

Remotely sensed habitat indicators for predicting distribution of impala (*Aepyceros melampus*) in the Okavango Delta, Botswana

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Abstract: We studied the spatial and temporal habitat use of impala in Botswana's Okavango Delta at landscape level with the aid of satellite imagery, with minimal fieldwork. We related remotely sensed vegetation to impala habitat preferences, by first distinguishing three vegetation types through a multi-temporal classification, and dividing these into subclasses on the basis of their Normalized Difference Vegetation Index (NDVI). This indicator for abundance and greenness of biomass was assessed for wet and dry season separately. Similarly, habitat use was assessed for both seasons by allocating vegetation classes to bimonthly impala observations. Impala distribution patterns coincided with NDVI-based subclasses of the landscape, nested within broad vegetation types, to which impala did not show a marked seasonal response. We suggest that this methodology, using limited field data, offers a functional habitat classification for sedentary herbivores, which appears particularly valuable for application in extensive areas with high spatial variability, but with restricted access.

Key Words: herbivore distribution, remote sensing, resource use, savanna, ungulates

INTRODUCTION

Basic needs of animals, that is forage, water and shelter, frequently vary spatially and temporally. Therefore, animals do not range randomly, but are distributed in relation to variation in these parameters (Hutchinson 1957, Krebs 1985, Sinclair 1983). The temporally changing features to be considered for studying herbivore habitat use are therefore to be sought at the landscape scale, and include vegetation cover, forage availability and forage quality. Remote-sensing techniques offer opportunities to map both shelter and shade, as well as forage characteristics. Physiognomic landscape features indicate the distribution of shelter and shade in the landscape, and these can be derived directly from spectral information on various imagery bands. Forage-related indices include the widely applied Normalised Difference Vegetation Index (NDVI) (Lillesand & Kiefer 2000).

Chlorophyll level, indicative of the greenness of the vegetation, and Leaf Area Index (LAI) indicating the vertical thickness of the vegetation, largely determine NDVI values. Generally, LAI will increase with the thickness of the green layer or with the number of green layers. Chlorophyll level and LAI have been successfully correlated with vegetation characteristics important to herbivores, such as phytomass, amount of green cover, productivity, photosynthetic activity (Huete 1989, Wessman 1994) and leaf nitrogen content (Turner *et al.* 1992). High NDVI values are usually associated with well-developed green vegetation such as closed canopy in woodland or a continuous green grass layer, whereas low NDVI values are generally associated with a non-continuous vegetation cover or a non-green cover like exposed bare soil or water.

Past studies on the modelling of animal habitat using remote-sensing techniques at landscape scale include bird habitat analyses (Homer *et al.* 1993, Osborne *et al.* 2001, Saveraid *et al.* 2001). Ottichilo *et al.* (2000) and Verlinden & Masogo (1996) related distribution of

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migratory large herbivores to rainfall data and satellite-derived NDVI at a regional scale, in the Masai Mara and the Kalahari respectively. Zinner *et al.* (2002) studied the distribution of grivet monkeys (*Cercopithecus aethiops*) in Eritrea, also at a regional scale, using vegetation classes and NDVI derived from Landsat satellite imagery, as well as auxiliary data concerning altitude, annual rainfall, and distance to settlements and rivers. These studies indicate the usefulness in relating NDVI and remotely sensed vegetation classes to herbivore distribution at landscape and regional scales, but it remains unclear whether this approach would also be applicable to non-migratory animals at a detailed, landscape scale, under seasonal conditions, without clear rainfall gradients, and in the absence of auxiliary data. We are particularly interested in this goal, using a limited input of ground data, while acknowledging spatial variability and gradual change in vegetation characteristics.

We propose that a functional differentiation in natural vegetation units can be reached with respect to herbivore distribution, by incorporating both physiognomy and NDVI into one nested classification system. Vegetation classified into broad physiognomic classes masks the variation in quality and quantity of forage within these broad types, and providing more detail in physiognomy-based classification does not achieve the goal of linking animal distribution to an index of habitat quality either. On the other hand, distinction of the vegetation based purely on NDVI is expected to yield a similarly broad distinction among vegetation classes as by physiognomic classification, since variation in NDVI between physiognomic vegetation classes will be much greater than within these classes (Peterson & Running 1989, Sellers 1989). Moreover, the addition of an NDVI-based classification, nested within a physiognomic classification, is expected to yield differences in the qualitative and quantitative aspects of potential forage. This paper describes a technique for creating a functional habitat differentiation at a detailed, landscape scale, by classifying the vegetation firstly in terms of its physiognomy, and secondly by differentiating these classes further based on their gradient in LAI and chlorophyll levels, as indexed by the continuum of NDVI values. Thus, the vegetation was first classified into broad, remotely sensed vegetation types, and each vegetation class was then subdivided into distinct NDVI classes.

Apart from ground-truthing for broad vegetation types, this classification does not require additional field information. We chose impala (*Aepyceros melampus*) as a model herbivore for our distribution study, as this species is widely distributed in Southern Africa. Impala are mixed feeders of medium size (females 40–45 kg, males 60–65 kg; Jarman & Jarman 1973), drinking-water dependent, and are known to occupy a wide array of habitats throughout much of southern and eastern Africa

(Kingdon 1997, Skinner & Smithers 1990). Our study site was situated in the vast and generally inaccessible Okavango Delta, Botswana. We hypothesize that impala shows a response in occupancy of habitat units based on broad vegetation classes and NDVI. The development of a widely applicable methodology for prediction of herbivore presence is especially relevant for large and mostly inaccessible areas, where field data are difficult to obtain.

METHODS

Study area

Our study area was located in the Okavango Delta in north-western Botswana (Figure 1), (23°06′–13′E, 19°30′–32′S). The Delta, including the sandveldt tongues and the dryland areas, comprises an area of approximately 22 000 km² (Ellery & Ellery 1997). The area is highly heterogeneous, largely difficult to access especially at some times of the year, and can be divided into four regions: the Panhandle, the upper permanent swamps, the lower seasonal swamps and a number of large sandveldt tongues and islands (Ellery & McCarthy 1994).

The dynamics of the Okavango Delta are largely driven by two phenomena, rainfall and inundation of the floodplains. Most rainfall occurs between November and April (Gieske 1997), and the dry season lasts from May until November. The relative flatness of the area in combination with rainfall in the Angolan highlands drive the flooding, which reaches its peak in our study area in August, some 6 mo after the upstream rainfall (Gieske 1997, McCarthy *et al.* 2000). Basically, the dryland nutritional value of the vegetation varies with the seasons, peaking in the early wet season, and declining thereafter until the late dry season. The flooding occurs during the local dry season, limiting the area available for foraging, but also inducing some regrowth of grasses on the floodplain after the water recedes.

Data collection

Impala locations. The data on impala habitat use were taken from three successive field study reports. These studies were carried out for nearly 1 y, from October 2000 until August 2001 (Hof 2003, Klop & van Goethem 2001, Slot 2002, Van Munster, unpubl. data). The data were collected on a bimonthly basis, and involved the use of four line transects (Figure 2): Croc (8 km), Lion (11 km), Bushcamp (13 km) and Mopane (5 km). All, with the exception of Croc transect, are situated in the

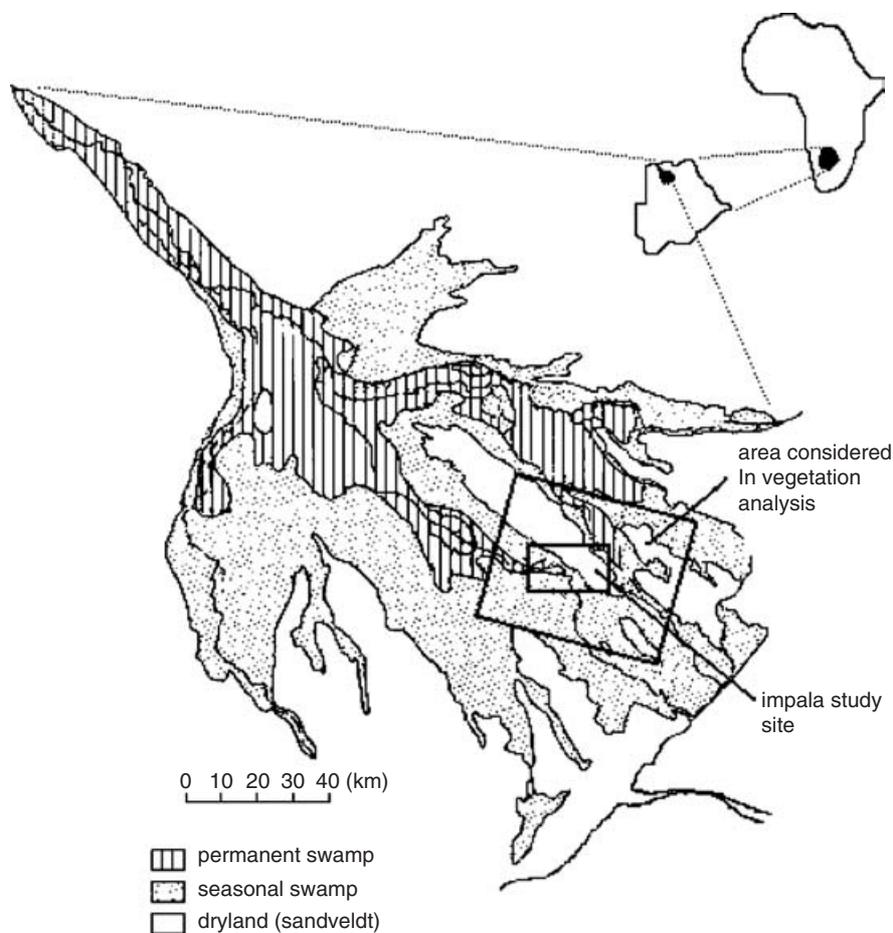


Figure 1. Map of the study area in the Okavango Delta, Botswana (adapted from Ellery & McCarthy 1994) and approximate location of the study site. The 'impala study site' is provided in more detail in Figure 2.

Moremi Game Reserve on Chief's Island, and comprise a somewhat smaller area than used for vegetation classification (Figure 1). Restricted accessibility due to flooding resulted in a slight alteration of the transects for the August period.

A handheld GPS was used to record the walked transect lines and the location where an animal or group of animals was observed. At each sighting the GPS coordinates, estimated sighting distance, and compass direction subtended from north were recorded. To avoid dependence, each group of animals was counted as one single observation. In case a group was encountered, the geometric centre of the group was considered in the recordings. An Arcview script was used to estimate the actual location of the animals, based on the observer's GPS location, estimated observation distance, and compass reading (Hof 2003, Klop & van Goethem 2001, Slot 2002, Van Munster, unpubl. data).

Remote-sensing imagery. The Landsat 7 ETM+ images, path 174 and row 074 covering the south-eastern part of

the Okavango Delta, were obtained from SAFARI 2000 (Swap & Privette 1999) through the Tropical Rain Forest Information Centre. Images from 3 April and 9 August 2000 (Figure 2) were used.

Geo-rectification of the Landsat images (30 m pixel size), to correct for the distortion in the images and place them into known geographic space (i.e. coordinate system), was reached through GPS-collected ground control points, resulting in a precision for the April and August image of 8.2 and 7.4 m respectively. To combine both images for classification, they were superimposed to form one multi-temporal image.

We gathered 600 training sets of representative vegetation classes during field visits in 2001. For each vegetation class the training set was randomly divided into two groups, one for training purposes, the second for accuracy assessment. These training sets were subsequently used for a supervised classification of the three vegetation types. The area considered in the training set gathering and classification, comprises a larger area than the impala-distribution study area (Figure 1). In doing so we expected that the adopted methodology

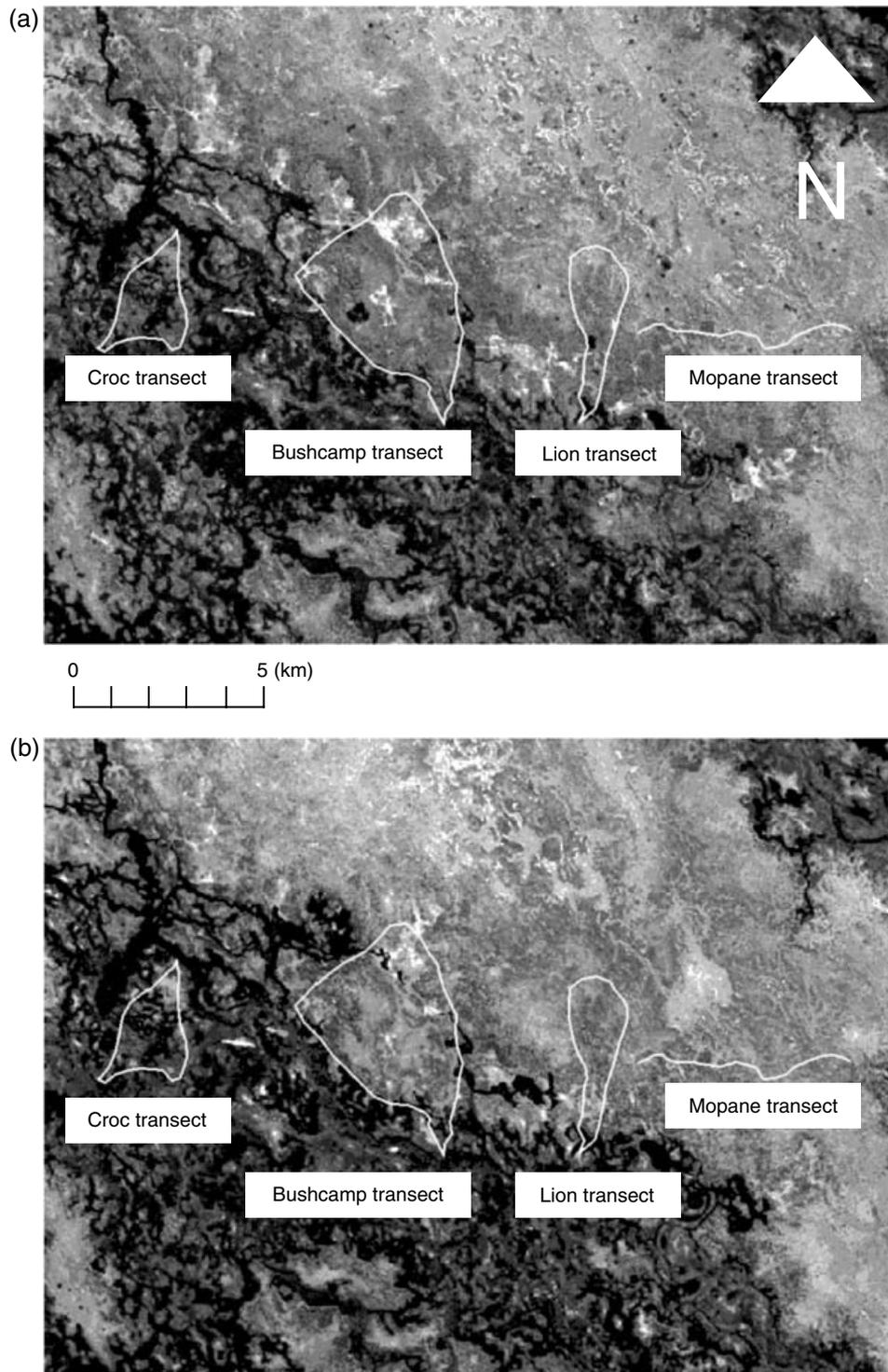


Figure 2. Study site, April (a) and August (b) Landsat image (black and white version of Landsat band combination 4, 5, and 3) of the impala study site in the Okavango Delta, Botswana, including transect locations.

would be strengthened in its general applicability and usefulness in extensive areas.

The NDVI was calculated for each pixel in both the April and August images. The April image represents the

end of the wet season, when peak biomass levels have been reached. The August image, the middle of the dry season, shows a strong difference between water-covered floodplain and the dryland covered with desiccated and

yellow grass, bare patches, and mostly leafless trees. The NDVI was calculated as follows (Lillesand & Kiefer 2000):

$$\text{NDVI} = (\text{NIR} - \text{R}) / (\text{NIR} + \text{R})$$

where NIR = near-infrared value and R = visible red value. High positive NDVI values are reported to correspond to dense green vegetation cover, whereas negative values are usually associated with bare soil and other non-vegetated surfaces.

Vegetation classification. The multi-temporal image was classified using the software package ERDAS Imagine. In the classification, three physiognomic vegetation types were distinguished, woodland, grass on dryland, and grass on floodplain. Each of these types was subdivided into three subclasses on the basis of the NDVI values available within each type. For all the pixels classified as one of the above-mentioned vegetation types, their respective NDVI value was determined, so that for each vegetation type a range of NDVI values is obtained. Subsequently, these ranges were divided into three subclasses, and consisted of low, intermediate and high NDVI values. This was reached through ranking the NDVI values for all pixels in each vegetation type, whereby the lowest one-third, the intermediate one-third and the highest one-third of all NDVI values were assigned to each subclass.

In order to assess the accuracy of the classification procedure, the overall accuracy of the classification gives the proportion of correctly classified reference pixels for all vegetation types combined, whereas accuracies specific per vegetation type are assessed through user and producer accuracy. Overall, producer and user accuracy are calculated as follows:

Overall accuracy: total number of correct pixels/total number of reference pixels \times 100%

Producer accuracy: number of correct pixels per vegetation type/number of reference pixels per vegetation type \times 100%

User accuracy: number of correct pixels per vegetation type/number of classified pixels per vegetation type \times 100%

Producer accuracy indicates the proportion of correctly classified reference pixels per vegetation type. A vegetation type with a high producer accuracy suggests that the vegetation type's presence in the field is well estimated. The user accuracy indicates the proportion of correctly classified pixels of the total number of pixels assigned per vegetation type. A vegetation type with a high user accuracy suggests that pixels are likely to be correctly classified.

Assessment of available habitat

The software package Distance 3.5, was used to estimate the so-called effective strip width (ESW), the area effectively surveyed from a transect for purpose of wildlife population assessments. We used the ESW as a correction factor for the classified images to estimate the availability of impala habitat (i.e. vegetation subclasses). The method is based on the locations of animals sighted from a transect. For each animal detected, the perpendicular distance between animal and transect was calculated. The ESW of the main vegetation types (i.e. woodland, grass on dryland, and grass on floodplain) was determined for each transect separately. Perpendicular distance from the sighted animal to the transect, was used as input for the Distance software. The derived effective strip widths were used to generate observation zones around the transect lines, representing the area estimated to be visible from these transects. To extract the available area for the vegetation subclasses, both April and August vegetation maps were superimposed on the calculated observation zones.

Analysis of habitat use

Selectivity of impala for vegetation classes was determined for both periods. We only used animal observations within a 12-wk period encompassing the image recording dates, to ensure that the observations related to each period's NDVI. A timespan of 12 wk was necessary to obtain enough validation data on impala locations, given the logistic constraints in our sampling efforts. Although this appears to be a large time-span, we were confident that the main phenological contrasts between the April and August periods would remain in place. The impala locations in the respective periods were superimposed on the classified maps for April and August, from which we calculated the impala habitat-use values.

The number of observations of a species within the recognized vegetation types were compared with the availability of each vegetation type, by following the methodology of Neu *et al.* (1974) and Byers & Steinhorst (1984). A χ^2 goodness-of-fit test ($\alpha = 0.05$, $n = 9$) was applied to test for selection of vegetation classes. When a significant difference was found, the Bonferroni approach was applied to determine which of the vegetation types were selected or avoided. The Bonferroni approach involves the construction of a set of simultaneous confidence intervals ($\alpha = 0.05$, $n = 9$) around the observed proportions of utilized vegetation types. Where the expected proportion of usage did not lie within the interval, it was concluded that the expected and observed utilization of that vegetation class were

significantly different, and either avoidance or preference occurred.

RESULTS

Vegetation classification

A mono-temporal classification for both images, resulted in a 77.7% overall accuracy for both April and August. A multi-temporal classification improved accuracy to 81.1%. However, the latter classification showed a considerable underestimation for grass on dryland (producer accuracy 18%) and a subsequent overestimation of the other two types. To improve upon this, a classification with adjusted maximum likelihood probabilities was applied, that enlarged the probability of the underestimated type, and vice versa. This resulted in an overall accuracy of 83.9% (Table 1), and decreased the underestimation of grass on dryland. User accuracies ranged from 80–87%, and producers accuracies from 81–93%, with the exception of grass on dryland (30%) (Table 1).

Table 1. Classification accuracy assessment. Overall, producer and user accuracy of the number of pixels correctly classified as landcover types (i.e. physiognomic vegetation types and open water) through a multi-temporal classification of the study area in the Okavango Delta, Botswana.

| Class name | Reference totals | Classified totals | Correct totals | Producer accuracy ² (%) | User accuracy ³ (%) |
|-------------------------------|------------------|-------------------|----------------|------------------------------------|--------------------------------|
| Grass on floodplain | 87 | 85 | 70 | 80.5 | 82.4 |
| Woodland | 152 | 178 | 142 | 93.4 | 79.8 |
| Grass on dryland | 43 | 15 | 13 | 30.2 | 86.7 |
| Open water | 73 | 77 | 73 | 100.0 | 94.8 |
| Column totals | 355 | 355 | 298 | | |
| Overall accuracy ¹ | | | | | 83.9% |

¹Overall accuracy: the proportion of the total correctly classified reference pixels (total number of correct pixels/total number of reference pixels × 100%).

²Producer accuracy: the number of correctly classified pixels of a specific class in comparison with the number of reference pixels of that class (number of correct pixels per vegetation type/number of reference pixels per vegetation type × 100%).

³User accuracy: the number of correctly classified pixels of a specific class in comparison with the number of pixels classified as that class (number of correct pixels per vegetation type/number of classified pixels per vegetation type × 100%).

Table 2. Range of NDVI levels for each subclass (low, intermediate, high NDVI) of physiognomic vegetation types, per season, of the study area in the Okavango Delta, Botswana.

| Vegetation type | April 2000 | | | August 2000 | | |
|---------------------|------------|--------------|-----------|-------------|--------------|-----------|
| | Low | Intermediate | High | Low | Intermediate | High |
| Grass on floodplain | −0.50–0.19 | 0.20–0.28 | 0.29–0.66 | −0.33–0.03 | 0.04–0.09 | 0.10–0.53 |
| Woodland | −0.38–0.22 | 0.23–0.29 | 0.30–0.65 | −0.33–0.01 | 0.02–0.06 | 0.07–0.46 |
| Grass on dryland | −0.28–0.16 | 0.17–0.22 | 0.23–0.55 | −0.10–0.01 | 0.00–0.01 | 0.02–0.30 |

The vegetation types distinguished were subdivided on the basis of their NDVI, for both April and August. The NDVI varied from −0.50 to 0.66 in the green, late-wet-season month of April, while NDVI in the dry month of August varied less, from −0.33 to 0.53 (Table 2). The accuracies of the subdivided types were assumed to approximate the accuracy of the classification for the broad physiognomic vegetation types. In both periods the largest variation in NDVI is shown for grass on floodplain, followed by woodland, and then by grass on dryland.

Available habitat

For each transect and for each vegetation class, the width of the observation zone was determined (Table 3). Due to the absence of grass on floodplain on the Mopane transect, there are no observations for this type, and estimation of the effective strip width could not be performed. Reliability of the ESW for grass on floodplain on the Lion transect and for grass on dryland on the Mopane transect is expected to be low, due to the limited number of impala observations here.

Vegetation-class availability figures from April and August differed slightly due to flooding-induced alteration of the transects in August (Table 4). Most of the observation area was covered by woodland, in April 57% and August 60%. Grass on floodplain made up 40% and 36% of the area, and grass on dryland 3% and 4%, for April and August respectively. Woodland and grass on dryland included relatively large areas with high NDVI values, whereas grass on floodplain had rather similarly sized NDVI subclasses.

Habitat use

The estimated impala locations were superimposed on the classified images. For the April period this resulted in 167 observations allocated to a vegetation subclass, against 97 impala observations around August (Table 5). Impala use of vegetation subclasses in April and August differed from the relative availability of those subclasses both in April ($\chi^2 = 38.5$, $P < 0.05$) and in August ($\chi^2 = 19.3$, $P < 0.05$). More specifically, impala preferred woodland with intermediate NDVI values in both April and August, but were indifferent to, or even

Table 3. Width of the observation zones (m), determined by Distance 3.5, for each transect (Bushcamp, Croc, Lion and Mopane) and for each physiognomic vegetation type (grass on floodplain, woodland, and grass on dryland), based on impala observations.

| Vegetation type | Bushcamp | Croc | Lion | Mopane |
|---------------------|----------|------|-----------------|-----------------|
| Grass on floodplain | 68 | 84 | 33 ¹ | — ² |
| Woodland | 29 | 22 | 32 | 52 |
| Grass on dryland | 39 | 53 | 63 | 35 ¹ |

¹Number of observations is considered too small for a reliable estimate of the Effective Strip Width (ESW).

²No observations, and no ESW determined.

avoided, other woodland subclasses (Table 5). Impala avoided grass on dryland with low NDVI values in both seasons, and were indifferent to the other subclasses in grass on dryland. Impala avoided grass on floodplain with high NDVI values in both periods, as was also the case with grass on floodplain with low NDVI values for the April period; they appeared indifferent to all other subclasses in both periods.

DISCUSSION

Classification accuracy

Our classification accuracies, mostly over 80%, compare favourably to previously published work where classification accuracies using Landsat imagery were actually reported. Tanser & Palmer (2000), studying heterogeneous vegetation cover of the Great Fish River basin in South Africa, found an accuracy of 77%. Conese & Maselli (1994) reported 85% for their study in southern Senegal on subtropical land cover types, whereas Gomasasca *et al.* (1992), studying the floodplain and dryland vegetation of the Niger River Interior Delta in the Republic of Mali, reported 77% (wet season) and 66% (dry season) accuracies. Furthermore, since all of our vegetation classes showed a high user accuracy, pixels were likely correctly classified. The low producer accuracy for grass on dryland (30%) suggests that this vegetation type is likely to be underestimated in our classification, whereas grass on floodplain and woodland – which covered the largest

parts of our study area – were for the larger part correctly represented.

Assessment of available habitat

The accuracy of the availability assessment is determined by (1) the observation zone estimate, and (2) the vegetation classification. The observation zones vary in width both within and between vegetation types. This can be explained by the vegetation structure and animal sightings in the field. The found observation zones appear to be plausible, as they correspond with differences in patchiness and visibility among the physiognomic vegetation types. Grass on floodplain generally offers a higher visibility than grass on dryland or woodland, as it generally covers extensive open areas that offer clear views. Grass on dryland is of a more patchy nature and thus generally offers more limited sighting, while the most restricted view is found in woodland, especially in dense types such as mopane woodland or riverine forest (van Bommel, *pers. obs.*). For grass on floodplain and woodland the availability appears to be well estimated as both classification and observation zones are accurate. The availability assessment for grass on dryland is hampered by the classification, which appears to underestimate the presence of grass on dryland, and therefore the availability data for this vegetation class should be interpreted with caution.

Impala habitat use

In the late-wet season (April), water levels are low and reflectance is mainly determined by green vegetation, rather than by water or soil background. High NDVI values in woodland are interpreted as closed-canopy riverine forest, and open-canopy mixed woodlands with a well-developed grass layer. Low NDVI probably represents mopane woodland, that has a low LAI due to the absence of a continuous grass layer. The intermediate NDVI values are likely to be found in open-canopy *Acacia* or mixed woodlands. Variation in NDVI for grass on floodplain might be explained by reedbeds high in LAI and chlorophyll level, while areas that experience a high

Table 4. Availability (ha) of the subdivided (low, intermediate, high NDVI level) vegetation types (grass on floodplain, woodland and grass on dryland) based on the through Distance 3.5 determined observation zones, for the classified April and August 2000 images.

| Period | | Grass on floodplain | | | | Woodland | | | | Grass on dryland | | | | Total |
|--------|------|---------------------|-------------------|------|-------|----------|-------------------|------|-------|------------------|-------------------|------|-------|-------|
| | | Low | Inter- mediate | High | Total | Low | Inter- mediate | High | Total | Low | Inter- mediate | High | Total | |
| April | (ha) | 29.6 | 33.8 | 43.5 | 106.9 | 9.1 | 44.0 | 98.6 | 151.7 | 0.4 | 0.8 | 6.0 | 7.2 | 265.9 |
| | (%) | 11.1 | 12.7 | 16.4 | 40.2 | 3.4 | 16.5 | 37.1 | 57.1 | 0.2 | 0.3 | 2.3 | 2.7 | 100.0 |
| August | (ha) | 19.4 | 32.5 | 40.5 | 92.4 | 17.0 | 55.1 | 80.7 | 152.8 | 0.5 | 2.4 | 5.9 | 8.8 | 254.1 |
| | (%) | 7.6 | 12.8 | 15.9 | 36.4 | 6.7 | 21.7 | 31.8 | 60.1 | 0.2 | 0.9 | 2.3 | 3.5 | 100.0 |

Table 5. Selection of vegetation subclasses by impala for the April and August 2000 periods, with Bonferroni simultaneous probability intervals.

| Vegetation type | NDVI subclass | Expected proportion | Impala sightings | Observed proportion | Selection ¹ |
|----------------------|---------------|---------------------|------------------|---------------------|------------------------|
| April period | | | | | |
| Grass on floodplain | low | 0.111 | 6 | 0.005–0.103 | – |
| Grass on floodplain | interm. | 0.127 | 16 | 0.032–0.160 | 0 |
| Grass on floodplain | high | 0.164 | 10 | 0.008–0.111 | – |
| Woodland | low | 0.034 | 11 | 0.012–0.120 | 0 |
| Woodland | interm. | 0.166 | 47 | 0.184–0.379 | + |
| Woodland | high | 0.371 | 71 | 0.318–0.533 | 0 |
| Grass on dryland | low | 0.001 | 0 | 0.000–0.000 | – |
| Grass on dryland | interm. | 0.003 | 1 | 0.000–0.023 | 0 |
| Grass on dryland | high | 0.023 | 2 | 0.000–0.036 | 0 |
| Sum | | 1.000 | 167 | | |
| August period | | | | | |
| Grass on floodplain | low | 0.076 | 5 | 0.000–0.115 | 0 |
| Grass on floodplain | interm. | 0.128 | 9 | 0.010–0.175 | 0 |
| Grass on floodplain | high | 0.159 | 6 | 0.000–0.131 | – |
| Woodland | low | 0.067 | 6 | 0.000–0.131 | 0 |
| Woodland | interm. | 0.217 | 36 | 0.233–0.509 | + |
| Woodland | high | 0.318 | 33 | 0.205–0.475 | 0 |
| Grass on dryland | low | 0.002 | 0 | 0.000–0.000 | – |
| Grass on dryland | interm. | 0.010 | 1 | 0.000–0.039 | 0 |
| Grass on dryland | high | 0.023 | 1 | 0.000–0.039 | 0 |
| Sum | | 1.000 | 97 | | |

¹: avoidance; 0: indifference; +: preference ($\alpha = 0.05$, $n = 9$).

grazing pressure or that are partly flooded will be low in LAI, and thus in NDVI. Grass on dryland is expected to vary in NDVI mostly with LAI, which is a function of grass height and density, and of the presence of sparse trees.

In the late-dry season (August), the dryland is covered with desiccated and yellow grass, bare patches, and mostly leafless trees, with the exception of riverine forest and grass on floodplain. The variation of NDVI in woodland is therefore expected to be caused by the high LAI and associated high NDVI in riverine forest, and on the other hand by leafless and grassless mopane woodland, with low LAI and chlorophyll levels. For grass on floodplain the large variation might be explained by the presence of recently flooded areas exposing only water, very low in NDVI, and reedbeds or fresh regrowth in the floodplains with high chlorophyll levels, and therefore high NDVI values. Factors influencing the NDVI of grass on dryland could be the presence of sparse trees or the variation in presence of bare soil.

Grass on floodplain. We interpret the avoidance or neutral preference by impala of grass on floodplain NDVI classes in April and August as a valid result for both periods. Reedbeds, high in NDVI, are notably poor impala habitat at any time of the year, and particularly hard to get to in August. The permanently wet part of the floodplain always offers little suitable forage to these herbivores. Low NDVI areas in April are likely dry or intensely grazed areas that are low in green biomass, such as lower

parts of the floodplain that were still flooded in prior months. Furthermore, impala are often observed near forest boundaries, which are notably absent near much of the floodplain.

Woodland. The preference of impala for woodland intermediate in NDVI values, and the indifference for other woodland types is also regarded as valid for both periods. For both April and August, areas of intermediate NDVI are likely associated with *Acacia* and mixed woodland, but not with mopane woodland or riverine forest. Mopane woodland is conspicuously poor in palatable grasses, and mopane leaves are generally believed to have a low palatability to large herbivores. The indifference towards riverine forest, which does offer food resources of mixed quality to impala, could be explained by the limited number of impala sightings, due to the particularly low visibility of this vegetation type, whereas impala do perhaps occur at higher densities here.

Grass on dryland. The avoidance and indifference of impala for grass on dryland subclasses have to be carefully interpreted, as grass on floodplain was underestimated in the classification, and therefore also in the assessment of available habitat. For a subclass covering only a minor area, such as grass on dryland low in NDVI values, the observed proportion of habitat use is zero (Table 5), and therefore the upper and lower boundary of observed

occurrence are also set to zero. This implies that the expected proportion of occurrence always falls outside the observed boundaries, making the avoidance for grass on dryland low in NDVI, for both April and August, questionable.

Seasonal impala distribution. Overall, the field data indicate that there is no important shift in impala preference for habitat between late-wet and late-dry season, and that this consistency is captured by the NDVI-based vegetation subclasses. This observation is in line with the finding that impala show an annually consistent habitat preference (Ben-Shahar 1995).

Remote-sensing in animal habitat studies

The findings of this study clearly suggest that the chosen methodology, to incorporate remote-sensing-derived NDVI subclasses into broad physiognomic vegetation types, can be applied to relatively sedentary animals like impala at landscape scale, under seasonally different conditions. This has brought the work conducted by Verlinden & Masogo (1996) and by Ottichilo *et al.* (2000) on relating migratory herbivores with NDVI, and the NDVI-based studies of Oindo (2002) and Seto *et al.* (2004) on animal biodiversity, to a more detailed, landscape level. Furthermore, contrary to other studies (Ottichilo *et al.* 2000, Parra *et al.* 2004) we omitted environmental gradients, such as rainfall patterns, from mapping functional landscape characteristics. Yet, our results suggest that impala displayed selectivity for vegetation subclasses assigned on the basis of NDVI characteristics only, which is also a simplification compared to the use of auxiliary data in the study of sedentary grivet monkeys by Zinner *et al.* (2002). Some of the shortcomings in our study included the arbitrary numerical split of NDVI subclasses into thirds according to the number of pixels in each vegetation type, and by the use of relative spatially coarse imagery in the classification of highly heterogeneous landscape elements. These should be overcome by further studies that can provide further insight in obtaining functional breakpoints of NDVI subclasses and the application of the NDVI within herbivore habitat studies in general. A necessary improvement of the classification should include an error analysis of the NDVI subclasses. Given the recent progress in the fields of satellite tracking of animals in the field (Amstrup *et al.* 2004) and remotely sensed vegetation quality assessment (Mutanga *et al.* 2004), a strong link between animal movements and functional vegetation analysis using remote sensing is within reach. This would be of particular relevance for the conservation and management of herbivores in inaccessible areas.

Conclusion

The results show that our classification methodology is capable of capturing habitat occupancy by a sedentary large herbivore, impala, in a spatially and seasonally diverse landscape. We suggest that this is due to differences in vegetation characteristics determining forage quality and quantity (NDVI) and that impala shows a functional response. Further studies, directed towards linking forage quality and availability with NDVI levels nested in physiognomic vegetation types, will further improve our understanding of remote-sensing based studies on habitat use. This study suggests that the application of remote-sensing techniques may contribute to animal habitat studies at a landscape scale, without the need to sample a wide range of field data under time and budget constraints. We suspect that this technique would work even better for other herbivore species with stronger habitat selection characteristics than the generalist impala. We therefore consider this approach to be useful for describing functional habitat types for a range of herbivore species, sensitive to forage quality changes over time, in large areas. Moreover, this approach will likely benefit the preservation of individual species in extensive conservation areas.

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