that patch drops due to a reduction in availability. Under these conditions the animal will spend most time in habitats richest in food, and habitat selection is likely to reflect food availability (Myterud, 1998; Fauchald, 1999). Given the dynamic nature of the Okavango Delta ecosystem, understanding the patterns of habitat utilization by key species such as impala and the consequences of that habitat's conservation are absolute necessities.

This study therefore examines seasonal patterns of habitat selection and habitat use by impala at a broad, between habitat scale. As a mixed-feeder capable of utilizing a wide range of habitats, impala is expected to show distinct habitat selection patterns in the mosaic of highly spatial heterogeneous habitats of the Okavango Delta, and that its habitat use is proportional to availability.

Study Area

The main study area covers Moremi Wildlife Game Reserve (NG 28), and controlled hunting areas (CHAs) NG17 and NG31 to NG34 (Figure 1). Moremi Game Reserve is situated in the northern part of the Okavango Delta and covers 4,872 km². NG32 borders Moremi Game Reserve and the buffalo (cordon) fence in a south-easterly direction, covering 1,225 km². Vegetation is predominantly *Colophospermum mopane* and mixed open woodland with floodplains and riparian woodlands running along the Boro River. NG34 borders Moremi Game Reserve and NG32 as well as the buffalo fence in a northwards direction, covering 870 km².

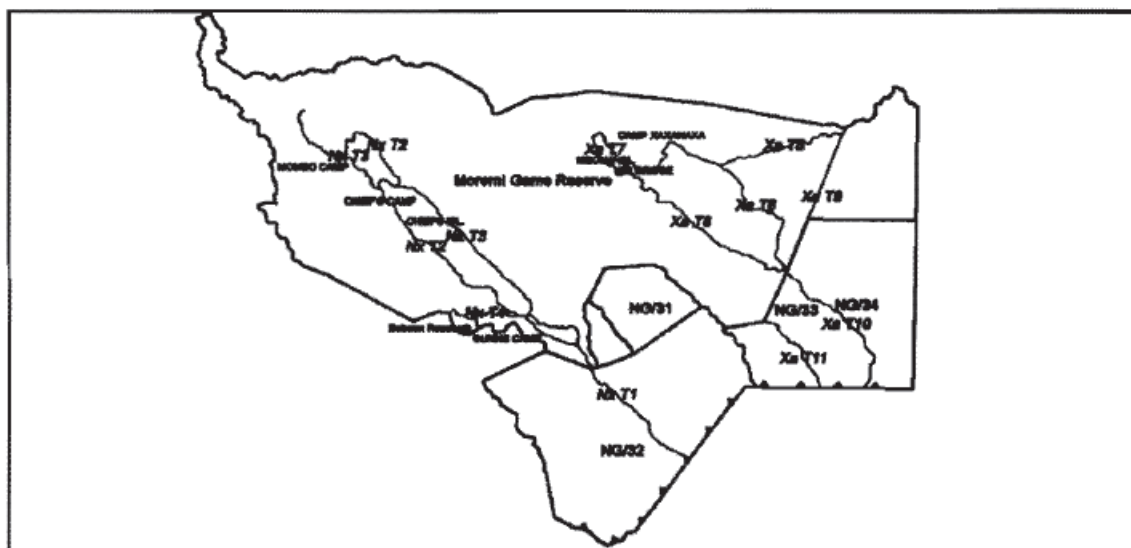


Figure 1. Map of the study area showing transect layout. (Source: Bonyongo 2004)

Methods

Description of the Transects

The transect layout is presented in Figure 1. Transect 1 (NxT1) runs for 46 km from the Daonara gate of the buffalo fence through NG32 to the HOORC camp near Nxaraga Lagoon. Transect 2 (NxT2) runs for 50 km from HOORC camp through floodplains and woodlands to Chief's Camp at Momo Island. Transect 3 (NxT3) runs for 76 km through the woodlands on the

southern edge of Chief's Island to Mombo Camp at Mombo Island. Transect 4 (NxT4) runs for 22 km from the HOORC Camp to Baboon Camp. Transect 5 (XaT5) runs for 49 km from South Gate to Third Bridge in the northern side of Moremi Game Reserve. Transect 6 (XaT6) runs for 50 km from South Gate to Xakanaka Wildlife Camp. Transect 7 (XaT7) runs for 22 km from Third Bridge to Mboma Island. Overall the study area covers 6,966 km² while transects cover 311 km. The frequency with which each vegetation type was encountered was measured by measuring vegetation parameters systematically every 1 km (Sinclair, 1985). The frequency was used as a measure of availability of vegetation types and to provide the expected numbers of animals for random association with vegetation types.

Habitat Types

Overall eight major habitat types were identified following classification by Biggs (1979) and Bonyongo (2000). The eight habitat types are Lower Floodplain, Upper Floodplain, Open Grassland, Mixed Open Woodland, Mixed Closed Woodland, Short Mophane, Tall Mophane and Mixed Mophane. The habitat types are described as follows (availability in parenthesis).

Lower floodplains (6%)

These are low-lying floodplains that are the first to flood, and last to dry when the floods recede. Duration of flooding ranges from six months during years with average rainfall to 10 months during years of above-average rainfall. They are dominated by flood resistant species, in particular sedges species *Cyperus articulatus*, *Schoenoplectus corymbosus* and grass species *Oryza longistaminata* and *Leersia hexandra*.

Upper floodplains (14%)

These are elevated areas of the floodplains, dominated by species adapted to periodic flooding. Duration of flooding range from 3 to 6 months depending on the intensity of flooding of a particular year. Common species include *Panicum repens*, *Setaria sphacelata*, *Eragrostis inamoena*, *Paspalidium obtusifolium* and *Cynodon dactylon*.

Open grasslands (28%)

These are areas with no or little woody vegetation, and are only occasionally flooded. Herb layer is dominated by grasses and in some cases forbs. They are mostly dominated by perennial species in areas of low grazing pressure while annuals species may dominate heavily grazed areas.

Mixed open woodlands (40%)

These are grassy woodlands, with woody cover ranging from 20-49%. These woodlands include *Acacia nigrescence-Croton megalobotrys* woodlands that occur in small stands on some of the small to medium sized islands. Palm savannah woodland are common in small and medium size islands of the upper floodplains.

Mixed closed woodland (4%)

These are mainly riverine woodlands with greater than 80% canopy cover. They are found on elevated islands surrounded by floodplains, within the proximity of surface water and areas of high ground water table. The prominent species are *Diospyros mespiliformis*, *Garcinia livingstonei*, *Ficus sycamore* and *Ficus burfiei*.

Scrub/short mophane (3%)

Pure stands of mophane woodland with average height of less than 3 m. Herbaceous layer is poorly developed.

Tall Mophane Woodland (4%)

Mophane stands with average height greater than 10 m. The herb layer is poorly developed.

Data Collection

Ground surveys were conducted from October 2000 to October 2002, using the classical transect method (Lamprey, 1963; Jarman, 1971). Preliminary surveys conducted at the beginning of each season showed that there were no significant differences in the number of sightings for morning and afternoon counts (student's *t-test*, $p > 0.05$). Transects were driven twice every month from 7:00 am to 11:30 am and 3:00 pm to 6:30 pm. For each animal observation, habitat type, dominant woody species, dominant grass species, grass height, dominant woody species height, distance from the car, and bearing were recorded. The position of the car was recorded using a global positioning system (GPS) device and the bearing to the animal was recorded using a standard compass.

Data Analysis

Comparison of Utilized and Available Habitat

Compositional analysis was used to compare habitat use and habitat availability as described in Aebischer *et al* (1993) and Catusse *et al* (2003). For the purpose of analysis, merging Mixed Mophane Woodland and Tall Mophane Woodland reduced the eight habitats to seven. The percentage number of sightings per animal species per habitat type in all the seven transects was used as a measure of habitat use. The number of surveys per season was used as the sample size. According to Aebischer *et al* (1993), compositional analysis requires a minimum of ten samples, but samples greater than 30 are recommended. In this study the sample size was 16. The number of observations - in this case, number of impala sightings per habitat type - varied with season (min. and max.). Zero percentage sightings were replaced by a default value of 0.1% since compositional analysis requires a logarithmic transformation.

Catusse *et al* (2003) suggested that replacing zeros with such small values is equivalent to postulating that the concern habitat is used but not enough to be detected by the analysis.

To test for overall differences in habitat use, Wilk's lambda test was applied, and levels of statistical significance were determined using a permutation test to avoid having assumed multivariate normality. When differences were detected, a pairwise comparison of habitats identified where the differences lay, and ranked habitats from most used to least used, relative to availability. This was done using a paired *t-test* to compare usage and availability for the ratio of log scale of percentages for the two habitats.

Habitat Selection Index

Impala selection for the seven broad habitat types was calculated using the electivity or selection index (*E*) of Jacobs (1974), as described by Gordon (1989):

$$E = (U_i - A_i) / \{ (U_i + A_i) - [2 \times (U_i \times A_i)] \}$$

where U_i is the proportion of sightings in habitat i and A_i is the proportion of the study area occupied by habitat i . E is defined as the relative difference between use and availability of the habitat type and gives an indication of relative feeding densities of animals in each habitat type. The value of E ranges from -1 to $+1$; values between -1 and 0 indicate the species avoids the habitat, and values between 0 and $+1$ indicate species selection of that habitat type (Gordon 1989).

Results

Habitat Use

Rainy Season

Impala were not randomly dispersed across the habitats types available to them in the rainy season ($X^2 = 45.2$; $p < 0.001$, $df = 7$; $p < 0.001$). During the rainy season, impala used habitats according to the following proportions: mixed open woodland (40%), open grasslands (19%), tall mophane woodland (16%); mixed closed woodlands (12%), upper floodplain (4%) lower floodplain (3%) and short mophane woodland (3%). Compositional analysis showed significant differences in habitat use ($\Lambda = 0.0058$, $p < 0.0001$, 1000 interactions). The pairwise ranking of habitat use is as follows: mixed closed woodland > tall mophane woodland > short mophane woodland > mixed open woodland >>> open grassland > lower floodplain > upper floodplain (Table 2). Generally, impala avoided grasslands and floodplains during the rainy season, while they showed greater utilization of woodlands.

Flooding Season

Impala were not randomly dispersed across the habitats types available to them in the rainy season ($X^2 = 62.3$; $p < 0.001$, $df = 7$; $p < 0.001$). Impala used habitats according to the following proportions: mixed open woodland (53%), tall mophane woodland (19%), open grasslands (16%), mixed closed woodlands (7%), upper floodplain (2%) and short mophane woodland (1%). From compositional analysis, impala showed significant differences in habitat use during the flooding season ($\lambda = 0.0000$, $p < 0.0001$, 1000 interactions). Pairwise ranking of habitat use by impala during the flooding season is as follows: lower floodplain > upper floodplain > open grassland >>> mixed open woodland > mixed closed woodland > short mophane woodland > tall mophane (Table 1).

Dry Season

Impala were not randomly dispersed across the habitat types available to them in the dry season ($X^2 = 13.8$; $p < 0.001$, $df = 7$; $p < 0.001$). Impala used habitats according to the following proportions: mixed closed woodland (37%), upper floodplain (25%), open grasslands (22%), mixed closed woodlands (5%), tall mophane woodland (5%), short mophane woodland (4%) and lower floodplain (3%). Significant differences in habitat use were registered during the dry season ($\lambda = 0.0666$, $p < 0.01$, 1000 interactions). Pairwise ranking of habitat use by impala during the dry season is as follows: lower floodplain > upper floodplain >>> open grassland > mixed open woodland > mixed closed woodland > short mophane woodland > tall mophane woodland (Table 1).

Habitat Selection

Impala were common and widely distributed throughout the study area. In all seasons impala strongly avoided short mophane woodland, while they strongly avoided upper floodplains during the rainy and flooding season (Table 2). They showed a weak avoidance of mixed

Table 1. Ranks of habitat use by impala derived from compositional analysis comparing seasonal habitat use to habitat availability. Triple signs represents significant deviation from random at $p < 0.05$. The rank column is calculated as a total of + and +++ signs in each row. Rank 0 is the least used habitat while rank 6 is the most used habitat. >>> indicates significant differences between consecutive ranks. Ranks with the same superscripts are not significant.

a) Rainy Season (MCW>TM>SM>MOW>>>OGL>LFP>UFP)								
	LFP	UFP	OGL	MOW	MCW	SMW	TMW	Rank and differences
LFP		+++	-	---	---	-	---	1 ^{ef}
UFP	---		---	---	---	---	---	0 ^f
OGL	+	+++		---	---	-	---	2 ^e
MOW	+++	+++	+++		---	-	---	3 ^{dc}
MCW	+++	+++	+++	+++		+++	+	6 ^a
SMW	+	+++	+	+	---		-	4 ^{bde}
TMW	+++	+++	+++	+++	-	+		5 ^{ab}
b) Flooding Season (LFP>UFP>>>OGL>MOW>MCW>SMW>TMW)								
	LFP	UFP	OGL	MOW	MCW	SMW	TMW	Rank and differences
LFP		+++	---	---	---	+++	-(---)	2 ^d
UFP	---		---	---	---	+++	---	1 ^e
OGL	+++	+++		---	---	+++	+	4 ^c
MOW	+++	+++	+++		-	+++	+++	5 ^a
MCW	+++	+++	+++	+		+++	+++	6 ^a
SMW	---	---	---	---	---		---	0 ^f
TMW	+(+++)	+++	-	---	---	+++		3 ^c
c) Dry Season (LFP>UFP>>>OGL>MOW>MCW>SMW>TMW)								
	LFP	UFP	OGL	MOW	MCW	SMW	TMW	Rank and differences
LFP		---	---	---	---	-	-	0 ^d
UFP	+++		+++	+++	+++	+	+++	6 ^a
OGL	+++	---		-	-	-	+	2 ^{bc}
MOW	+++	---	+		-	-	+	3 ^c
MCW	+++	---	+	+		-	+	4 ^b
SMW	+	---	+	+	+		+	5 ^{abcd}
TMW	+	---	-	-	-	-	+	1 ^{bcd}

mophane woodland during the rainy and flooding season, while they weakly avoided lower floodplains in all seasons. Generally impala made more use of mixed open woodlands and mixed closed woodlands. Impala also made high use of open grasslands during the rainy and dry seasons.

Table 2. Habitat use (%) and selection index (in parenthesis) for impala. S = Season, RS = rainy season, DS = dry season, FS = flooding season, LFP = lower floodplain, UFP = upper floodplain, OGL = open grassland, MOW = mixed open woodland, MCW = mixed closed woodland, SMW = short mopane, TMW = tall mopane, MMW = mixed mopane woodland — = Strong avoidance (-0.5 to -1.0), - = weak avoidance (-0.1 to -0.49), 0 = neutral (0.09 to -0.09), + = weak selection (0.1 to 0.49), ++ = strong selection.

Animal	S	LFP	UFP	OGL	MOW	MCW	SMW	TMW	MMW
Impala	RS	4 (-)	4 (-)	20 (+)	41 (+)	12 (+)	3 (-)	12 (+)	4 (-)
	FS	2 (-)	2 (-)	16 (0)	53 (++)	7 (+)	1 (-)	4 (+)	3 (-)
	DS	3 (-)	25 (+)	22 (+)	36 (+)	5 (-)	4 (-)	16 (-)	1 (-)

Discussion

In fine scale mosaics of habitats that characterize the Okavango Delta, patterns of seasonal habitat selection are complex and difficult to isolate since animals move short distances between habitats. The fine scale mosaics probably influenced the results in this study since animals could be sighted in areas where they do not feed in while in transit to feeding areas. This may obscure the patterns of habitat selection and use to some extent. Despite this reduction of accuracy, impala showed distinct patterns of habitat use and seasonality in habitat selection as expected. In all three seasons, impala made relatively extensive use of mixed open woodlands, presumably due to a high diversity of micro-habitats there.

The striking selection for open grasslands and mixed open woodland during the rainy season is explained by the presence of palatable forbs and annual grasses such as *Urochloa trichopus*, *Dactyloctenium aegyptium* and *Chloris virgata*. Kingdon (1997) described impala as edge (ecotone) species, preferring light woodland with little undergrowth and grassland of low to medium height, thus explaining the high number of sightings in mixed open woodlands which are normally characterized by patches of open grasslands. Highest utilization of woodlands was recorded during the flooding season due to the inaccessibility of floodplains. Field observation has shown that when water levels rise in floodplains, impala concentrate on high grounds and later disperse into the floodplains when floods recede. On a large scale, both temporally and spatially, dispersal of various wildlife species throughout the Delta which results from fluctuations in floodplain water level and food availability is reflected by the differences in population densities and herd sizes in different habitats. Unlike other grazing species like zebra, wildebeest and buffalo, impala has never been observed feeding on flooded grasslands.

The increased utilization of floodplains when floods recede (dry season) was influenced by the emergence of the probably highly nutritious green flush of grasses and forbs. This makes floodplains key fallback areas during the dry season, when forage is limited everywhere. These results indicate that during the dry season impala used mixed open woodlands, upper floodplains and open grasslands in almost equal proportions. In particular woodlands with high proportions of *Acacia* species were highly selected during the dry season because impala utilize *Acacia* pods which drop during the dry season. Similar observations were reported by Kaunda *et al* (2002), who noted impala picking *Acacia tortilis* pods in Gaborone Game Reserve.

Impala are water-dependent only when feeds are dry (Jarman and Sinclair, 1979; Kingdon, 1997), a scenario which further explains an increased selection for floodplains during the dry season, since both surface water and green forage are available in the floodplains during that time.

The results of this study agree with those presented in previous studies on free ranging impala populations (e.g. Omphile, 1987; Kaunda *et al*, 2002; Matson, 2003). The main weakness of this study is that it did not consider that animals within the same population may fall into distinct categories, determined for instance by age or size class, sex or region, or by a combination of all these factors. Several studies of habitat use by male and female impala (Jarman & Sinclair, 1979; Kaunda *et al*, 2002; Matson, 2003), have shown that males occupy habitats of poorer quality; a scenario which appears to be common among many several dimorphic ungulates (e.g red deer) (Myrterud, 1998). Determining the available habitat is often very difficult. Moreover the boundaries of available habitat are often arbitrary (Johnson, 1980). Not all habitats perceived and believed to be available for use by an animal are always available. Access to a particular habitat may be constrained by the presence of other animals.

Conclusions

The persistent selection of mixed open woodlands by impala all year round is a clear indication that this is the key habitat for impala in the Okavango Delta. However, woodlands are generally extensively utilised during the rainy season. Open grasslands and upper floodplains are also key habitats for impala during the dry season. The high use of mixed open woodlands, which were the most available habitat, suggests that impala used habitats proportional to availability. This study yielded meaningful insights from a conservation point of view because it showed which habitats are more important than others for impala. This is especially significant in that the management of wildlife populations entails habitat management that presupposes some understanding of habitat preferences. These results confirmed earlier predictions that impala are capable of utilizing a wide range of habitats since it is a mixed feeder.

References

- Aebischer, N.J., Robertson, P.A. & Kenward, R.E. (1993) Compositional analysis of habitat use from radio-tracking data. *Ecology*, 74, 1313-1325.
- Allaby, M. (2003) *Oxford Dictionary of Zoology*. Oxford: Oxford University Press.
- Bell, R.H.V. (1982) The effect of soil nutrient availability on community structure in African ecosystems. *Ecology of Tropical Savannas*. Eds. B.J. Huntley & B.H. Walker. pp. 193-216. Berlin: Springer-Ver.
- Biggs, R.C. (1979) *The ecology of Chief's Island and the adjacent floodplains of the Okavango Delta, Botswana*. MSc thesis, Pretoria: University of Pretoria.
- Bonyongo M.C. (2004) The ecology of large herbivores in the Okavango Delta, Botswana. PhD thesis. UK:Bristol University.
- Catusse, M., Corda, E.M., & Aebischer, N.J. (2002) Winter habitat selection and food choice of the capercaillie (*Tetrao urogallus*) in the French Pyrenees. *Game and Wildlife Science*, 19, 261-280.
- Fauchald, P. (1999) Foraging in a hierarchical patch system. *American Naturalist*, 153, 603-613.
- George, T.L. & Zack, S. (2001) Spatial and temporal considerations in restoring habitat for wildlife. *Restoration Ecology*, 9, 272-279.
- Gordon, I.J. (1989) Vegetation community selection by ungulates on the Isle of Rhum II: Vegetation community selection. *Journal of Applied Ecology*, 26, 53-64.

- Jacobs, J. (1974) Quantitative measurement of food selection. A modification of forage ratio and Ivlev's electivity index. *Oecologia*, 14, 413-417.
- Jarman, P.J. & Sinclair, A.R.E. (1979) Feeding Strategy and Patterns of Resource Partitioning in Ungulates. *Serengeti, Dynamics of an ecosystem*. Eds. A.R.E. Sinclair & M. Norton-Griffith), pp. 130-150. Chicago: University of Chicago Press.
- Jarman, P.J. (1971) Diets of large mammals in the woodlands around Lake Kariba, Rhodesia. *Oecologia*, 8, 157-178.
- Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 65-71.
- Kaunda, S.K., Mapolelo, M.M., Mathaku, K. and Mokgosi, J. (2002) Habitat utilisation and sexual segregation of impala in the Gaborone Game Reserve. *Botswana Notes and Records*, 34, 79-90.
- Kingdon, J. (1997) *The Kingdon Field Guide to African Mammals*. San Diego: Academic Press.
- Lamprey, H.F. (1963) Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. *East African Journal of Wildlife*, 1, 63-92.
- Matson, T.K. (2003) *Habitat use and conservation of the black-faced impala (Aepyceros melampus petersi) of Namibia*. PhD thesis. Queensland: University of Queensland.
- Morrison, M.L., Marcot, B.G. & Mannan, R.W. (1998) *Wildlife-Habitat Relationships; concepts and applications*. 2nd Ed. Madison: The University of Wisconsin Press.
- Mysterud, A. (1998) *Habitat Selection by Roe Deer Relative to Resource Distribution and Spatio-temporal Scale*. PhD thesis. Oslo: University of Oslo.
- Omphile, U. (1997) *Seasonal diet selection and quality of large savanna ungulates in Chobe National Park, Botswana*. PhD thesis. University of Wyoming.
- Rolstad, J., Loken, B. & Rolstad, E. (2000) Habitat selection as a hierarchical spatial process: the green woodpecker at the northern edge of its distribution range. *Oecologia*, 124, 116-129.
- Thain, D. & Hichman, M. (2000) *The Penguin Dictionary of Biology*, 2nd Ed. London: Penguin Books.