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Space-time pattern of habitat utilization for the Chobe riverfront elephant population



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Abstract

In order to examine potential contributing explanations to the high biodiversity seen along the Chobe riverfront in Northern Botswana, the space-time pattern of habitat use for the area's elephant population was investigated during the dry season 2004. Bulls and family groups were monitored in four different habitats in the north eastern corner of Chobe National Park using line transect sampling method. The results show that the areas closest to the Chobe river had the highest densities of elephants during the day-night cycle. This implies that a high proportion of faeces and urine are deposited in this small area. Since the elephants mainly forage in the vast woodlands further away from the river they mediate a transport of nutrients from the woodlands in the interior part of the park to the areas close to the river, mainly to the floodplain. The Chobe and Zambesi rivers are the main available surface water in the area during the dry season but the vicinity of water can not alone explain the high biodiversity seen at the riverfront. The net import of nutrients to the floodplain, facilitated by the elephants, should be considered as one potential contributing factor to the high biodiversity, and should be taken into account for decisions of management of the area in general and its elephants in particular. Further, the results indicate that family units forage at greater distances from the Chobe river than what has been recorded before. The causes for this new pattern are, however, uncertain.

Table of contents

| | |
|---|----|
| 1. Introduction | 3 |
| 1.1 Large herbivores and ecological heterogeneity | 3 |
| 1.2 Large herbivores and habitat utilization..... | 4 |
| 1.3 Elephants as ecological engineers in Northern Botswana..... | 5 |
| 1.4 Objectives..... | 7 |
| 2. Methods | 8 |
| 2.1 Study area..... | 8 |
| 2.2 Habitat classification..... | 9 |
| 2.3 Sampling design | 10 |
| 2.4 Distance analyses..... | 14 |
| 2.5 Other analyses | 15 |
| 3. Results | 17 |
| 3.1 Elephant densities in various habitats | 17 |
| 3.2 Densities as time utilization and related to browsing data..... | 18 |
| 3.3 Detection density at different periods of the day-night cycle | 19 |
| 3.4 Space-time pattern for different sex/group-types | 21 |
| 4. Discussion | 22 |
| 4.1 Elephant densities in various habitats | 23 |
| 4.2 Time utilization and nutrient transportation..... | 23 |
| 4.3 Space-time pattern during the day-night cycle..... | 25 |
| 4.4 Space-time pattern for different sex/group types | 25 |
| 4.5 Sampling design and statistical analyses | 26 |
| 4.6 The elephant debate in Southern Africa and in Chobe | 27 |
| 4.7 Conclusions | 29 |
| Acknowledgements | 29 |
| References | 30 |

1. Introduction

Herbivores affect vegetation and ecosystem processes directly or indirectly in many different ways (Huntly 1991, Davidson 1993, Jefferies et al. 1994, Hixon & Brostoff 1996). Large herbivores often have great impact on ecosystem processes through their ability to affect both abiotic and biotic factors (Hobbs 1996). They affect the vegetation and the ecosystems on different scales and the effects can be long lasting (Pastor & Naiman 1992). The large herbivores mainly affect ecosystem processes by their feeding, trampling, defecation, urination and by leaving carcasses (Mckendrick et al. 1980, Owen-Smith 1988, Pastor & Naiman 1992, Pastor & Cohen 1997). The direct effects from the large herbivores on the vegetation and on the landscape can have significant indirect effects on ecosystem processes, not least by interfering with the nutrient cycle (Augustine & McNaughton 1998, Ritchie et al. 1998). They are therefore not just influenced by heterogeneity in the landscape but also affect the spatial and temporal heterogeneity themselves. Hence, large herbivores can be seen as regulators of ecosystem processes and indirectly controlling the form and the function of the ecosystem (Pastor & Naiman 1992, Lawton 1994).

1.1 Large herbivores and ecological heterogeneity

Heterogeneity understood as the degree of difference among a set of things (Pickett 2003) is the ultimate source of biodiversity (Pickett 1998 in Pickett 2003) and its mechanisms is therefore essential to study. Heterogeneity in a landscape results both from abiotic and biotic factors. While temporal and spatial differences in soil and climate are important abiotic causes of heterogeneity in a savannah ecosystem (Venter et al. 2003), herbivores and specifically large herbivores can be important biotic drivers (Scholes et al. 2003). Sometimes specifically one kind of organism affects the availability of resources to other organisms; a process defined as ecological engineering (Jones et al. 1994). Ecological engineering is the basic mechanism by which organisms affect heterogeneity and it can operate via physical, chemical, or transport processes (Pickett et al. 2003). The physical engineering by e.g. large herbivores has ecological consequences modulating the flow of resources used by other species (Venter et al. 2003).

One of the most important ways in which large herbivores can have influence on heterogeneity is by affecting the distribution and availability of nutrients in the soil

(Augustine & McNaughton 1998). By selective herbivory large herbivores can alter the structure and composition of a plant community and therefore also affect the nutrient cycling rate (ibid.). Further, by consuming large amounts of biomass and by their often high mobility large herbivores are important in determining in what location the nutrients enter the decomposition subsystem. Hence, large herbivores play a key role in creating spatial and temporal heterogeneity.

1.2 Large herbivores and habitat utilization

In order to understand how large herbivores affect the vegetation and the distribution of nutrients it is important to examine their foraging pattern as well as their general spatial and temporal use of different habitats. All herbivores have certain requirements of their habitat which are vital for the survival of the individuals within the species. For large herbivores these include food sources, surface water, and refuges from weather extremes (Owen-Smith 1988). In order to secure their requirements the individuals engage in many activities such as feeding, moving between feeding sites, drinking, resting, and various forms of social interaction. These activities need to be scheduled optimally within the day-night cycle in certain space-time patterns which are established within the animal's home range (ibid.). There may be variations in terms of time utilization between different sections of the home range and the animals may also move seasonally between different home ranges defining what can be called an 'annual range' (ibid.).

There are great variations in space-time patterns between different species of large herbivores. While African elephants (*Loxodonta africana*) tend to be equally active during day and night and devote about three quarters of their time to foraging (Hendrichs 1971 in Owen-Smith 1988, Wyatt & Eltringham 1974), Hippos (*Hippopotamus amphibius*) devote only one third of their time to foraging, and exclusively at night (Verheyen 1954 in Owen-Smith 1988). The space-time patterns can also vary significantly between different populations of the same species. There are for example recorded home range sizes for African elephants varying from 14-52 km² from the ground water forest habitat of Lake Manyara Park in Tanzania (Douglas-Hamilton 1973) up to a mean home range size of 1800 km² in the semi-arid steppe of Tsavo East National Park in Kenya (Leuthold 1977 in Owen Smith 1988). Many large herbivores are so called "central place foragers" with a home place centred on a water source around which

they tend to forage (Stuth 1991). Thus, water is often an important constraint on regional movement (Senft et al. 1987).

1.3 Elephants as ecological engineers in Northern Botswana

The African elephant, the world's largest herbivore, is at high densities known to have profound effects on vegetation (Laws 1970, Pellew 1983, Jachmann & Bell 1985, Jachmann & Croes 1991, Ben-Shahar 1993, van de Vijver et al. 1999) and on biodiversity in general (Laws 1970, Cumming et al. 1997). They can affect the vegetation species composition through selective feeding (Jachmann & Croes 1991) and therefore play a key role in determining the distribution and cycle rate of nutrients (Augustine & McNaughton 1998). Further they affect other herbivores in several ways and directions by directly influencing the availability of food and shelter or the fire regime in a certain area (Owen-Smith 1988, van de Koppel & Prins 1998, Skarpe et al. 2000, Fritz et al. 2002), even though the direction of the influence from elephants on other herbivores varies between competition and/or facilitation (van de Koppel & Prins 1998, Fritz et al. 2002). By their ability of direct or indirect modulation of the availability of resources to other organisms, the elephants in some areas function as ecological engineers.

The northern part of Botswana and adjacent areas in neighbouring countries have the continent's largest coherent population of elephants (Blanc et al. 2007). The size of the population is estimated to be around 150 000 individuals (DWNP 2006 in Blanc et al 2007), with highest densities along the Chobe riverfront in Chobe National park (Gibson et al. 1998). The elephant population in Botswana and Chobe has gone through some dramatic changes during the past two centuries (Vandewalle, 2003) and the great variation in numbers and distribution of elephants over time has led to locally vast ecosystem changes in several directions. As in some other areas in southern Africa the elephant population along Chobe riverfront has grown rapidly during the last decades (ibid.). During the same period the vegetation structure and composition in this area has shown significant changes. Some tree species have decreased in distribution while others have increased (Mosugelo et al. 2002, Skarpe et al. 2004), and scenic woodlands along the river have been replaced by shrub vegetation (Addy 1993 in Skarpe et al. 2004, Herremans 1995). Although alterations in water availability could have contributed to the observed changes, these changes are believed to be caused mainly by the increasing elephant population (Simpson 1974, Addy 1993, Simpson

1975, KCS 1990, Chafota & Owen-Smith 1996 all in Skarpe et al. 2004, Ben-Shahar 1996), in interaction with increasing populations of smaller browsers, primarily impala, preventing rejuvenation by browsing on seedlings (Moe et al. in press).

Perhaps more than in any other location in Southern Africa the high local densities of elephants along the Chobe river has led to major concern regarding their potential to harm biodiversity by degrading the ecosystem. This was the reason for the launching by DWNP, Botswana Department of Wildlife and National Parks in 1998 of a large research and capacity building project (BONIC) in cooperation with Norwegian institutions. The project found little evidence of adverse ecological effects. On the contrary, they found that the heavily elephant impacted areas close to Chobe River had the highest biodiversity and was favoured by many animals from insects to guineafowl, antelopes and lions (Motsumi 2002, Skarpe et al. 2004). The observed increases of buffalo (Taolo 2003 in Skarpe et al. 2004) and impala (Rutina 2004) in the heavily elephant impacted areas is contrary to the findings of Fritz et al., in their study over 31 conserved African ecosystems (Fritz et al 2002). The different pattern in Chobe can perhaps be partly explained by the intermittent pattern of herbivory. Browsing and grazing pressure is highest during the dry season when plants largely are dormant and lowest during the wet growing season when animals disperse to other areas (Skarpe et al. 2004). Another contributing factor could be that of elephants as nutrient transport agents, mediating a net transport of nutrients from the woodlands in the interior of the park to the shrublands and floodplains close to the river (ibid.).

Knowledge about the impact from the elephants on the ecosystem in Chobe is of considerable importance for protection of biodiversity, and is essential for decisions of management of the area in general and its elephants in particular. It is therefore of greatest interest to gain more knowledge about the dynamics of Chobe's elephant population. In order to understand the elephants' role as ecological engineers and as key elements of creating heterogeneity it is essential to map not only their foraging strategies but also their total utilization of different habitats along the Chobe riverfront. The elephants in Chobe have been subject for many studies (Sommerlatte 1976, Craig 1990, Stokke 1999, Stokke & du Toit 2000, Stokke & du Toit 2002, Skarpe et al. 2004), but the spatial dynamics of the population has not yet been investigated in terms of time utilization in different sections of their home range. As described, this has potential influence not only on the shape of the landscape and the structure

of the vegetation, but also on the nutrient cycle and consequently the potential heterogeneity in terms of primary production within the area.

To investigate the possible nutrient transport mediated by the elephants it is necessary to map their space-time pattern; how much time they spend in different sections of their home range, and relate that to the proportion of forage taken from the different areas. We suspected high elephant densities close to the river, where they drink, bathe and socialise. High densities would imply a proportionally large amount of time utilization, which in turn would indicate that a relatively large amount of faeces and urine is deposit in this area. By spending a proportionally large amount of time close to the river, the elephants would import nutrients to this area from the woodlands in the interior part of the park, where they mainly forage (Skarpe et al. 2004).

1.4 Objectives

The main aims of my study were

- To estimate the density of elephants in different habitats within the Chobe riverfront in the dry season, in order to obtain a space-time pattern of habitat utilization.
- To relate the space-time pattern of habitat utilization to foraging patterns.
- To investigate variations in habitat utilization between different periods during the day-night cycle.
- To investigate variations in habitat utilization between different sex/group types.

2. Methods

The field study was conducted in a selected part of Chobe National Park in northern Botswana (Fig. 1) July-September 2004. The distribution of elephants in the area was monitored by driving transects and doing road-side counts. The collected data were analysed using mainly Distance statistical methods.

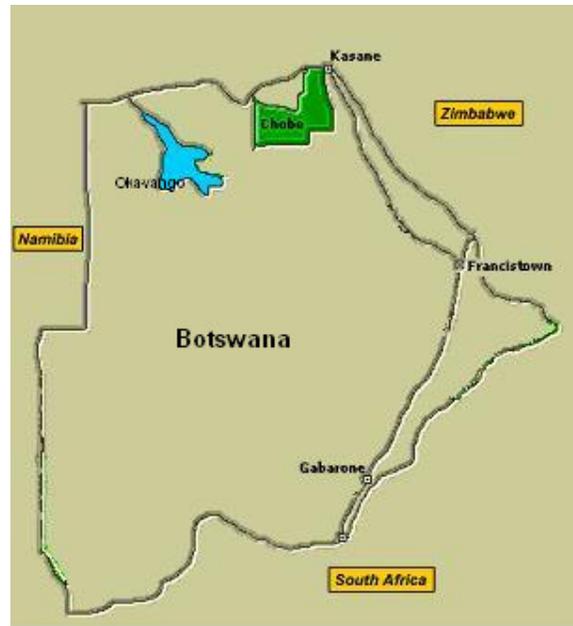


Fig. 1. Map of Botswana and Chobe National Park in the north.

2.1 Study area

Chobe National park is divided into four distinctly different ecosystems: The Chobe riverfront with its lush plains and dense forests in the Chobe river area in the extreme north-east; the Savuti Marsh in the west; the Linyanti Swamps in the north-west and the hot dry hinterland in between (http://www.botswanaturism.co.bw/attractions/chobe_national_park.html). The study area was located in the north-eastern corner of the park (approx. 17°50'-18°08'S 24°50'-25°07'E) in the Serondela region. It included a 50 km wide section along the Chobe River and stretched from Ngoma in the west to Kasane in the east. The area was bounded by the Chobe River in the north and extended around 34 km to the south from the river.

The area is flat to gently undulating and the average altitude is about 1000 m. The stretch of the river running along the study area is bounded by floodplain grassland, fragments of riparian forest and shrubland in the adjacent uplands (Mosugelo et al. 2002). Further away from the river the shrubland vegetation becomes woodland vegetation with a mixture of species including *Baikaea plurijuga*, *Combretum elaeagnoides*, *C. apiculatum*, *C. mossamicense* and *Baphia massaiensis*. With distance from the river *B. plurijuga* gradually becomes more dominant.

The climate in the study area is semi-arid and there are two distinctive seasons, one rainy season in summer lasting November-March and one dry in winter lasting May-August (April and September/October are regarded as transition periods). The rainy season is hot with an average day-night temperature of 26 °C (<http://www.climate-zone.com/climate/botswana/celsius/kasane.htm>). The annual average rainfall during the rainy season in the study area is about 650 mm (<http://www.weather.info.bw/index.html>). The dry season is warm during the day and cool at night with an average day- night temperature of 21°C. Rainfall during the dry season is scarce (<http://www.climate-zone.com/climate/botswana/celsius/kasane.htm>).

2.2 Habitat classification

The distribution of the elephants within the study area was analysed in terms of density of individuals in four different habitats: floodplain, shrubland, mixed woodland and baikaea woodland. When analyzed, each habitat was regarded as homogenous even though local variation in vegetation density and species composition occurred. For example patches of shrubland occurred in the woodlands and some parts of the baikaea woodland had a similar density as the vegetation seen in the mixed woodland. However, generally the four habitats were distinctively separate.

- The **floodplain** is a wide open grassland defined by the annual inundations by the Chobe river and runs along and within (as islands) the river. The vegetation is dominated by the grazing-adapted grasses *Cynodon dactylon* and *Vetiveria nigritana*. The examined part of the floodplain is constituted by the river shore, the islands in the

river and the water in between (the river itself). The floodplain occupies 3% of the area studied.

- The **shrubland** is located parallel to the river in the adjacent uplands stretching 0.3-1.7 km away from it. These elevated alluvial plains are covered by shrubs with *Capparis tomentosa* and *Combretum mossambicense* as dominating species. The shrubland occupies 5% of the area studied.
- Away from the river the alluvial soil changes into Kalahari sand and the shrubland vegetation changes into woodland vegetation. In this study the habitat bordering the shrubland is classified as **mixed woodland**. The vegetation in this habitat is mainly composed of *Baikaea plurijuga*, different *Combretum* species and *Baphia massaiensis*. The mixed woodland occupies 16% of the area studied.
- Further south the woodland vegetation becomes more dominated by *Baikaea plurijuga* and the habitat is classified as **baikaea woodland** in this study. The baikaea woodland habitat continues south of the main road running through the park, even though the vegetation density is thinner there due to the occasional occurrence of fires, which are virtually absent north of the main road. The baikaea woodland occupies 76% of the study area, where the part north of the main road stands for 55% and the part south of the main road for 21% of the total area studied.

2.3 Sampling design

The densities of elephants within the study area were estimated using line-transect sampling, which is one of several Distance sampling methods (Thomas et al. 2002). When using line-transect sampling a series of lines (transects) is traversed by an observer searching for an object and when an object is detected the distance and angle between the line and the object is recorded (ibid.).

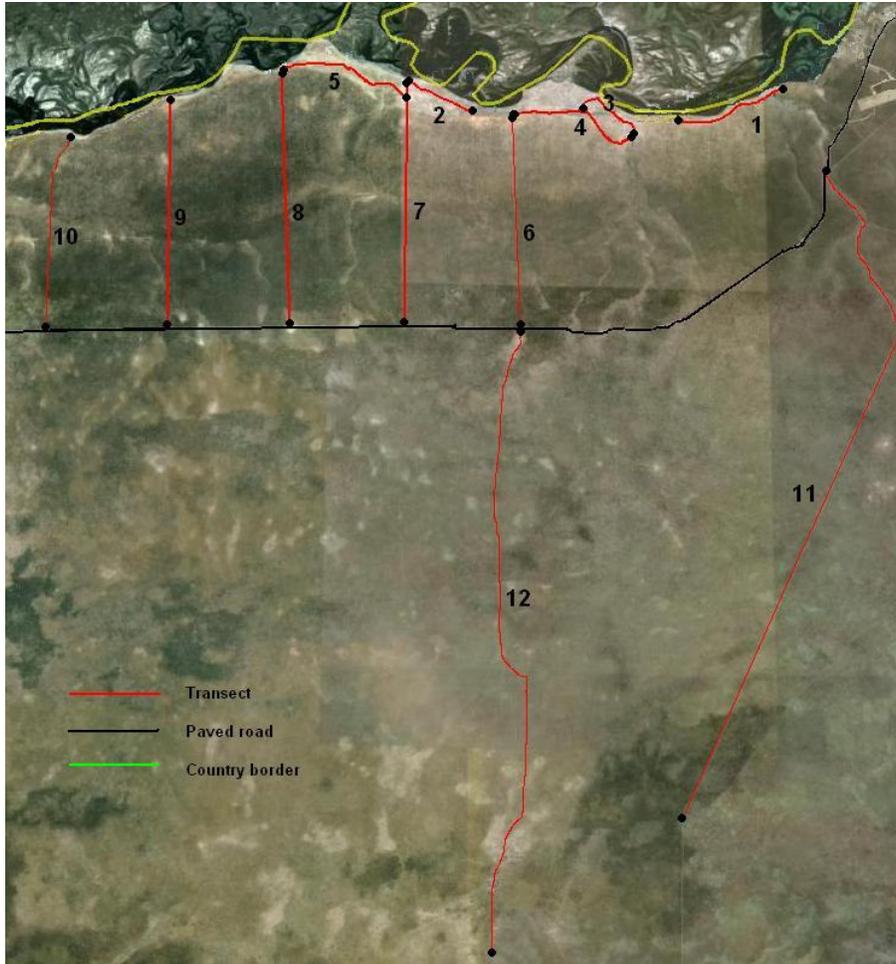


Fig. 2. Map showing the study area with the 12 transects used. The Chobe river and the country border to Namibia is seen at the top of the picture.

We were driving a total number of 12 fixed transects, together covering all four habitats. Transects 1-2 ran along the floodplain parallel to the Chobe River, transects 3-5 in the shrublands close to the river, transects 6-10 ran about 10 km perpendicularly from the river through shrubland, mixed woodland and baikaea woodland, and transects 11-12 ran about 24 km further away from the river, exclusively in baikaea woodland (Fig. 2, Table 1). Already existing tracks and roads were used as transects in all cases. The transects on the floodplain and in the shrubland (transects 1-5) were tourist roads and the ones in the mixed and baikaea woodland (transects 6-12) were roads used by park staff and scientists. The tracks and roads used as transects were chosen so that they would be representative for each habitat (even though transects 6-10 ran through three different habitats) and for practical reasons (they were close enough to each other to save time and fuel and far enough from each other not to risk counting the same observation twice).

Table 1. Length in km of each transect in the various habitats

| Transect No | Habitat | | | | Total |
|----------------|------------|-----------|-------------------|---------------------|--------|
| | Floodplain | Shrubland | Mixed woodland | Baikaea woodland | |
| 1 | 3,4 | - | - | - | 3,4 |
| 2 | 2,9 | - | - | - | 2,9 |
| 3 | - | 3,1 | - | - | 3,1 |
| 4 | - | 5,5 | - | - | 5,5 |
| 5 | - | 5,4 | - | - | 5,4 |
| 6 | - | 0,84 | 4,98 | 4,23 | 10,05 |
| 7 | - | 1,68 | 5,12 | 5,12 | 11,92 |
| 8 | - | 0,33 | 1,66 | 8,96 | 10,95 |
| 9 | - | 0,75 | 1,59 | 8,0 | 10,34 |
| 10 | - | 0,37 | 1,29 | 6,72 | 8,38 |
| 11 | - | - | - | 28,7 | 28,7 |
| 12 | - | - | - | 23,9 | 23,9 |
| Total | 6,3 | 17,97 | 14,64 | 85,63 | 124,54 |

The transects were driven both during the day and the night at all different times with the exception of 06-07 and 18-18.45 because of the difficulties in light conditions. At these hours it was too dark to use the day method and too light to use the night method (see below for explanation of the different methods). The total number of driven transects was 135 during the day and 122 at night. Each transect was driven between 9 and 13 times in the day and 9 and 11 times at night. Each transect was also driven at all different times of the day and night. The time of day or night a transect was driven was spread out over the study period so that no transect was driven only at night in the beginning and only during the day in the end of the study period. During our study we collected data of habitat use by driving line transects over a total distance of 2 428 km.

The transects were run using a 4x4 vehicle. The transect drive included 3 persons, one driver and two standing on the back of the car. Before starting each transect drive, date, running no. (every drive got an individual no.), the name of the transect, period of the day (day or night), the direction of the drive (east, west, north or south), weather, actual time, and actual GPS coordinates were noted. The speed while driving transects was approximately 25 km/h in the day and 20 km/h at night. Each drive was carried out as similar to one another as possible, but if the visibility was extremely good as on the floodplain and some parts of the baikaea

woodland at daytime, the transects could be run with a higher speed without affecting the detection probability.

During the drive, the two persons standing on the back of the car were looking for elephants on each side of the road (transects 3-12) and the driver was looking for elephants on the road. While driving the two transects along the river covering the floodplain habitat (transect 1-2) only one side of the road was examined (the actual floodplain) and the elephants observed on the other side of the road were disregarded.

As soon as one or more elephants were spotted, the driver stopped the car and the two people at the back started to note information about the observation. The actual time, the distance driven along the transect and the coordinates of the car position were noted using a GPS. Further, the distance to the animal(s), the direction from the car to the animal(s) and the direction of the road (degrees from north), were recorded using a rangefinder. The number of spotted individuals was noted. Also, sex (if there was a single elephant) or composition of the group, either “family group” or “male group”, were recorded. To be classified as family group there had to be at least two individuals in the group, of which at least one had to be a cow. A male group consisted exclusively of bulls. At the end of every transect drive, the actual time, the total distance covered and the actual GPS coordinates were noted.

During the night transects two spotlights connected to a car battery were used. The two persons on the back of the car were sweeping the spotlights between the road in front of the car and 90 degrees out of the car on each side, back and forth. When an observation was made the same procedure as described above was used.

To be regarded as a separate observation there had to be 200 m or more between the groups or the individuals. If the observation regarded a group, both the distance and the direction were measured to the centre of the group. The recorded distance and direction to the elephant(s) were always taken to the spot where they were first observed. If they for example started to move during recording, the data still refer to their position where they were first observed. If there were difficulties in deciding any of the variables during the observation that variable was left out.

2.4 Distance analyses

The densities of elephants in the various habitats were analysed using the software Distance

4.1. Animal density \hat{D} is estimated in Distance by

$$\hat{D} = \frac{n}{2wL\hat{P}_a} \quad (1)$$

where n is the number of observed animals, w the distance from the line beyond which animals are not recorded (the truncation distance) and L the total length of the lines traversed by the observer.

To estimate P_a we can define the detection function $g(x)$ to be the probability that an object at distance x from the line is detected, $0 \leq x \leq w$ and assume that $g(0) = 1$, in other words that all objects on the line are detected (Thomas et al. 2002). The distance x is the perpendicular distance between the line and the object observed. $x = r \sin \theta$ where r is the distance to the animal from the observer and θ the recorded angle between the line and the animal from the observer. Further, we introduce the parameter μ as the effective strip width, which is defined as the distance from the line for which as many objects are detected beyond μ as are missed within μ .

If we define $\mu = \int_0^w \hat{g}(x)dx$, then $P_a = \frac{\mu}{w}$ and we get

$$\hat{D} = \frac{n}{2wL\hat{P}_a} = \frac{n}{2wL\frac{\hat{\mu}}{w}} = \frac{n}{2L\int_0^w \hat{g}(x)dx} \quad (2)$$

We can from this identify a probability density function (pdf) as the detection function $g(x)$ rescaled with the factor $1/\mu$ so that it integrates to unity. By fulfilling the requirements of being a probability density function the problem of finding the density is reduced to modeling the probability density function of the perpendicular distances (Thomas et al. 2002). While analyzing in Distance a parametric key function is selected and the program adds polynomial or cosine series adjustments to model $\hat{g}(x)$ until an adequate fit is provided.

Many of the observations in this study were clusters (groups) of individuals. Distance calculates the density of clusters and multiplies it with an estimate of mean cluster size in order to obtain the estimated density of individuals. Distance also provides confidence limits of the estimated parameters. 95% confidence intervals were used throughout this study.

The data collected during the day and the night were analysed separately in Distance since the methods varied between these periods. Further, to be able to compare the different habitats the data collected in each habitat were analysed separately. Data collected from all four habitats during both day and night were analysed by Distance except for the data collected on the floodplain during daytime (see below). The distribution of elephants in the baikaea woodland was analyzed by Distance as two separate data sets both day and night (north and south of the main road) due to differences in visibility and therefore detection probability between these two areas. A mean value of these two different baikaea woodland densities was then calculated where the different sizes of these areas were taken into consideration. Since the calculated density in the total baikaea woodland is constituted of two different densities with different confidence intervals, no overall confidence interval is obtained for this habitat. Further, due to low number of observations in shrubland and mixed woodland during night-time, the data collected here were brought together and the two different habitats were assumed as one homogenous habitat when the density was calculated by Distance. The common density is, however, presented as two separate but equal densities (Fig. 3, Table 2). The assumption made when bringing the data from the two different habitats together is discussed on page 28.

2.5 Other analyses

The data collected on the floodplain during daytime were not analysed by Distance. The Distance analyses stands on the assumption that the detection probability decreases when the distance from the transect increases. This is however not the case on the floodplain during the day since the visibility is perfect and all animals are detected. Elephants could be spotted as easily several hundred metres away as on the actual transect and the only limitation was the rangefinder used while recording the distance. Therefore this data set was analyzed separately as strip transects which is a form of quadrat sampling method (Thomas et al. 2002). The density of elephants was calculated by dividing the number of elephants recorded by the floodplain area covered. The covered floodplain area was calculated by multiplying the transect distance covered with the transect width (370 m). One transect drive was considered as one experimental unit giving the possibility to calculate variance and a confidence interval. The density for the overall study area was obtained by simply calculating a mean density of all habitats, where the habitats were weighted for their different areas.

The mean elephant densities from all habitats were related to already existing elephant browsing intensity data (Skarpe, unpublished). A proportion of time utilization was calculated for each habitat as the mean day-night-time density, weighted for the size of the habitat, related to the total time utilization. A proportion of the amount of browsing in each habitat was likewise calculated as the mean browsing intensity, weighted for the size of the habitat, related to the total amount of browsing. The two different proportions were then compared.

The data were further analysed in terms of variations in detection density of elephants within day- and night-time. Note that this is not the density of elephants, but a relative measure of the density of detected elephants while driving transects in the various habitats. All observations from each habitat were grouped in early or late day and night observations. The observations made on transects during daytime with starting time before noon were regarded as early day observations and the observations made on transects started after noon were regarded as late day observations. The observations made on transects started at night before midnight were regarded as early night observations and consequently the observations made on transects started after midnight were regarded as late night observations. The detection density of elephants was calculated by dividing the total number of elephants recorded by the total distance covered for each habitat.

The representation of different sex/group types in each habitat was analysed in terms of proportion of observations in relation to the total number of observations. The number of observations represented by each sex/group type category was simply divided by the total number of observations for each habitat.

3. Results

A total number of 3840 elephants were counted. 2449 of these were observed during the day and 1391 at night. The total number of observations was 418 divided up into 315 in the day and 103 at night.

3.1 Elephant densities in various habitats

The overall elephant density in the study area was 5.2 elephants/km² (Table 2). The highest density daytime, 21 individuals/km², was found on the floodplain. The densities then became consecutively lower in the habitats further away from the river with the lowest density, 6 individuals/km², found in the baikaea woodland. Also at night the floodplain with 35 individuals/km² showed the highest density of elephants. The lowest density, 2 individuals/km², was found in the baikaea woodland at night as well (Fig. 3, Table 2). The only statistically significant difference in density between day and night is detected in the shrubland.

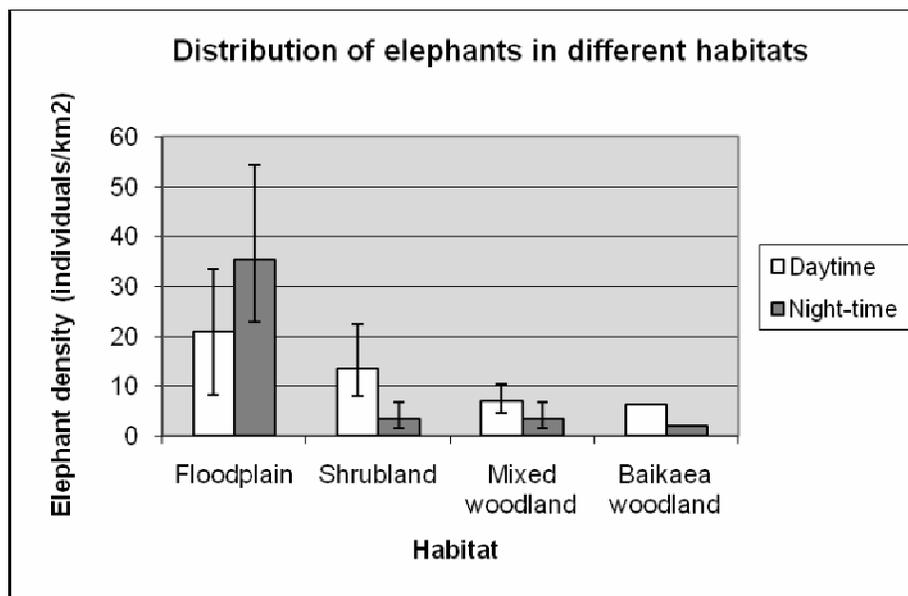


Fig. 3. Densities of elephants in all four habitats, day- and night-time. 95 % confidence intervals inserted when possible.

Table 2. Elephant densities in all habitats and statistical details from Distance analyses.

| Habitat | Day/ night | Distance analyses details | | | | | 95% conf. interval | | |
|------------------------------|---------------------|----------------------------|------------------------|--------------------|----------------------------------|------|--------------------|----------------|----------------|
| | | Detection function | Truncation distance | No of intervals | Density (No/km ²) | %CV | Df | Lower limit | Upper limit |
| Floodplain | Day | - | 370 m (5% of obs) | - | 20.9 | 150 | 23 | 8.3 | 33.4 |
| | Night | Half- normal/ Cosine | 250 m (12% of obs) | 5 | 35.2 | 21.9 | 56.9 | 22.8 | 54.3 |
| Shrubland | Day | Uniform/ Cosine | 250 m (9% of obs) | 5 | 13.5 | 23.9 | 11.8 | 8.1 | 22.5 |
| | Night | Uniform/ Cosine | No truncation | 6 | 3.3 | 35.6 | 19.9 | 1.6 | 6.8 |
| Mixed woodland | Day | Half- normal/ Cosine | 180 m (9% of obs) | 5 | 7.0 | 20.4 | 31.8 | 4.6 | 10.5 |
| | Night | Uniform/ Cosine | No truncation | 6 | 3.3 | 35.6 | 19.9 | 1.6 | 6.8 |
| Baikaea woodland north | Day | Uniform/ Cosine | 150 m (12% of obs) | 4 | 7.9 | 34.0 | 7.2 | 3.6 | 17.1 |
| | Night | Half- normal/ Cosine | No truncation | 4 | 1.4 | 38.2 | 26.5 | 0.6 | 2.9 |
| Baikaea woodland south | Day | Uniform/ Cosine | 400 m (9% of obs) | 5 | 1.9 | 22.9 | 5.5 | 1.1 | 3.4 |
| | Night | Uniform/ Polynomial | 100 m (5% of obs) | 6 | 3.5 | 24.2 | 29.7 | 2.2 | 5.8 |
| Baikaea woodland total | Day | - | - | - | 6.2 | - | - | - | - |
| | Night | - | - | - | 2.0 | - | - | - | - |
| Overall mean | Day and night | - | - | - | 5.2 | - | - | - | - |

3.2 Densities as time utilization and related to browsing data

Mean elephant densities, represented as proportion of time utilization in different habitats, compared to existing browsing intensity data (Skarpe, unpublished), show that the time utilization is comparatively higher than the amount of browsing on the floodplain and in the shrubland. The woodland habitats show an opposite pattern with comparatively higher amount of browsing than time utilization (Fig. 4).

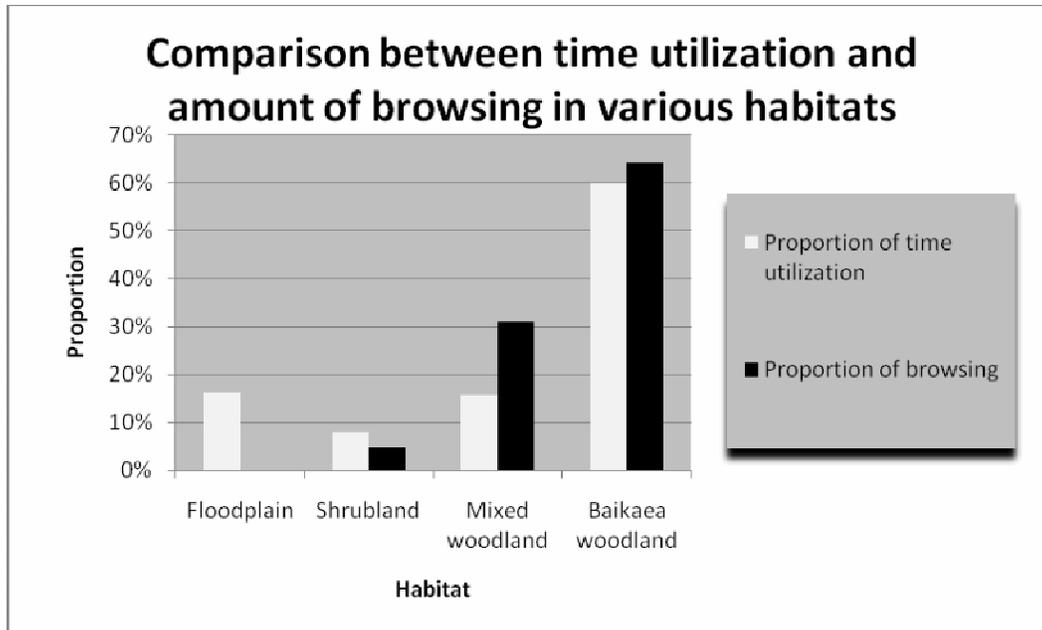


Fig. 4. Proportion of the time the elephants spend in various habitats compared to the proportion of the amount of browsing.

3.3 Detection density at different periods of the day-night cycle

In the floodplain and shrubland habitats the density of detected elephants was higher after noon than before, and on the floodplain all observations but one were made after noon (Fig. 5a, 5c). Early night had the highest detection density on the floodplain whereas differences were small in the shrubland (Fig. 5b, 5d). In the woodland habitats the differences were generally smaller even though it seemed to be a higher density of observations after noon in the mixed woodland than before noon (Fig. 5e) and a higher density before midnight in the baikaea woodland than after midnight (Fig. 5h).

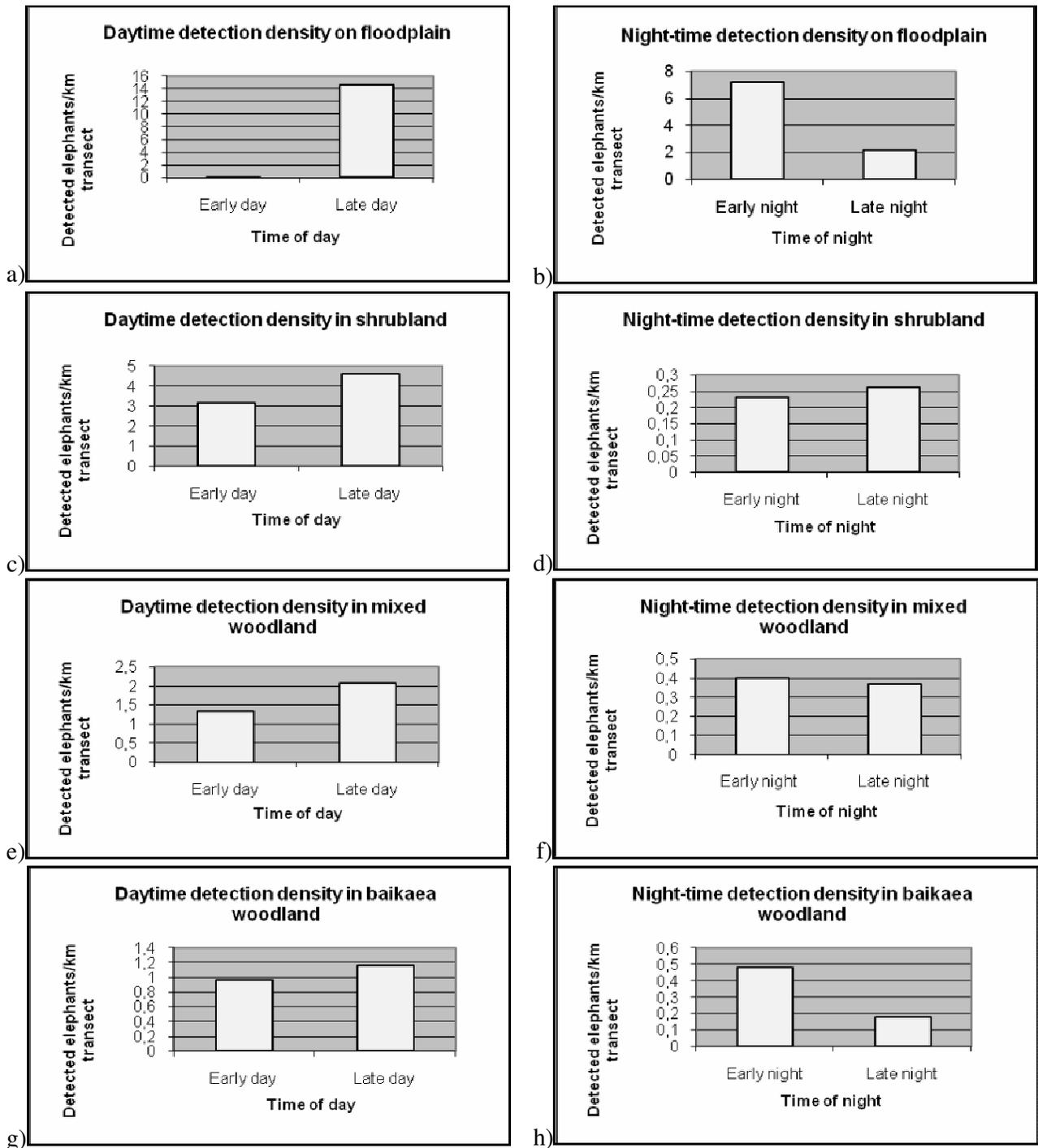


Fig. 5 a-h. Detection density at different periods of day and night in the various habitats.

3.4 Space-time pattern for different sex/group-types

The sex/group type dominating in all four habitats is family groups ranging from 63 to 66 % of the observations in each habitat. All other group types varied from 0 to 18 % of the observations in the four different habitats. Single females were the least observed sex/group-type with a maximum of 3 % of the observations in the mixed woodland. The proportions of observations that were impossible to classify into a specific sex/group-type varied from 9 to 20 % in the four habitats with the highest representation in the baikaea woodland (Fig. 6, Table 3).

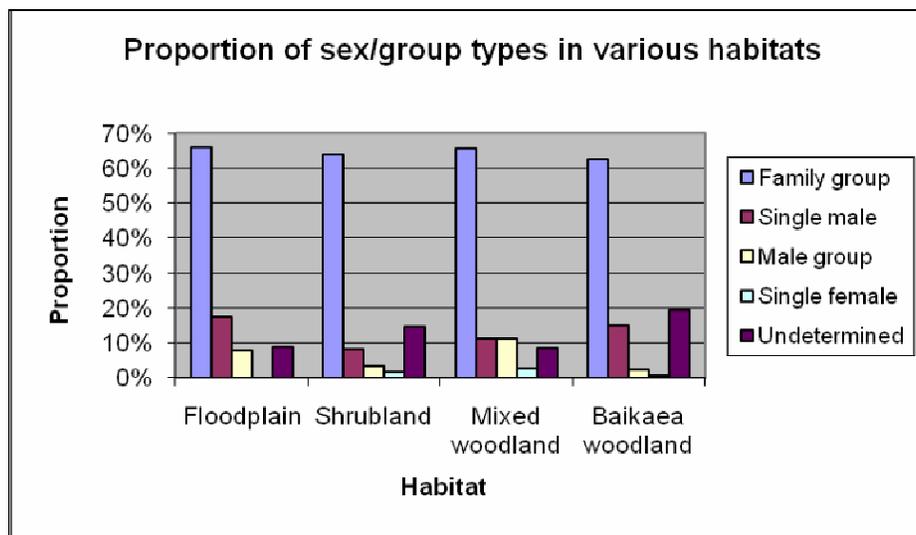


Fig. 6. Proportion of different sex/group types in the four different habitats.

Family groups account for a higher proportion of the observations at night than during the day in all habitats except for the baikaea woodland. Due to a low total number of night-time observations in the shrubland and mixed woodland, these proportions are not accurate. 15 % of the total number of daytime observations and 17 % of the total number of night-time observations were not possible to classify into any sex/group-type (Table 3).

Table 3. Representation of different sex/group types in various habitats day- and night-time

| Habitat | Sex/group type | No of observations | | Total |
|------------------|----------------|--------------------|------------|-------|
| | | Daytime | Night-time | |
| Floodplain | Family group | 36 | 24 | 60 |
| | Single male | 12 | 4 | 16 |
| | Male group | 7 | 0 | 7 |
| | Single female | 0 | 0 | 0 |
| | Undetermined | 3 | 5 | 8 |
| Shrubland | Family group | 69 | 9 | 78 |
| | Single male | 9 | 1 | 10 |
| | Male group | 4 | 0 | 4 |
| | Single female | 2 | 0 | 2 |
| | Undetermined | 17 | 1 | 18 |
| Mixed woodland | Family group | 19 | 4 | 23 |
| | Single male | 4 | 0 | 4 |
| | Male group | 3 | 1 | 4 |
| | Single female | 1 | 0 | 1 |
| Baikaea woodland | Undetermined | 3 | 0 | 3 |
| | Family group | 80 | 32 | 112 |
| | Single male | 18 | 9 | 27 |
| | Male group | 3 | 1 | 4 |
| | Single female | 1 | 0 | 1 |
| | Undetermined | 23 | 12 | 35 |

4. Discussion

4.1 Elephant densities in various habitats

In the whole study area there is a mean density of about 5 elephants per km² (Table 2). Gibson et al. (1998) found in their study that the mean density along the Chobe riverfront in the dry season is about 4 animals per km². The increase in elephant density of about 25% over the time between the two studies matches reasonably well with the estimated population growth rate of 5.3% per annum for Northern Botswana's elephant population (Vandewalle 2003); a growth rate that appears to have been reasonably stable over the past decades (ibid.). Looking at the density of elephants in the study area's four different habitats we clearly see that the habitats closest to the Chobe river and especially the floodplain habitat have the highest concentrations of individuals during the day-night cycle (Fig. 3, Table 2). The elephant density on the floodplain is higher than in all other habitats both during day and night, and the mean density in the shrubland is higher than in the two woodland habitats. Considering that the Chobe and Zambezi rivers are the main available surface water sources in the dry season in this area, these results might not be a surprise. The elephants are dependent on regular access to surface water and besides drinking they use muddy holes and river shores for wallowing and also immerse themselves into deeper bodies of water, for example the Chobe river (Hendrichs 1971 in Owen-Smith 1988, personal observations). However, the availability of food resources is much higher in the woodlands in the interior part of the park and considering the enormous amount of biomass the elephants are dependent on, they have to browse in these areas further away from water to secure their nutritional needs.

4.2 Time utilization and nutrient transportation

The recorded elephant densities in the various habitats within the study area can be understood as a pattern of the elephants' time utilization. A high density in one habitat automatically implies a high time use per area unit in the same habitat. Further, the time spent in one area gives an estimate of the amount of faeces and urine deposited there, since elephants like other large herbivores are believed to defecate and urinate more or less regularly throughout the night and day (Brodén, unpublished). However, Coe (1972) suggested there might be a minor peak in defecation rate in the early morning hours and a higher peak in the afternoon. High elephant densities, however, do not correspond to their food intake in a linear way. As seen, both the availability of food and the activity varies

between the different habitats within the elephants' home range. Accordingly the time the elephants spend in one area gives an estimate of the amount of faeces and urine deposited there but not an estimate of the amount of food consumed.

The high elephant density on the floodplain relative to the other habitats, and especially relative to the two woodland habitats, indicates that a relatively large amount of faeces and urine are deposited on the floodplain. However, the relatively large amount of time spent close to the river is not proportional to the food intake. It is known that the elephants forage mostly in the woodlands in the interior part of the park (Skarpe et al. 2004) with highest browsing intensity in the mixed woodland (Skarpe, unpublished). When relating the elephant densities to existing data on elephant browsing intensity, an asymmetric pattern is clearly identified (Fig. 4). The proportion of time the elephants spend on the floodplain (16%) is comparatively high (in fact there is no elephant browsing at all on the floodplain since there are no trees or shrubs there). Also the shrubland habitat has a higher proportion of time utilization than of browsing, even though the difference is smaller (8 compared to 5%). In the woodland habitats, however, we see an opposite pattern. Both woodland habitats have lower proportion of time utilization than of browsing; 16 compared to 31% in the mixed woodland and 60 compared to 64% in the baikaea woodland. This indicates that there is an import of plant biomass to the floodplain and shrubland and an export of biomass from the two woodland habitats. Even though not quantified in this study, the transportation of biomass from the woodland habitats to the habitats closest to the river indicates a transportation of nutrients in the same direction.

The elephants' food intake on the floodplain, constituted by grass, is not considered in this comparison. However, the availability of food – in terms of biomass per area unit – is much smaller on the floodplain and additionally, this habitat is used for many activities apart from feeding. Studies in other areas indicate that the elephants are more dependent on woody browse in the dry season when there is less available green grass (Guy 1976 in Owen-Smith 1988, Barnes 1982). This further strengthens the conclusion of a net transportation of nutrients from the woodlands in the interior part of the park to areas close to the river and mainly to the floodplain.

4.3 Space-time pattern during the day- night cycle

A total number of 605 elephants were observed while driving a distance of 41.2 km on transects with a starting time after noon in the floodplain habitat. This can be compared to one single elephant observed on the 34.4 km covered with a transect driving start time before noon in the same habitat. The results further show that the elephant density on the floodplain is higher at night than during the day as a whole, but lower than in the late hours of the day. More than three times as many elephants were observed during the first half of the night than during the second, in the floodplain habitat; 7.2 animals per km transect compared to 2.2 animals per km transect. This suggests that the elephants move their way back to the woodland habitats at night and mainly during the second half of the night. Since the Chobe and Zambezi rivers provide the main available drinking water for the Chobe riverfront population in the dry season and since the peak drinking time of African elephants occurs in the early evening (du Preez & Grobler 1977, Weir & Davison 1965 in Owen-Smith 1988) we would expect high concentrations of elephants in the floodplain habitat during the afternoon and the early night hours. My results confirm this general knowledge of the elephants' day-night cycle activities drawn from earlier studies.

One would perhaps expect that as a consequence of the high concentration of elephants on the floodplain in the afternoon we would see a decrease in number of elephants observed during the same period in one or more of the other habitats. However, we see no such decrease in the other habitats. The reason for this is most likely that the floodplain occupies a much smaller area than for example the baikaea woodland (3% compared to 76% of the total area). Relatively low increases in numbers of animals on the floodplain give rise to a relatively high increase in density. The corresponding decrease in numbers of animals in the large woodland habitats might, however, not be observable.

4.4 Space-time pattern for different sex/group types

My results indicate that there are no significant differences in representation of different sex/group types in the various habitats (Fig. 6). Stokke and du Toit (2002) found that male elephants move further away from the river than family groups tend to do. They found that family groups congregated within 3.4 km from the river in the dry season while bulls roamed to more than 10 km from the water (ibid.). My results indicate, however, that family groups

move much further from the river than just a few km and in the baikaea woodland family groups stood for more than 60% of all observations. The baikaea woodland starts at 1.6 to 6.8 km from the river depending on transect and stretches south to a distance of about 34 km from the river (Table 1, Fig. 2). Even in the southern part of the baikaea woodland (transects 11 & 12) which starts at about 10 km from the river the family groups stood for the majority of observations. This fact could have several explanations; since the time of Stokke and du Toit's study, permanent water has been artificially established in Nogadsaa, south of our study area, and perhaps some of the family groups observed far from the Chobe river use this new location as their main water source. The new pattern observed could also partly be caused by a depletion of food resources close to the Chobe river. Such depletion can be temporary and seasonal (the end of the dry season). It can also be a more long-ranging effect from the increasing elephant population who might be about to use up its food resources close to the Chobe river. This could force more elephants to forage at larger distances from the river in order to secure their nutritional needs.

4.5 Sampling design and statistical analyses

One assumption made when using line transect sampling is that the transects used should be randomly chosen and placed (Buckland et al. 1993). However, in order to make our study possible and safe, we used already existing tracks and roads as transects. Sometimes we noticed that elephants used these tracks or roads as their walking trails, at least on the tracks that were not used by tourists and not frequently used. On the floodplain and in the shrubland, where tourist roads were used as transects, there might be reason to expect the opposite; that some elephants avoided the roads in order to keep away from cars. Another factor influencing the detection probability could be disturbance of elephants on or close to the road while driving transects. The noise and light of the car could make them walk away from the road before they were spotted which would result in observations at generally larger perpendicular distances from the transect. This could perhaps be a factor while driving transects at night, where one had to come much closer to the elephants to be able to spot them. It is much too dangerous and slow to do a line transect sampling by foot. In order to avoid these methodological problems aerial surveys, if possible, might therefore be a useful alternative or complement, although also that method has problems.

Due to low number of observations, reliable results could not be obtained when trying to analyse the night-time data from the shrubland and the mixed woodland habitats separately in Distance (see page 16). I therefore brought these data together and regarded the new dataset as coming from one homogenous habitat. An assumption when analyzing in Distance is that the visibility and hence the detection probability within a habitat should be homogenous. Daytime, this is not the case between shrubland and mixed woodland since the mixed woodland is more densely vegetated. Night-time however, the difference in visibility between the two habitats are believed to be small or insignificant, since it was impossible to spot elephants through the shrubs or at large distances in the shrubland habitat.

The number of observations in the various habitats was too low to be able to compare the density of elephants within day- and night-time between different habitats, something that would be interesting to investigate in further studies. Instead of elephant densities within day- and night-time a relative measure – number of elephants per km transect – was used. This measure can not be compared between the different habitats because of differences in visibility. However, it provides an indication of variation in densities between early and late day and night in each habitat.

4.6 The elephant debate in Southern Africa and in Chobe

The ecological effects of high densities of elephants are a main concern for conservation managers in Southern Africa. The African elephant has become locally extinct across much of its former range and it is categorized as Near Threatened by IUCN, mainly because populations in Central, East and West Africa are in decline (IUCN 2008). However, several locations in Southern Africa show another pattern and in some protected areas populations grow rapidly (van Aarde & Jackson, 2007). Authorities responsible for management decisions are concerned about the possible negative effects of the elephants on the biodiversity, and solutions such as culling, translocation or birth control in order to limit the impact of the elephants are discussed in several areas (Owen-Smith et al. 2006). The effects from the elephants on biodiversity are still heavily debated in several locations in Southern Africa. Some argue high densities of elephants reduce the diversity of habitats and hence the diversity of species (Cumming et al. 1997, Herremans 1995). There are examples of local species loss such as of lesser kudu and bushbuck or of different plant species (Skarpe et al. 2004) as a probable indirect effect of high densities of elephants. It is especially the examples of how

high densities of elephants through feeding and trampling turn former woodland into shrubland or grassland vegetation, that have highlighted the concern from conservation managers and authorities throughout Southern Africa.

However, some of the harmful effects on biodiversity ascribed to the elephants have poor scientific support and there may be reason to believe some of the concerns of adverse ecological effects are exaggerated (Owen-Smith et al. 2006). Further, an observed pattern of elephant impact on a given ecosystem can not easily be generalized and valid for other locations (ibid.). The consequences of the elephants' feeding depend on a large number of factors such as elephant densities, the plant species selected and also interactive effects of other factors such as fire, rainfall and soil properties (Owen-Smith 1988). In order to understand the dynamics of any ecosystem we must take each area's ecological and historical uniqueness into account.

In the Chobe riverfront area, the changes in vegetation structure and composition seen during the last 50 years are assumed to be caused mainly by the large and still increasing elephant population (Simpson 1974, Addy 1993, Simpson 1975, KCS 1990, Chafota & Owen-Smith 1996, Ben-Shahar 1996). Results from the BONIC project showed that there is not much scientific support for adverse ecological effects - in terms of loss in biodiversity - due to the elephants. As mentioned before, they found that areas close to the Chobe river, where the elephant impact was highest, also had the highest biodiversity (Motsumi 2002, Skarpe et al. 2004). The availability of the surface water from the river is one obvious explanation to the high biodiversity seen there, but for highly mobile species like birds or larger mammals this explanation alone is not satisfactory. It is known that elephants, especially when densities are high, can play a key role in determining the distribution and cycle rate of nutrients (Augustine & McNaughton 1998). The nutrients released in faeces and urine, are immediately available for quick uptake by plants, and an increase of available nutrients implies a rise in primary production (Ruess & McNaughton 1984) and in extent also potentially higher biodiversity. The results from my study indicate that transportation of nutrients created by the elephants' asymmetric space-time pattern should be added as one potentially important contributing factor to the high biodiversity seen at the Chobe riverfront.

4.7 Conclusions

The Chobe riverfront elephant population shows a clear asymmetric space-time pattern in the dry season, where the areas close to the Chobe river are favoured in terms of time utilization during the day-night cycle. The great deal of time spent close to the river implies that the elephants deposit a proportionally high amount of faeces and urine there. Since the elephants forage mostly in the woodlands in the interior part of the park, they mediate a net transport of nutrients from the woodlands to the areas close to the river, mainly to the floodplain. The consequences and importance of this nutrient transportation are not easily predicted. It should, however, be regarded as one potential factor to the rise in primary production close to the Chobe river, and in turn, a contributing factor to the higher biodiversity seen in these areas. Further, I found no difference in habitat use between different sex/group types. Unlike results from previous studies family groups were represented as much in the baikaea woodland furthest away from the Chobe river as in the habitats closest to the river.

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