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

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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 mophane* 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.

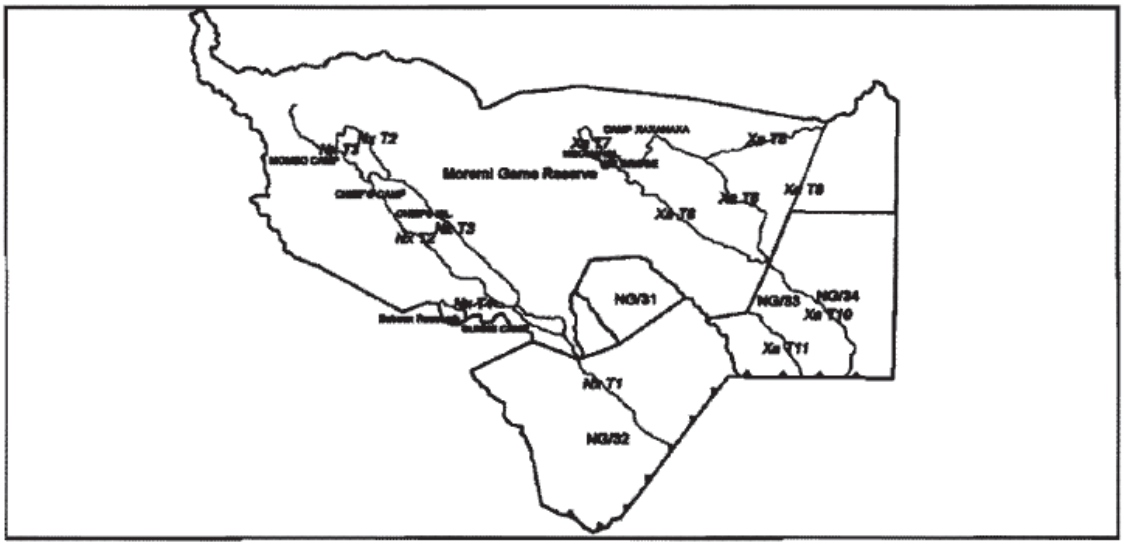

Figure 1. Map of the study area showing transect layout. (Source: Bonyongo 2004)

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 Mombo 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 km^2 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 coodland, SMW = short mophane, TMW = tall mophane, MMW = mixed mophane 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*, *Dactyloctinum egyptium* 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 diamorphic angulates (e.g red deer) (Myterud, 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.

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