Elephants in the Waterberg: impacts on woody vegetation by breeding groups compared with bachelors

by

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ABSTRACT

In May 1994 IFAW funded the relocation of 50 elephants from the Kruger National Park to Welgevonden Private Game Reserve in the Northern Province, South Africa. Impact by the elephants on the vegetation of this reserve has since become a concern. The aim of this study was to quantify impact by the elephants on the woody vegetation by investigating vegetation and habitat use by elephant bachelor and breeding groups. This was determined by comparing resource use between sexes within seasons, and within sexes between seasons. Data were collected at two ecological scales: feeding patch scale and habitat scale. Feeding data were collected from 202 food plots, defined from 161 elephant sightings. In the dry season, when resources are often limited, no difference in feeding patch use was found between bachelor groups and breeding groups. This may suggest a lack of inter-sexual competition and could therefore suggest that the elephant population is currently below carrying capacity. Three habitat types are available to the elephants: plateau, hillslope and valley bottom. Both bachelor groups and breeding groups preferred valley bottom in comparison with habitat availability, in both seasons. When sexes were compared within seasons, in the dry season, bachelor groups used valley bottom more and breeding groups used hillslope more.

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CHAPTER 1

INTRODUCTION

African elephant (*Loxodonta africana*, Blumenbach 1797) impact on woody vegetation in reserves across Africa has received much attention in the literature over the past 50 years (Buss 1961; Agnew 1968; Laws 1970; Caughley 1976; Jachmann & Bell 1985; Mwalyosi 1987; Viljoen & Bothma 1990; Tchamba & Mahamat 1992; Ben-Shahar 1993; Whyte *et al.* 1998; Lombard *et al.* 2001). Research concerning elephant impact on vegetation has become more concentrated in recent years as human population growth has lead to a decrease in space available for conservation areas. This is important where elephants are concerned since limiting these megaherbivores (Owen-Smith 1988) to confined areas results in increased impact to the vegetation as their populations expand. The Kruger National Park (KNP) is one of the many reserves to experience this and the problem there was compounded by the suspension of elephant culling in 1995 (van Aarde *et al.* 1999). In an attempt to alleviate this problem, in 1994 KNP captured 148 elephants comprising a number of complete herds, and relocated them to various small game reserves in South Africa (du Toit unpubl.). The results of this were that as those populations numbers grew, the land owners began to notice the impacts the elephants were having on the vegetation in those reserves. One such reserve was Welgevonden Private Game Reserve (WPGR) in the Waterberg, Northern Province of South Africa, to which 50 elephants were introduced during May 1994.

On WPGR, the visible effects of elephant on the woody plants were evident and a cause of concern to management, landowners and tourists. Damage to woody vegetation is often simply attributed to elephant impact, but other possible causes should not be overlooked. Both wind and lightning are known to have a profound effect on, especially, the felling of trees (Spinage & Guinness 1971). Fire, combined with impact by elephants, also has a detrimental effect on savanna vegetation (Buss 1961; Dublin *et al.* 1990; Ben-Shahar 1996; Eckhardt *et al.* 2000). It is therefore important for landowners and managers of reserves to clarify the reasons for having elephants on a property and accept that a certain level of vegetation structure modification is going to occur. Ultimately, landowners and wildlife managers who are concerned about changes to the vegetation, have to set levels of acceptable change, and manage the elephant population numbers accordingly. Concerns regarding changes to the vegetation were the motivation for this research.

One approach to testing hypotheses regarding elephant impact on woody vegetation is to investigate sex differences in resource utilisation. If males and females are found to utilise the woody vegetation differently in relation to each other, one management option may be to adjust the sex ratio to reduce impact on the vegetation. Many studies have been done to investigate possible reasons why some ungulate species segregate into single sex groups outside of the breeding season. This phenomenon is known as sexual segregation (Main *et al.* 1996) and is most likely influenced by social, spatial and temporal factors such as the periodicity of mating opportunities, population densities, resource distribution and environmental conditions. Elephant family structure exists as a matriarchal society and the population forms bachelor and breeding groups (Douglas-Hamilton 1972; Poole 1996). Elephants, however, do not exhibit clear seasonal mating periods (Estes 1993), as has been recorded in other ungulate species. Sexual segregation has been well documented in many species of sexually dimorphic ungulates (see Main *et al.* 1996; Gross 1998; Mysterud 2000 and Ruckstuhl & Neuhaus 2000 for reviews). Sexual segregation has, however, only been investigated on a limited basis in one population of elephants in Botswana by Stokke (1999), Stokke and du Toit (2000; in press). They propose that investigations into sex related differences concerning forage and habitat use by elephants are relevant to evaluating the impacts of elephant populations on savanna vegetation.

Underlying mechanisms of segregation by sex are still poorly understood (Kie & Bowyer 1999; Ruckstuhl & Neuhaus 2000). From the literature it is possible to define two main explanations of sexual segregation, as defined from studies on various species of sexually dimorphic ungulates. Firstly, that which arises from the direct use of vegetation and secondly, that which arises as a result of other factors such as predator avoidance or social preference. Habitat segregation (Conradt *et al.*1999) may be a combination of these factors.

Ruckstuhl and Neuhaus (2000) provide a clear overview of the current hypotheses regarding sexual segregation. Three of the hypotheses defined in the literature may be considered as possible explanations for sexual segregation in elephants. Firstly, the forage selection hypothesis (Ruckstuhl & Neuhaus 2000), also termed the sexual dimorphism-body size hypothesis (Main *et al.* 1996) and the body size hypothesis (Stokke & du Toit 2000) is directly based on forage use by herbivores. It predicts that the sexes segregate because sex differences in body size lead to different energy requirements and therefore food selection, and hence their choice of habitat. The second hypothesis is the scramble competition hypothesis, which applies when resources are limited or plant height is greatly reduced, resulting in competitive interactions between sexes (Ruckstuhl & Neuhaus 2000). This hypothesis does not apply to browsers in the same way it would to grazers, because in large, sexually dimorphic browsers, the competitive displacement would be vertical as opposed to horizontal (du Toit 1995). The taller body height of the bull elephants in bachelor groups therefore ensures that they would be able to utilise the upper strata of vegetation, while the breeding groups exploited the lower strata, when feeding in the same immediate patch, consequently, sexual segregation would not necessarily be spatial along the horizontal component. Main and Coblentz (1990) examine a third hypothesis to explain sexual segregation whereby males select habitats on the basis of optimal foraging opportunities, while females choose habitats based on their suitability for raising young. This hypothesis is based on energetics and the relative differences in the reproductive strategies of males and females of polygynous ungulates. Main *et al.* (1996) referred to this hypothesis as the reproductive-strategy hypothesis. This hypothesis includes the principle of predator avoidance, and therefore Ruckstuhl and Neuhaus (2000) later referred to it as the predation risk hypothesis.

This research project was not designed to test any of the above hypotheses, but rather to determine whether the elephants on WPGR display any sexual segregation in terms of their use of habitat or feeding patch. The data collected for this research have been analysed and assessed at two ecological scales. The first was the habitat scale, and the second was the narrower scale of feeding patch choice. Since large herbivores interact with forage resources at several levels of ecological resolution (Senft *et al.* 1987), it is often necessary to work at different scales when researching ecological concepts, since one scale is often too broad or too narrow in relation to the specific subject. When research focuses on a megaherbivore such as the African elephant, knowledge regarding habitat and vegetation utilisation by these large animals is of crucial importance in population control and habitat management (Afolayan & Ajayi 1980). This is because, as large-bodied animals, they have high dietary requirements, and therefore elephants have the potential to have a high impact on their environment. This can have both direct and indirect consequences for the population itself, as well as other species.

1.1 Objectives

In this study I focus on the elephant's use of the vegetation, their impact thereon, and the possible differences exhibited by bachelor and breeding groups within this framework. Elephant impact on woody plant species was the focal point of this project, as opposed to the grass or herb layer mainly because, on WPGR, both reserve managers and landowners are concerned about elephant impact on the woody component, due to the visible effect it has on the aesthetic value of vegetation to tourists. Woody plants in this study were defined as perennial plants whose stems do not die back at the end of the growing season (Van Wyk & Malan 1998). Elephant activity in conjunction with woody vegetation is referred to in this thesis as "impact" rather than "damage" owing to the concern over the use of this term due to its implication of excessive vegetation destruction (Anderson & Walker 1974). The term impact, as used in this study, is intended to include all types of vegetation utilisation by elephants, whether excessive or not. Aspects such as population numbers, sex and age ratios, and individual identification of the elephants were investigated on a secondary basis to the main study.

1.2 Key questions

This study was designed around five key questions, combinations of which form the basis of each chapter in this thesis:

1 Do preferences for woody plants differ between elephant group types (breeding groups and bachelor groups) in each season?

2 Do bachelor and breeding groups differ with respect to the woody plant species they fell, barkstrip or uproot?

3 Do bachelor groups have a greater impact on the woody vegetation than breeding groups?

4 What are the main habitat types available to the elephants on WPGR?

5 What habitat types are preferred, and do habitat preferences differ between group types, in each season?

1.3 Approach

The major objectives for this study were to investigate sex differences in elephant resource utilisation at two ecological scales. Firstly, that of the local feeding patch scale (chapter three) which addresses key questions one, two and three. The two hypotheses tested in this chapter were defined from the research done by Stokke (1999) and Stokke and du Toit (2000; in press) in Chobe, Botswana concerning sexual segregation in elephants:

1. An elephant population can be divided into two functional groups with regard to their relative impact on the woody vegetation:
    a Bachelor groups
    b Breeding groups
2. Elephant bachelor groups have a greater impact on the woody vegetation than do breeding groups.

Secondly, chapter four addresses key questions four and five at the habitat scale. Chapter five presents a final discussion and brief implications of the results from data chapters three and four to reserve management.

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CHAPTER 2

STUDY AREA

2.1 Reserve location and history

This study was conducted on Welgevonden Private Game Reserve (WPGR), situated in the Waterberg region of the Northern Province, South Africa. The reserve is located at 24° 10' 03" - 24° 25' 03" S and 27° 45' 07" - 27° 56' 01" E, and shares 13.8 km of its western boundary fence with Marakele National Park. WPGR, proclaimed early in 1993, is a group of 15 old farms (both cattle and crop farms) and has a total surface area of 334.3 km^2. Included in this surface area are two new farms which were incorporated into the main reserve between August and October 1998. This new portion of land extends from the vegetation type of the main reserve (Waterberg Moist Mountain Bushveld (Low & Rebelo 1996)) into a new vegetation type (Mixed Bushveld (Low & Rebelo 1996)). WPGR has 38 (of the proposed 62) lodges, which are fully operational.

2.2 Climate

This region has distinct wet and dry seasons from October to March and April to September respectively. The summers are hot and wet, and the winters are cold and dry. The mean annual rainfall was recorded as 670 mm by Elandshoek Weather Station. The mean annual rainfall as recorded by Vaalwater Weather Station was 613 mm. Climatic data from the Vaalwater Weather Station (Station number: 0632/077LO; Latitude 24° 17' S; Longitude 28° 03' E; Altitude: 1215m above sea level) was obtained from the weather bureau. This weather station lies approximately 10 km east of WPGR. The average maximum temperature is 26.5°C and the average minimum temperature is 11°C. The mean temperature is 18.8°C. An average of 91.7% of years (from 1979 to 1998) experienced a moderate frost, with mean frost season length being 51 days.

2.3 Geology and soils

The Waterberg Group consists chiefly of a succession of course clastic sedimentary rock, which shows two upward-fining sequences (Callaghan 1987). The Waterberg strata form rugged topography, and some striking krantzes. Topography is less well developed, however, in a lower portion of the sequence in which there are more shales and also more felspathic sandstones (Truswell 1970). This semi-mountainous terrain is derived from Waterberg sandstone and is therefore predominantly sandy (mean sand content 97.2%; SEM=0.039), with a very small percentage of clay (mean clay content 2.45%; SEM=0.029) (Frost & Peres unpubl.). The soil composition of the Waterberg plateau and its foothills, is mostly yellow and grey fersiallitic sands and loams derived from weathered sandstones and conglomerates (Harmse 1978).

2.4 Vegetation

Acocks (1988) classifies the Waterberg region into two main vegetation types; Sourish Mixed Bushveld on the gentle slopes to the mountains, and Sour Bushveld which forms the open savanna and occupies the largest part of the bushveld mountains of the Waterberg. According to Acocks (1988) the following are examples of the species which can be found in the Sourish Mixed Bushveld: *Acacia caffra, Grewia spp., Pappea capensis, Dichrostachys cinerea, Dombeya rotundifolia, Combretum zeyheri, Ziziphus mucronata* and *Burkea africana.* In the less rocky parts of the region, the Sour Bushveld is characterised by species such as: *Faurea saligna, Englerophytum magalismontanum, Lannea discolor, Vangueria infausta, Gardenia volkensii* and *Pachystigma triflorum* to name a few.

Low and Rebelo (1996) offer a more recent perspective on the vegetation types of the Waterberg. According to their vegetation map, the reserve spans two vegetation types namely: Waterberg Moist Mountain Bushveld and Mixed Bushveld. Both these vegetation types are categorised under the Savanna Biome, which is the largest biome in southern Africa and occupies one-third of the area of South Africa itself (Low & Rebelo 1996). Many of the woody plant species which comprise these two vegetation types are the same as those given by Acocks (1988) with a few more examples provided by Low and Rebelo (1996): Waterberg Moist Mountain Bushveld (also known as Sour Bushveld (Acocks 1988)), includes *Terminalia sericea, Protea caffra, Diplorhynchus condylocarpon, Pseudolachnostylis maprouneifolia, Grewia flavescens, Ochna pulchra* and more. In Mixed Bushveld (Acocks (1988) referred to this as Mixed Bushveld and Sourish Mixed Bushveld), the following species are commonly found: *Combretum apiculatum* (where the soils are shallow), *Grewia flava and Peltophorum africanum* as well as all the other species mentioned by Acocks (1988) for this vegetation type, many occurring on deeper and more sandy soils.

2.4.1 Habitats types on WPGR

An official vegetation map is not yet available since the vegetation survey is still in progress. An habitat map was compiled using aerial photographs and a GIS program (Arcview). For the purpose of this project three main habitat types were used during the collection of data namely: plateau, hillslope and valley bottom (Fig. 2.1). These habitat types were defined on the basis of physical landscape features, as well as prominent vegetation structure and distinguishing woody species present.

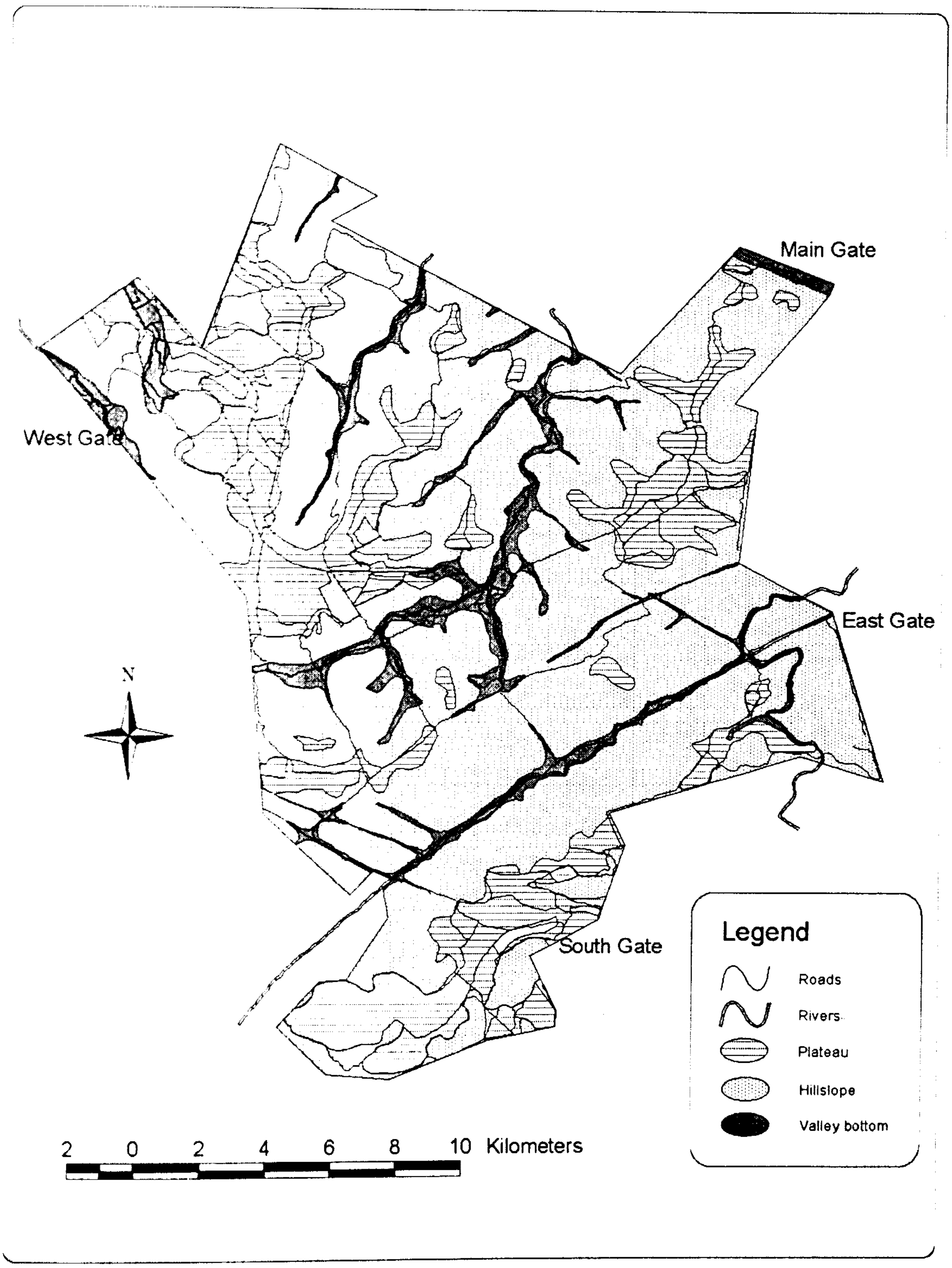

Fig. 2.1. Map of Welgevonden Private Game Reserve showing habitat types, roads & rivers.

2.5 Elephant relocation details

During May 1994, 50 elephants were reintroduced to WPGR from the Kruger National Park. The sex ratio composition of this population was 21 males (two adults, eight subadults, ten juveniles and one calf) and 29 females (seventeen adults, six subadults and six juveniles).

Between 1994 and 1999, eight elephants died and three calves were bom during the first few months of introduction (duToit unpubl.). A game census was conducted on Welgevonden during August 1999. The total elephant count was 64. Since then, one young bull died when it slipped into an erosion gully, one calf (± six months old) was found dead and at least one birth has been reported. Assuming a birth rate of four calves per year, a maximum of 72 elephants can be present on WPGR. This birth rate was calculated based on the number of elephants introduced in 1994 and the number of elephants counted at the time of the September 2001 game count (70 elephants).

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CHAPTER 3

SEXUAL SEGREGATION AT THE FEEDING PATCH SCALE: IMPACT ON WOODY VEGETATION BY ELEPHANTS (*LOXODONTA AFRICANA*) REINTRODUCED TO WATERBERG WOODLAND

Abstract

Differences in the use of woody vegetation by bachelor and breeding group types were examined on Welgevonden Private Game Reserve. Data were collected from 203 food plots, and 173 control plots. A total of 92 woody species were recorded as being available in food plots to the elephants on this reserve. Bachelor groups used 38 woody species (36% of those available) and breeding groups used 36 (34% of those available), with 29 woody species appearing in both the diets of bachelor groups and breeding groups. Species diversity of woody plants utilised in food plots, available in food plots and present in control plots did not differ between bachelor groups and breeding groups within seasons. Elephant bachelor groups selected feeding sites with higher species richness and woody plant density than did breeding groups, in the dry season. A consistently higher species diversity, species richness and species density at food plots, when compared with control plots, indicated that bachelor groups and breeding groups are selective in their choice of feeding paths. Bachelor groups and breeding groups generally did not differ with respect to the types and degree of impact they exerted on the woody vegetation. This research therefore suggests that, in the Waterberg, elephant bachelor groups and breeding groups may not represent separate functional groups (bachelor and breeding groups) on the basis of their feeding behaviour.

3.1 Introduction

In 1995 when the Kruger National Park (KNP) suspended culling operations (van Aarde *et al.* 1999), a number of herds of elephant (*Loxodonta africana*, Blumenbach 1797) were relocated to various private game reserves throughout South Africa (du Toit undated.). One such group of 50 animals was relocated to Welgevonden Private Game Reserve (WPGR) in the Waterberg region of the Northern Province. Elephants, being megaherbivores (Owen-Smith 1988), are bound to have some impact on the vegetation, and as elephant numbers increase in confined conservation areas, it is possible that evidence of their feeding activities may also increase. It is well known that the African elephant has a noticeable impact on the vegetation in its environment (Buss 1961; Laws 1970; Caughley 1976; Eckhardt *et al.* 2000), but despite their visible impact on habitats, they may also have beneficial effects such as seed dispersal and opening up of closed woodland (Viljoen 1991).

Elephants are sexually dimorphic in size and the males tend to segregate into groups generally referred to as bachelor groups. The term breeding group refers to the group comprising of related females, their offspring (including males younger than twelve years) and migrant adult male visitors (Douglas-Hamilton 1972). The reasons for this segregation in elephant are not entirely understood, yet it presents a convenient framework for the observation and comparison of feeding strategies between the two group types. Although the concept of sexual segregation has been researched in a wide range of sexually dimorphic ungulates (see chapter 1 for a brief review), research concerning this subject in elephants is limited to one elephant population (Stokke 1999; Stokke & du Toit 2000; In Press). It is thought, however, that the investigation of whether the two group types have different impacts on the vegetation or not, may be fundamental to their management. Knowledge of the ways in which bachelor groups and breeding groups use their habitats and the vegetation in comparison with each other, and importantly, whether that use differs between the group types, can be used to understand elephant interactions with their environment. If there are no differences in the utilisation of resources between sexes, it could suggest that they select for similar features of their environment, and that there is unlikely to be competition between the sexes for resources. This is what we would expect at low population densities. However, if differences exist in habitat or vegetation utilisation between group types, it may suggest that such competition exists between the sexes for access to resources. Which of these scenarios applies for the Waterberg forms the basis of this study. Hence, the aim of this chapter was to determine resource use by the two elephant group types in terms of use of woody vegetation in the Waterberg, with reference to WPGR specifically.

Two important hypotheses were defined from the research done on sexual segregation in elephants (Stokke 1999; Stokke & du Toit 2000; In Press). These were tested for the elephant population in the Waterberg:

1 An elephant population can be divided into two functional groups with regard to their relative impact on the woody vegetation:
   a Bachelor groups and
   b Breeding groups
2 Elephant bachelor groups have a greater impact on the woody vegetation than do breeding groups.

Key questions to be addressed in the Waterberg, therefore include the following :

1 Do feeding preferences for woody plant species differ between elephant bachelor groups and breeding groups in each season?
2 Do bachelor groups and breeding groups differ with respect to woody species they fell, barkstrip or uproot, in each season?
3 Do bachelor groups have a greater impact on the woody vegetation than breeding groups?

3.2 Study Area

See chapter 2 for details.

3.3 Methods

3.3.1 Data collection

Data were collected from July 1999 to November 2000, thereby incorporating one dry season and one wet season into the data set. During this time, research focused on the woody vegetation within the boundaries of WPGR (Appendix 3.1). Van Wyk and Malan (1998) define woody plants as perennial plants whose stems do not die back at the end of the growing season. They define a herb plant as one which does not develop persistent woody tissue above ground and either dies at the end of the growing season or overwinters by means of underground organs (e.g. rhizomes, bulbs, corms). Only woody plant species (trees and shrubs) were assessed because even though it is well known that grass forms the largest percentage composition of an elephant's diet during the wet season (Buss 1961; Owen-Smith 1988), browse forms the largest part of the diet in the dry season (Anderson and Walker 1974). This is because graze components decrease in nutritional value (and palatability) during this time, as the plants draw the nutrients out of the above-ground parts, downwards into underground storage organs. Due to the fact that elephants concentrate their feeding activities more on woody plant species during the dry season, their effects on the woody vegetation are much greater and longer lasting than on grassland and herbs because woody species have longer growth cycles and therefore a longer replacement time (Laws 1970). Therefore, the impact of elephants on the woody vegetation component is most relevant to the question of how elephants influence plant community dynamics.

Elephant locations were based largely on radio reports from lodge guides, which were then followed up independently. There were usually more than two game drive vehicles operating in WPGR during the morning or evening. These game drives always originated from different lodges (only one vehicle per lodge) and the lodges are evenly distributed throughout the entire reserve. The focus of these game drives was to locate any members of the "big five", as well as a number of other species, therefore they did not concentrate on finding the elephants, but were more likely to encounter them randomly. Therefore, although a certain bias may exist, it was assumed that this bias was minimal and that the method provided equal chances that any elephant(s) would be sighted in any one habitat. Once an elephant or herd was encountered, the characteristics of the sighting were recorded in terms of:

1) Location [descriptive and GPS (Global Positioning System)] was recorded; sightings were recorded in one of six habitat types: riverine, valley bottom, hillslope, terrace, plateau and old lands.
2) Group type (i.e. whether the sighted herd was a bachelor or a breeding group).
   Group types were categorised as either bachelor groups or breeding groups based on the classification by Stokke and du Toit (2000), where only pure male associations were recorded as bachelor groups. Herds were recorded as breeding groups if only a family unit was present or if a family unit had bachelor groups associated with it.
3) Specific attention was paid to the vegetation which was being utilised by the group type, so that food plots could be defined later in which feeding data would be collected.

When a group or individual (in the case of bulls) of elephants were sighted, the plant which the first sighted elephant was utilising was recorded. Feeding activities of the elephant(s) were observed until they willingly vacated the area and any other plants which were utilised by the elephant(s) as they moved along the chosen forage path were also noted. No behavioural data were collected during these observation periods. If the elephants displayed any signs of aggression or distress, they were left alone and only later were food plots defined around the first recorded utilised woody plant. Once the elephant(s) had moved away, feeding data were collected from within sample plots defined by Stokke and du Toit (2000) as food plots; the area within a circle with a radius of 5m, which had a recently browsed woody plant at its centre (Food Plot$_1$; Fig. 3.1). All subsequent food plots identified along a forage path (Food Plot$_2$; Fig. 3.1) were placed no less than 50 m apart.

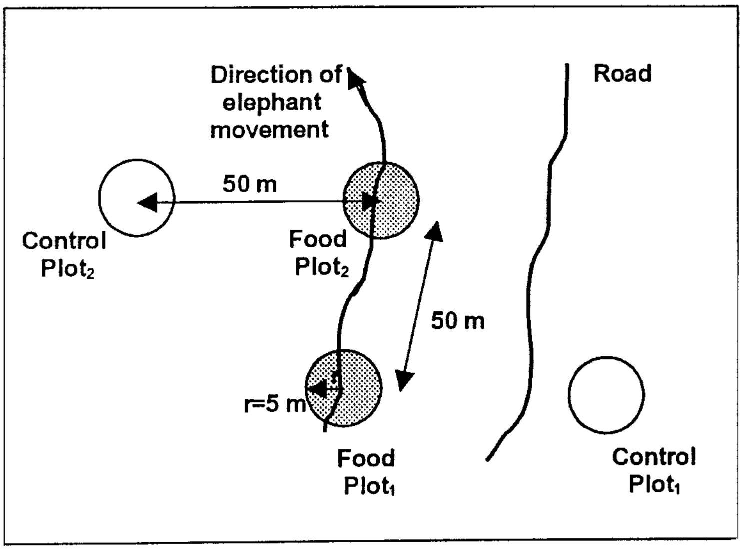


Fig. 3.1. Representation of the method used to locate plots. Not to scale. Modified from Stokke (1999).

Food plots were delineated (where possible) as soon as possible after the utilisation took place to ensure that new damage was identifiable from wet sap in breaks (Stokke & du Toit 2000). Details of all woody vegetation (trees and shrubs) within these food plots were recorded and assessed in terms of:

a) the species name;
b) the height of each plant;
c) a code system to indicate the type of impact sustained by each woody plant where: 0 = no impact ; 1 = felled (stem broken) ; 2 = felled (uprooted) ; 3 = barkstripped ; and 4 = branches broken;
d) the diameter of the largest branch broken, measured on the plant side, to the nearest millimetre using vernier callipers (Stokke & du Toit 2000); the height of this break above the ground was measured to the nearest 20 cm using a 4 m collapsible pole;
e) the stem diameter of felled trees (both stem broken and uprooted) was measured at the bottom of the stem immediately above the ground, using vernier callipers or a 30 cm ruler if the diameter was more than 10 cm;
f) following Anderson and Walker (1974) a damage score for each impacted woody plant using eight classes of percentage damage as follows: 1 (0%); 2 (1-10%); 3 (10-25%); 4 (25-50%); 5 (50-75%); 6 (75-90%); 7 (90-99%) and 8 (100%); if more than one type of impact was inflicted on an individual plant, the plant was given an overall score of damage;
g) the number of other breaks (besides the measured one) sustained to a plant during utilisation by the elephant(s).

No attempt was made to differentiate between impacted vegetation and consumed vegetation, all plants clearly utilised by elephants were simply assessed in terms of damage sustained to the plant by either group type (bachelor or breeding groups). Note the definition of "damage" from Anderson and Walker (1974).

As with Viljoen (1989), no attempt was made to quantify old utilisation – this is too subjective since some plant species coppice or recover and some do not, and collection and interpretation of this type of data would require a longer time frame than was allocated to this study. Only new elephant damage was recorded so as to be sure that it was caused by an identified elephant group and not another factor such as lighting or fire. Therefore, all of the other possible causes of damage, including old elephant damage, were ignored (impact code 0) because it was impossible to determine the cause (in some cases) or the elephant social grouping responsible (in all cases).

Some food plots were recorded under an "inferred elephant group type" when no elephant groups were actually sighted, but feeding activity was fresh and obvious. These inferred "food plots" were included in order to increase the sample size. "Inferred" food plots were only used if the elephant group type could be inferred from evidence such as foot print size and number and/or dung bolus size [calves and juveniles in breeding groups would have small dung boli whereas bachelor groups would have very large dung boli (Jachmann & Bell 1984)]. The centre (utilised) plant in each food plot was identified in these "inferred group type food plots" by identifying the forage path, and then walking along that path and noting the first freshly utilised plant encountered as the centre plant of the first food plot. Sometimes a very distinct forage path could be identified. In such cases, the centre plant for each successive food plot was identified as explained above. The minimum distance between all food plots (inferred or otherwise) was kept to 50 m to exclude any possibilities of pseudoreplication. A total of 203 food plots (Fig. 3.2) were recorded over the two seasons (one full wet season from October to March; and one full dry season from April to September). Of these, 82 food plots were defined for bachelor groups (16 inferred plots and 66 from sightings) and 121 for breeding groups (92 inferred plots and 29 from sightings).

Data were collected from 173 control plots (almost one control plot for every food plot). The data for control plots was recorded as in Stokke and du Toit (2000): a circle with a 5 m radius was placed 50m (centre to centre) away from the food plot, and perpendicular to the path of movement of the elephants being observed (Control $Plot_1$; Fig. 3.1). Data collected from control plots were the same as for food plots except that no plant utilisation data were recorded, i.e. only the species names and heights of all the woody plants were recorded. The direction in which the control plots were placed, either to the left or to the right of the corresponding food plot, along the elephant's path of movement, was randomised by flipping a coin on each occasion. Where consecutive food plots were paired with control plots, they were defined as in Fig. 3.1 (Food $Plot_2$ and Control $Plot_2$).

3.3.2 Data analysis

Although a total of 203 food plots were defined, data from 202 food plots (121 for breeding groups and 81 for bachelor groups) were used in analyses. One food plot for a bachelor group was excluded because it had a non-woody plant species at its centre. Higher sightability of elephants in groups (hence, breeding groups) resulted in feeding data being collected from more food plots for breeding groups than for bachelor groups. Many areas become inaccessible due to flooding during the wet season, therefore sample sizes are smaller for the wet season.

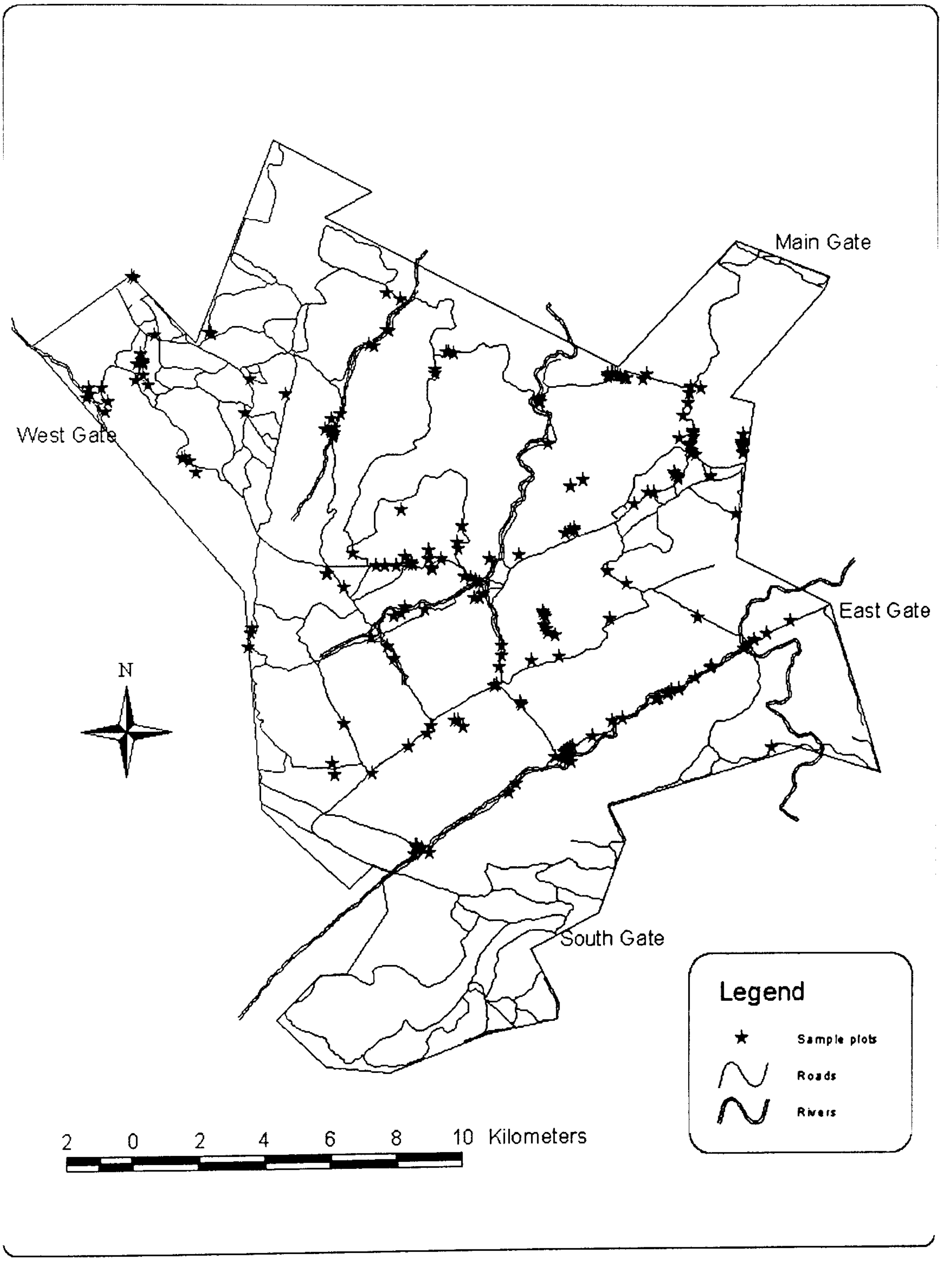


Fig. 3.2. Map of WPGR showing distribution of 203 food plots from which feeding data were collected.

The problem of unequal sample sizes was overcome in the data analysis by using statistical techniques such as chi-square (Gravetter & Wallnau 1999) and t-tests (Gravetter & Wallnau 1999) which are sensitive to sample size. Feeding data were collected in food plots from all three habitat types available to the elephants: 53 food plots were defined in plateau (26% of the total 203 food plots); 70 in hillslope (35% of 203 food plots); 80 in valley bottom (39% of 203 food plots).

The Shannon Index of diversity (Magurran 1988) was used to determine whether the diversity of woody plant species utilised, available in food plots and present in control plots, differed between bachelor groups and breeding groups. These analyses were applied plot-wise on a paired (food-control) plot basis, within elephant group types, between seasons. A total of 202 food plots and 158 control plots were used in the analysis of species diversity. Eight control plots for bachelor groups and seven control plots for breeding groups were excluded from the Shannon diversity index calculations because these contained no woody vegetation and were hence "empty", as Stokke and du Toit (2000) noted. These plots could obviously not be given a value of zero since that exists as a valid index value, they were therefore excluded from the analysis. The formula used to calculate the *H'* (the Shannon index) was taken from Krebs (1978). The Mann-Whitney U test was used to compare whether diversity of species (*H'*) was significantly different for food and control plots, between bachelor and breeding groups, in each season. To determine whether bachelor groups and breeding groups (separately) selected feeding patches with differing species diversity to the corresponding control plots, the Wilcoxon test for non-parametric paired data was used. Shannon indices for each food plot and control plot were grouped into the three habitat types and a one-way ANOVA (Gravetter & Wallnau 1999) was used to test for significant differences in species diversity between habitats.

Preference of woody species by bachelor groups and breeding groups was determined by calculating a preference ratio as adapted from Petrides (1975) and Ishwaran (1983) and Tchamba and Mahamat (1992), of use to availability for each woody species where:

$$\text{Use of species } i = \frac{\text{the number of food plots in which species } i \text{ was utilised}}{\text{the total number of food plots sampled}}$$

$$\text{Availability of species } i = \frac{\text{the number of food plots in which species } i \text{ was available}}{\text{the total number of food plots sampled}}$$

$$\text{Preference ratio for species } i = \frac{\text{use of species } i}{\text{availability of species } i}$$

This preference ratio (PR) returns a value between 0 and 1. The closer the PR is to 1, the more preferred the species is considered to be. A woody plant species was considered available to an elephant if it occurred within at least one of the food plots. Preference ratios were calculated for woody plant species which were utilised at least once by both bachelor groups and breeding groups in each of the dry and wet seasons, and which were available to both bachelor groups and breeding groups in both dry and wet seasons. A preference rank was then allocated to each of those species to denote degree of preference in the diet of bachelor groups and breeding groups, in each season. A Spearman Rank Correlation (Sokal & Rohlf 1995) was used to determine whether there was any correlation between bachelor groups and breeding groups in the species they preferred.

Chi-square tests with contingency tables (Gravetter & Wallnau 1999) were used to test for differences in frequencies of woody species used, and individual woody plants used, between group types within seasons and between seasons within group types. Chi-square tests with contingency tables were used to test if there was a significant difference between woody plants that were utilised and unutilised by bachelor groups and breeding groups, within the dry and wet season, and then for each group type between seasons. Proportions of utilised to available individual woody plants were calculated per food plot for bachelor groups and breeding groups, in dry and wet seasons. The non-parametric Mann-Whitney U test (Sokal & Rohlf 1995) was used to test for differences between bachelor groups and breeding groups within seasons, and then for each group type, between seasons.

The Mann-Whitney U test was used to compare heights of woody plants utilised by the elephants (group types together) with heights of those available to the elephants in the food plots. The same statistical technique was also used to compare the height of browsed (utilised) trees between bachelor groups and breeding groups, between seasons.

A chi-square test with contingency tables was used to test for differences between bachelor and breeding groups for four impact types [felling (main stem broken-off), uprooting, barkstripping and branches broken] within dry and then wet seasons. A chi-square test was then used to compare impact types for each group type (separately), between seasons. These analyses were conducted for data pooled for all woody species. Sample sizes were too small for species-specific analyses, therefore this analysis was re-done for the nine woody plant species which were utilised more than five times by both bachelor groups and breeding groups. This was to eliminate spurious effects of rare species. Data from all the individual woody plants belonging to those nine species were pooled and a chi-square test with contingency tables was used to test for differences in impact type exerted by bachelor groups and breeding groups on the woody vegetation over the whole year. Differences between bachelor groups and breeding groups were investigated for utilised plants regarding the measurements relating to three of the impact types, namely stem diameter [of plants that were felled (main stem broken-off) or uprooted], break diameter and break height (of branches broken). Differences between these measurements were tested for using Student's t-test where data were parametric and Mann-Whitney U test for non-parametric data. Data were transformed using log transformations where necessary. All counts were analysed using chi-square tests. Analyses were first conducted using data from all species pooled together, then on a species-specific basis where sample sizes were sufficiently large to provide reliable results. Where Student's t-test and Mann-Whitney U test were used, the minimum sample size used was 12 values. The relationship between browse height (break heights) and tree height of utilised woody plants was investigated using non-parametric Spearman Rank correlation.

Chi-square contingency tables were used to test for differences in damage score between bachelor groups and breeding groups, between seasons. Average percentage damage was calculated for woody species which were used more than 5 times by both bachelor groups and breeding groups together (data pooled) in each season. The midpoint of each category of damage was found, this single percentage was then summed to the frequency of each corresponding damage score, providing a total percent damage which was then averaged using the total number of times the species was utilised in each relevant season.

3.4 Results

3.4.1 Diversity of woody plant species

The diversity of woody plant species utilised in food plots, available in food plots, and present in control plots did not differ between bachelor groups and breeding groups within seasons, or within group types between dry and wet seasons (Table 3.1). The number of woody species available to each group type in their respective food plots was significantly greater for bachelor groups than for breeding groups, but only in the dry season (Table 3.1). This did not differ significantly within each group type, between seasons (Table 3.1). The number of woody plants (all species pooled) available was greater in the food plots of bachelor groups than of breeding groups in the dry season (Table 3.1). Number of Woody plants available in food plots did not differ between bachelor groups and breeding groups for wet season data, nor did it differ for bachelor groups between dry and wet season. This did, however differ in food plots of breeding groups where the number of woody plants available in the food plots was greater in the wet season data than in the dry season data (Table 3.1).

Table 3.1. Comparisons made between elephant bachelor and breeding groups, in each season in terms of the following variables: diversity of woody species utilised in food plots, available in food plots and present in control plots; number of woody species available in food plots; number of woody plants available in food plots. Mean ± standard error are shown for each variable in each category (each elephant group type, in each season). Where significant differences were found between categories, < or > were used to designate which mean was significantly different (where < indicates that the mean on the left hand side of the sign was significantly less than the mean on the right hand side of the sign, and conversely for >). The test statistic and *P* value are reported beneath these categories.

Variable tested	Bachelor groups		Breeding groups		Dry season		Wet season	
	Dry season	Wet season	Dry season	Wet season	Bachelor groups	Breeding groups	Bachelor groups	Breeding groups
Diversity of woody species utilised in food plots	0.562 ± 0.088	0.561 ± 0.131	0.531 ± 0.069	0.694 ± 0.123	0.562 ± 0.088	0.531 ± 0.069	0.561 ± 0.131	0.694 ± 0.123
Diversity of woody species available in food plots	2.53 ± 0.087	2.54 ± 0.221	2.43 ± 0.081	2.54 ± 0.139	2.53 ± 0.087	2.43 ± 0.081	2.54 ± 0.221	2.54 ± 0.139
Diversity of woody species present in control plots	2.29 ± 0.112	2.15 ± 0.219	2.18 ± 0.107	1.98 ± 0.169	2.29 ± 0.112	2.18 ± 0.107	2.15 ± 0.219	1.98 ± 0.169
Number of woody species available in food plots	9.63 ± 0.492	10.3 ± 1.17	8.40 ± 0.376	9.91 ± 0.810	9.63 ± 0.492 >	8.40 ± 0.376	10.3 ± 1.17	9.91 ± 0.810
					t = 1.99, *P* < 0.05			
Number of woody plants available in food plots	37.2 ± 2.65	70.4 ± 28.6	28.3 ± 2.10 <	40.5 ± 4.16	37.2 ± 2.65 >	28.3 ± 2.10	70.4 ± 28.6	40.5 ± 4.16
			Mann-Whitney U = 942, *P* < 0.05		Mann-Whitney U = 1837, *P* < 0.05			

Species diversity of woody plants available in food plots, number of woody species available (species richness) in food plots and number of woody plants available in food plots were compared (separately) with that present in the corresponding control plots. Species diversity of woody plants available in food plots of bachelor groups was significantly higher than those present in the corresponding control plots, in the dry season (Table 3.2). Species diversity of food and control plots of bachelor groups in the wet season did not differ (Table 3.2). Species diversity in food plots of breeding groups was significantly higher than in control plots in both dry and wet seasons (Table 3.2). Species richness differed significantly between plot types for bachelor groups in dry season data, being higher in food plots than in control plots (Table 3.2). No significant difference in species richness was found between food and control plots of bachelor groups in the wet season. The number of woody species available to breeding groups in food plots in the dry season was significantly greater than the number present in the corresponding control plots in the same season (Table 3.2). This was also significantly different for breeding groups in wet season data, with more species available in food plots than in control plots (Table 3.2). The number of woody plants available in food plots was significantly greater than that present in control plots for bachelor groups in the dry season, bachelor groups in the wet season, breeding groups in the dry season and breeding groups in the wet season. See Table 3.2.

A significant difference in species diversity was found between the three habitat types ($F = 10.4$, $P < 0.0001$). Where plateau had the lowest species diversity (mean = 2.04, n = 95), valley bottom (mean = 2.40, n = 133) and hillslope had the highest species diversity (mean = 2.52, n = 132).

3.4.2 Utilised and available woody species and plants

A total of 113 woody species and 11 308 individual woody plants were recorded as available to the elephants over all food plots and control plots (Appendix 3.1). However, only 92 woody species and 7 579 woody plants were recorded as available to the elephants in the food plots. The elephants (both group types together) utilised 48 woody species (52% of the available 92), and within these species, they utilised 548 individual woody plants (7% of the available 7 579). Bachelor groups utilised 38 different woody species (42% of available 92 species) and 180 individual woody plants (2% of available 7 579 plants), while breeding groups used 36 different species (39% of available) and 368 individual plants (5% of available). Only 29 species were recorded as being common to the diets of both group types (31% of available 92 species) (Appendix 3.1). There were 5 636 individual woody plants available in the food plots, of the 29 woody species common to both bachelor groups and breeding groups. The number of woody

Table 3.2. A comparison of food and control plots within group types, between seasons, on a paired food-control plot basis for diversity of woody species available; number of woody species available and number of woody plants available. Mean ± standard error are shown for each variable in each category (each elephant group type, in each season). Where differences were found, < or > were used to designate which mean was significantly different (where < indicates that the mean on the left hand side of the sign was significantly less than the mean on the right hand side of the sign, and conversely for >). The test statistic and *P* value are reported beneath these categories.

Variable tested	Bachelor groups				Breeding groups			
	Dry season		Wet season		Dry season		Wet season	
	Food plot	Control plot	Food plot	Control plot	Food plot	Control plot	Food plot	Control plot
Diversity of woody species available in food plots and present in control plots	2.54 ± 0.104 >	2.29 ± 0.112	2.24 ± 0.320	2.15 ± 0.219	2.43 ± 0.084 >	2.18 ± 0.107	2.66 ± 0.149 >	1.98 ± 0.169
	W = 319, *P* < 0.0001		ns		W = 795, *P* < 0.0001		W = 236, *P* < 0.0001	
Number of woody species available in food plots and present in control plots	9.60 ± 0.556 >	6.96 ± 0.535	8.47 ± 1.10	5.93 ± 1.14	8.15 ± 0.358 >	6.81 ± 0.438	10.0 ± 0.846 >	6.30 ± 0.754
	W = 609, *P* < 0.0001		ns		W = 840, *P* < 0.0001		W = 296, *P* < 0.0001	
Number of woody plants available in food plots and present in control plots	38.3 ± 3.03 >	20.2 ± 1.90	78.7 ± 41.9 >	24.5 ± 5.73	27.2 ±2.16 >	20.2 ± 1.68	38.3 ± 3.95 >	25.5 ± 3.36
	W = 848, *P* < 0.0001		W = 89, *P* < 0.05		W = 771, *P* < 0.0001		W = 261, *P* < 0.0001	

plants utilised within those 29 common species was 511 [159 by bachelor groups (31% of available) and 352 by breeding groups (69% of available)].

3.4.3 Preference of woody plant species by the elephants

A total of 29 woody species were utilised at least once by bachelor groups and by breeding groups over the period of data collection. Of these species, 21 were used by both bachelor groups and breeding groups in the dry season, and 14 in the wet season. Only nine species were used by both sexes, in both seasons. Preference ratios were calculated for each species used at least once by either bachelor groups or breeding groups over both seasons, and available at least five times to both group types over both seasons, 37 species in the dry season (Table 3.3; Fig. 3.3) and 25 species in the wet season (Table 3.4; Fig 3.4). No significant correlation was found between preference ratios of species preferred by bachelor groups and breeding groups in either of the seasons. Species with preference ratios of zero were not utilised by the specific group type in the specific season, even though they were available to both group types.

3.4.4 Numbers of woody species and individual woody plants utilised

No significant difference in seasonal variation of the number of woody species used by bachelor and breeding groups was found. There was also no significant variation in the number of woody plants used by bachelor and breeding groups, in each season (Table 3.5).

3.4.5 Utilised vs unutilised woody plants

Comparison of number of woody plants that were utilised with the number that were unutilised per food plot between bachelor groups and breeding groups showed a significant difference for both dry and wet season data taken together. Within seasons, bachelor groups and breeding groups showed a significantly different utilisation of woody plants compared with unutilised woody plants in food plots in the dry and wet season. In all three of these tests (for whole year, then dry and wet seasons separately), bachelor groups were consistently observed to utilise fewer woody plants than expected, whereas the opposite was observed for breeding groups. Between seasons, bachelor groups exhibited significantly different utilisation of woody plants, compared with those that remained unutilised however, no significant difference was found for the breeding groups (Table 3.6). Both sexes were observed to use more woody plants than expected in dry season, and fewer than expected in the wet season.

3.4.6 Utilised vs available woody plants

Dry season data showed that bachelor groups and breeding groups utilised significantly different proportions of woody plants to those available in the food plots. Wet season data showed the

Table 3.3. Percentage use, percentage availability and preference rank for 37 woody species used at least once by either bachelor groups or breeding groups in the dry season, but available to both in that season. Species are listed in order of mean preference ratio over both sexes for the dry season. Preference rank indicates preference of species by each sex individually where a rank of 1= highest preference ratio.

Species name	Bachelor groups			Breeding groups		
	% Use	% Availability	Preference rank	% Use	% Availability	Preference rank
Ficus thonningii	5.09	6.78	2	1.12	1.12	1
Pterocarpus rototundifolius	18.6	32.2	3	12.4	18.0	3
Vitex pooara	1.7	3.39	4	3.37	5.62	7
Diplorhynchus condylocarpon	6.78	17.0	8	28.1	42.7	5
Dombeya rotundifolia	11.9	49.2	16	11.2	14.6	2
Peltophorum africanum	1.7	1.69	1	0	2.25	35
Combretum zeyheri	5.09	13.6	10	8.99	14.6	6
Strychnos pungens	5.09	11.9	7	12.4	23.6	8
Acacia galpinii	1.7	10.2	21	2.25	3.37	4
Elephantorrhiza burkei	1.7	6.78	14	6.74	14.6	11
Englerophytum magalismontanum	8.48	27.1	11	12.4	32.6	13
Lannea discolor	11.9	39.0	12	16.9	43.8	12
Grewia spp.	25.4	66.1	9	7.87	28.1	17
Rhus leptodictya	6.78	25.4	13	4.49	14.6	16
Brachylaena rotundata	0	1.69	29	1.12	2.25	9
Clerodenrum glabrum	0	13.6	30	1.12	2.25	10
Pseudolachnostylis maprouneifolia	1.7	10.2	22	2.25	6.74	15
Rhus pyroides	8.48	18.6	5	0	2.25	36
Dichrostachys cinerea	6.78	15.3	6	0	3.37	33
Ozoroa paniculosa	1.7	6.78	15	2.25	20.2	26
Rhus dentata	3.39	17.0	19	2.25	15.7	20
Terminalia sericea	5.09	23.7	17	2.25	18.0	25
Faurea saligna	0	10.2	32	2.25	6.74	14
Pappea capensis	3.39	18.6	20	1.12	7.87	19
Burkea africana	8.48	42.4	18	7.87	74.2	27
Rhoicissus revoilii	1.7	27.1	26	3.37	24.7	22
Terminalia brachystemma	0	10.2	36	1.12	6.74	18

Table 3.3. Continued

Species name	Bachelor groups			Breeding groups		
	% Use	% Availability	Preference rank	% Use	% Availability	Preference rank
Ochna pulchra	3.39	22.0	23	0	25.8	34
Ziziphus mucronata	3.39	22.0	24	0	10.1	37
Vitex rehmanni	0	1.69	37	1.12	7.87	21
Gardenia volkensii	0	5.08	33	1.12	8.99	23
Indigophera spp.	0	5.08	35	2.25	18.0	24
Bridelia mollis	1.7	17.0	25	0	5.62	31
Gymnosporia spp.	0	17.0	34	3.37	37.1	28
Euclea crispa	1.7	57.6	28	1.12	24.7	29
Combretum molle	1.7	45.8	27	0	51.7	32
Euclea natalensis	0	35.6	31	1.12	34.8	30

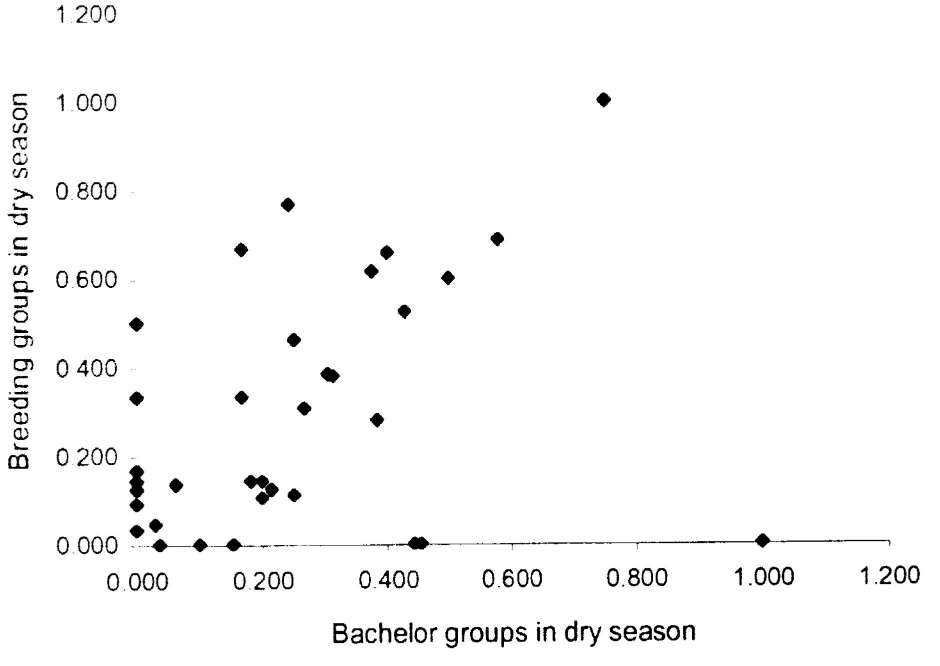


Fig. 3.3 Scatterplot of the correlation between preference ratios for 37 woody species used at least once by bachelor groups or breeding groups in the dry season, but available to both groups in that season. The relationship was not significant (r_s = 0.28, P = 0.10).

Table 3.4. Percentage use, percentage availability and preference rank for 25 woody species used at least once by either bachelor groups or breeding groups in the wet season, but available to both in that season. Species are listed in order of mean preference ratio over both sexes. Preference rank indicates preference of species by each sex individually where 1= highest preference ratio.

Species name	Bachelor groups			Breeding groups		
	% Use	% Availability	Preference rank	% Use	% Availability	Preference rank
Rhus pyroides	22.7	22.7	1	15.6	25.0	4
Elephantorrhiza burkei	9.09	18.2	2	12.5	18.8	3
Pterocarpus rotundifolius	0	13.6	23	9.38	9.38	1
Ziziphus mucronata	9.09	18.2	5	12.5	28.1	6
Englerophytum magalismontanum	18.2	45.5	6	21.9	40.6	5
Strychnos pungens	13.6	27.3	3	6.25	21.9	14
Combretum zeyheri	0	4.55	20	6.25	9.38	2
Rhus dentata	13.6	50.0	8	12.5	34.4	8
Grewia spp.	9.09	31.8	7	15.6	46.9	10
Dombeya rotundifolia	4.55	18.2	10	6.25	18.8	9
Vitex rehmanni	4.55	9.09	4	0	3.13	25
Burkea africana	9.09	59.1	12	25.0	78.1	12
Lannea discolor	4.55	45.5	18	15.6	46.9	11
Rhus leptodictya	4.55	31.8	13	6.25	21.9	13
Vitex pooara	0	0	25	9.38	25.0	7
Faurea saligna	4.55	22.7	11	3.13	18.8	17
Gymnosporia spp.	4.55	36.4	14	3.13	18.8	18
Clerodenrum glabrum	4.55	18.2	9	0	21.9	21
Gardenia volkensii	0	9.09	22	3.13	12.5	15
Rhoicissus revoilii	0	18.2	24	6.25	28.1	16
Combretum molle	4.55	40.9	16	3.13	50.0	20
Diplorhynchus condylocarpon	0	4.55	21	3.13	21.9	19
Ochna pulchra	4.55	36.4	15	0	21.9	24
Indigophera spp.	4.55	45.5	17	0	18.8	23
Euclea crispa	4.55	50.0	19	0	31.3	22

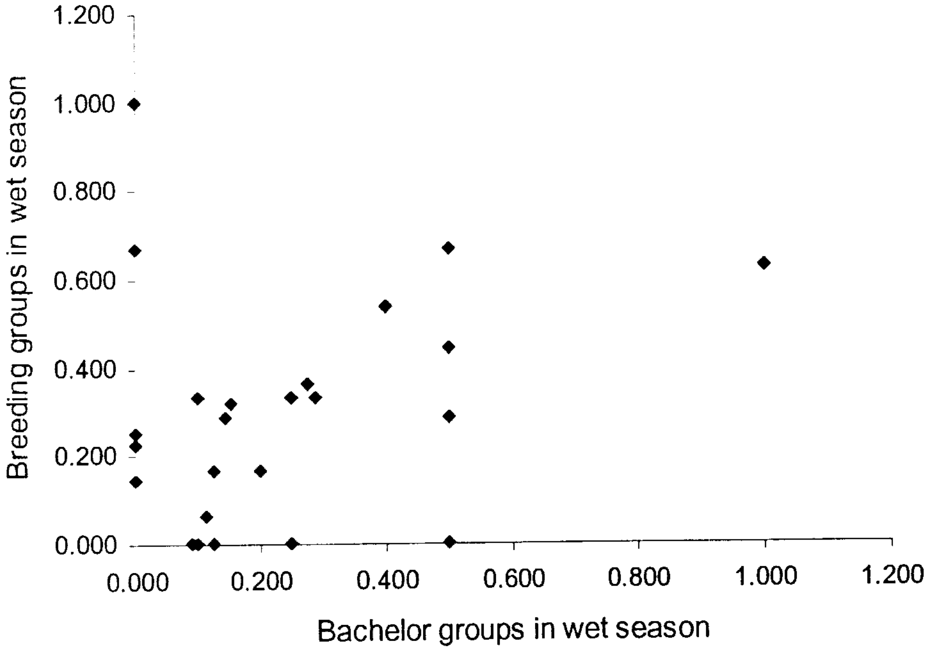


Fig. 3.4 Scatterplot of the correlation between preference ratios for 25 woody species used at least once by bachelor groups or breeding groups in the wet season, but available to both groups in that season. The relationship was not significant (r_s = 0.23, P = 0.29).

Table 3.5. Number of woody species and individual woody plants used, a comparison between elephant bachelor groups and breeding groups in dry and wet seasons

	Dry season		Wet season	
	Bachelor groups	Breeding groups	Bachelor groups	Breeding groups
Number of woody species used	31	33	21	21
Number of individual woody plants used	138	258	42	110

Table 3.6. Comparison of the number of woody plants utilised, with those unutilised, in food plots between group types over both seasons together (whole year) and within seasons and then within group types, between seasons.

		Utilised	Unutilised	n	χ^2
Whole Year:	Bachelor groups	180	3580	3760	66.4 *
	Breeding groups	368	3451	3819	
Dry Season:	Bachelor groups	138	2058	2196	23.7 *
	Breeding groups	258	2267	2525	
Wet Season:	Bachelor groups	42	1522	1564	47.6 *
	Breeding groups	110	1184	1294	
Bachelor groups:	Dry Season	138	2058	2196	26.0 *
	Wet Season	42	1522	1564	
Breeding groups:	Dry Season	258	2267	2525	2.90
	Wet Season	110	1184	1294	

Note: The χ^2 values calculated in this table are for d.f. = 1; all significant χ^2 are with $P < 0.05$ and are indicated by *.

same results. Between seasons, bachelor groups and breeding groups did not exhibit any difference in the proportions of woody plants utilised, to those available (Fig. 3.5).

3.4.7 Heights of utilised and available woody plants

The mean height of woody plants utilised by the elephants was 3.3 m however, the most frequently used height category (by bachelor groups and breeding groups in each season) was 2.0–2.4 m. Fourteen percent of utilised woody plants, and seven percent of all woody plants available in food plots and present in control plots fell within this height interval. With all species pooled, the trend (Fig. 3.6) suggests that the elephants (both sexes together) utilised woody plants of different heights to those available to them in food plots over the whole year, although this difference was not statistically significant.

Elephant bachelor groups browsed from significantly taller woody plants than breeding groups in the dry season. There was no difference in the height of plants utilised by bachelor groups and breeding groups in the wet season. Bachelor groups did not differ in the heights of plants they utilised between seasons. The same result was found for breeding groups (Fig. 3.7.).

3.4.8 Impact types

The observed frequencies of impact types exerted by bachelor groups and breeding groups on the woody vegetation did not differ from the expected values within dry and wet seasons. No difference between observed and expected values of impact type frequency was found for bachelor groups between dry and wet seasons (Table 3.7). Breeding groups, however, showed a significant difference between observed and expected frequencies of types of impact they exerted on the woody vegetation, between dry and wet seasons (χ^2 = 14.8, d.f. = , $P < 0.05$). Breeding groups were observed to uproot and barkstrip more woody plants (not necessarily both impact types on one plant) in the dry season than was expected, and broke branches more than was expected in the wet season. These analyses were conducted for data pooled over all utilised woody species. None of the utilised woody species had large enough sample sizes for analysis on a species-specific basis. Chi-square results for data pooled from nine species (*Burkea africana, Dombeya rotundifolia, Elephantorrhiza burkei, Englerophytum magalismontanum, Grewia spp, Lannea discolor, Pterocarpus rotundifolius, Rhus pyroides* and *Strychnos pungens*) that were used more than five times, showed no significant difference between bachelor groups and breeding groups in the types of impact they exerted on the woody vegetation over both dry and wet seasons.

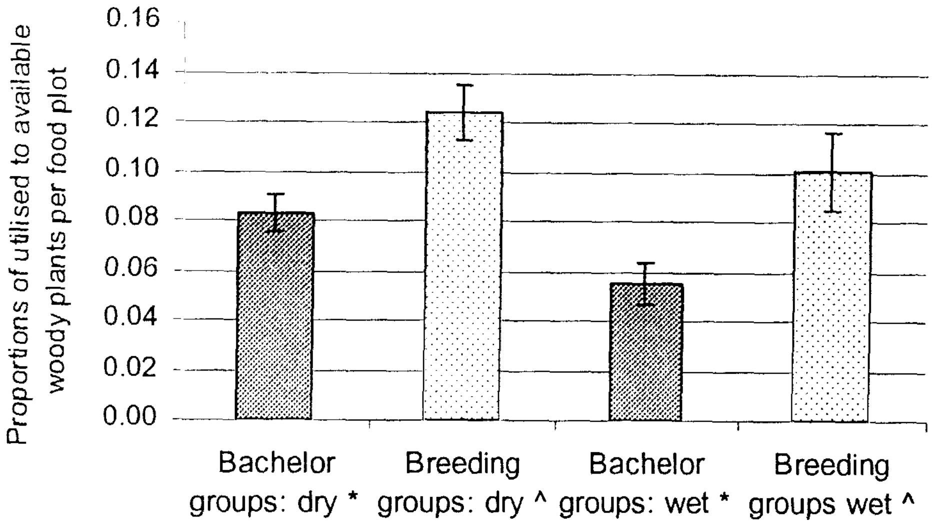


Fig. 3.5. Mean (and standard error bars) of the proportions of utilised woody plants to those available in food plots for each elephant group type, in each season. Bachelor groups and breeding groups utilised significantly different proportions of woody plants to those available in their respective food plots in the dry season (Mann-Whitney U = 1987, $P < 0.05$) and wet season (Mann-Whitney U = 232, $P < 0.05$). Different symbols indicate where categories were significantly different. No significant differences were found within group types, within seasons.

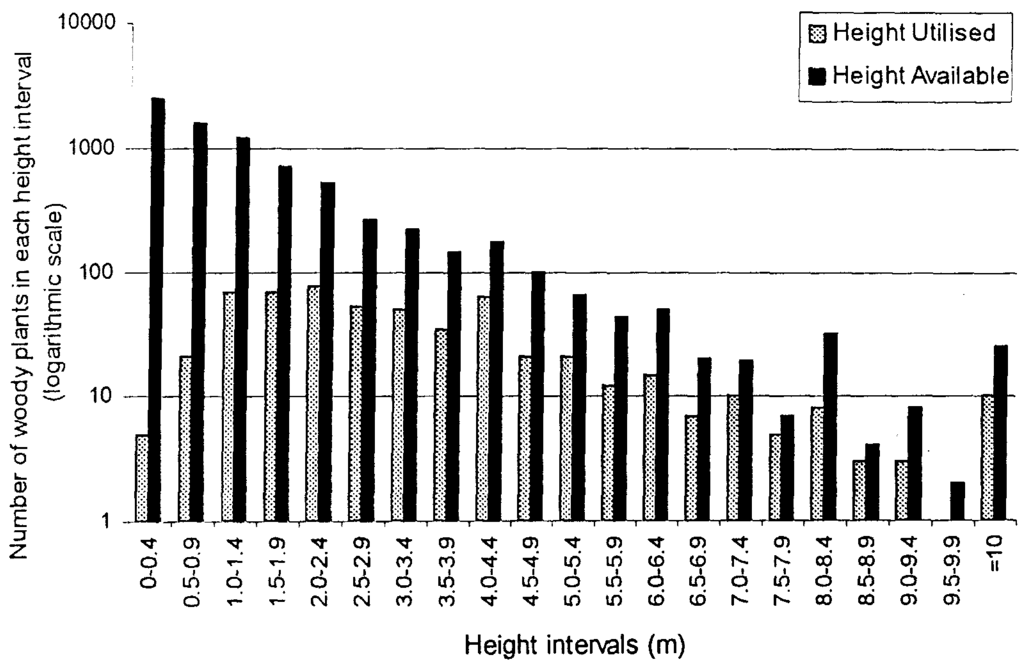


Fig. 3.6. A comparison of heights of woody plants utilised by both elephant group types, with the heights of woody plants available to them in food plots, over both seasons.

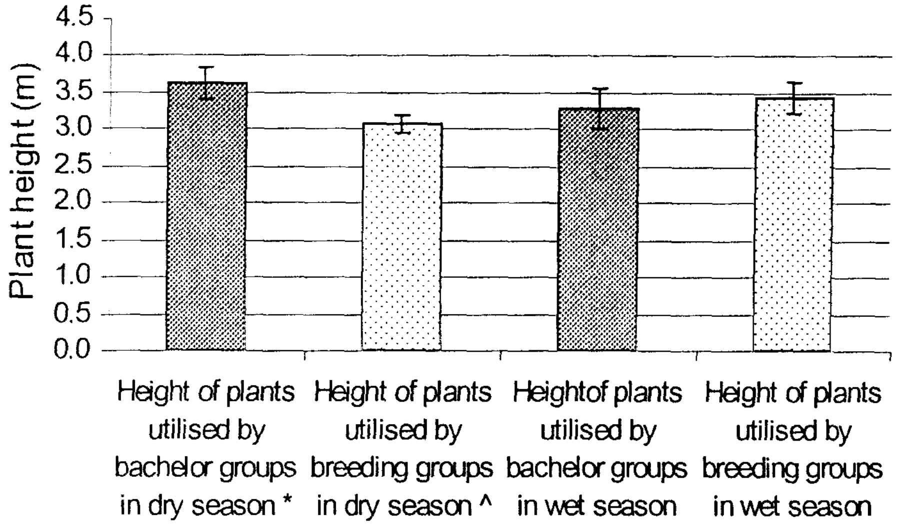


Fig. 3.7. Mean (± standard error) height of woody plants utilised by bachelor groups and breeding groups in each season are shown. Different symbols indicate that bachelor groups browsed from significantly taller woody plants (3.62 ± 0.20 m) than breeding groups (3.08 ± 0.12 m) in the dry season (Mann-Whitney U = 45 950, $P < 0.0001$).

Table 3.7. Percentage frequency of types of impact exerted by bachelor groups and breeding groups (separately) on woody vegetation between dry and wet seasons. Data are pooled within each impact type over all utilised woody species.

Elephant group type and season	% Felling	% Uprooting	% Barkstripping	% Branch breaking
Bachelor groups: dry season	5	11	29	55
Bachelor groups: wet season	7	15	13	65
Breeding groups: dry season	6	9	35	50
Breeding groups: wet season	10	7	20	63

3.4.9 Stem diameter of felled and uprooted woody plants

In the dry season bachelor groups felled woody plants with significantly larger stem diameters than breeding groups (Fig. 3.8a). Bachelor groups and breeding groups did not differ significantly with respect to the stem diameter of the plants they felled in the wet season. Bachelor groups did not fell woody plants with significantly different stem diameters in dry and wet seasons. The same result was found for breeding groups between seasons.

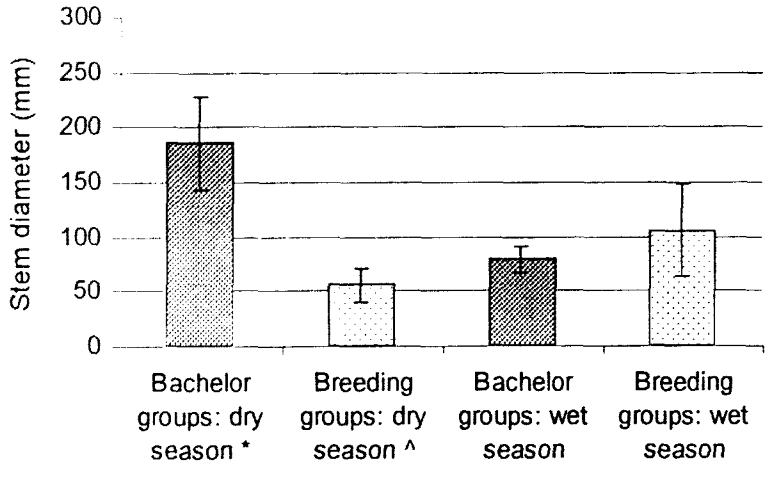
Stem diameter of woody plants that had been uprooted did not differ between bachelor groups and breeding groups in the dry season or the wet season. Bachelor groups did not exhibit any difference in the stem diameter of the plants that they uprooted between dry and wet seasons. The same results were found for breeding groups between dry and wet seasons (Fig. 3.8b).

3.4.10 Break diameter of branches

Bachelor groups and breeding groups showed no difference in the diameter of branches they broke in the dry season or in the wet season. A comparison of the diameter of branches broken by bachelor groups between seasons also revealed no significant difference. Breeding groups also did not break branches with significantly different diameters between seasons (Fig. 3.9a). The above results were obtained from data from all species pooled together. Two woody species were analysed further (*Grewia spp* and *Pterocarpus rotundifolius*), on the basis that they were utilised 12 times or more by either breeding groups or bachelor groups. Mann-Whitney U tests were used to test for differences in break diameter of branches broken, between group types over the whole year (seasons together) because sample sizes were not large enough to test between seasons. Bachelor groups and breeding groups showed no difference in the diameter of branches they broke from *Grewia spp* over both seasons. The same results were found for *Pterocarpus rotundifolius*, where bachelor and breeding groups did not show any significant difference in the diameter of branches they broke.

3.4.11 Break height of branches broken

Height at which branches were broken did not differ between bachelor groups and breeding groups in the dry season. The height at which branches were broken by elephants in the wet season did however differ between group types, being at a slightly higher level in the canopy for bachelor groups than for breeding groups. The height of branches broken by bachelor groups differed significantly between seasons. No difference in break height was found for breeding groups between dry and wet seasons (Fig. 3.9b). On the basis that their sample sizes were large enough, *Grewia spp* and *Pterocarpus rotundifolius* were also used for species-specific analysis of break height. The height at which the elephants broke branches of *Grewia spp* did a)



b)

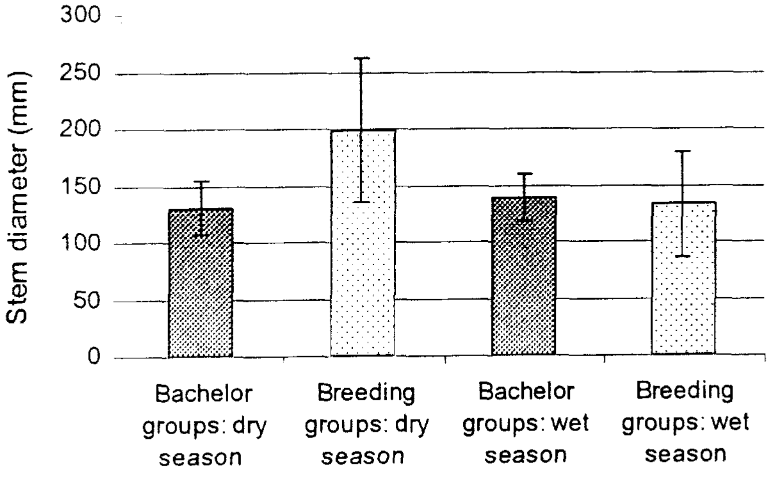
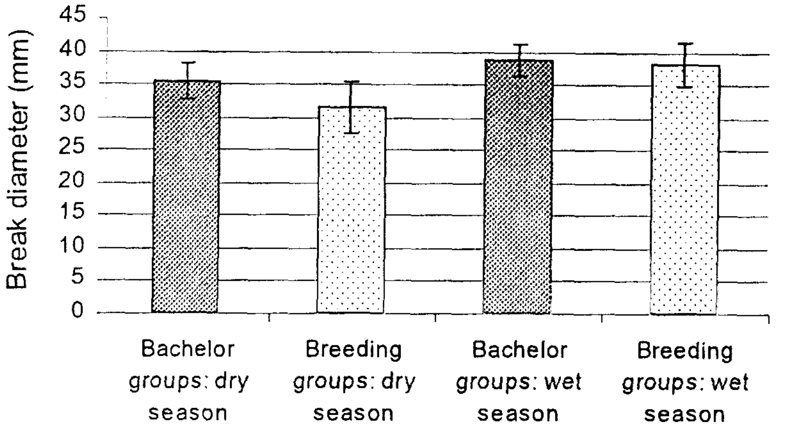


Fig. 3.8. Comparisons between bachelor groups and breeding groups, between seasons, of a) stem diameter of felled plants where main stem was broken-off and b) stem diameter of uprooted plants. Different symbols indicate significant differences between group types or seasons. In the dry season bachelor groups felled woody plants with significantly larger stem diameters than breeding groups (Mann-Whitney U = 71.0, $P < 0.05$).

a)



b)

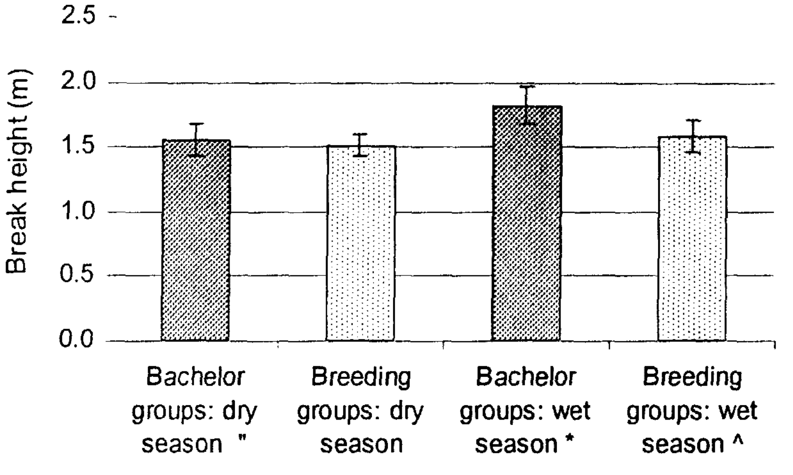


Fig. 3.9. Comparisons between bachelor groups and breeding groups, between seasons, of a) break diameter and b) break height of branches. Different symbols indicate significant differences between group types or seasons. Break height by bull elephants was significantly higher (Mann-Whitney U = 1362, $P < 0.05$) than by breeding groups in the wet season. Break height differed significantly between seasons for bachelor groups (Mann-Whitney U = 1601, $P < 0.05$).

not differ between bachelor groups and breeding groups over the whole year (seasonal data was pooled to allow for larger sample sizes). However, bachelor groups broke branches from *Pterocarpus rotundifolius* at a significantly lower height than breeding groups did (Mann-Whitney $U = 311$, $P < 0.05$).

3.4.12 Number of branches broken

Bachelor groups and breeding groups did not break significantly different number of branches from woody plants in the dry or wet season. Number of branches broken by the elephants also did not differ within sexes, between seasons.

3.4.13 Break height in relation to height of browsed plant

The relationship between browse height and height of the browsed plant (Fig. 3.10) was positive and significant for all four categories (each elephant group type, in each season).

3.4.14 Damage scores

The two most frequently occurring damage scores for woody species used by both bachelor groups and breeding groups, in both dry and wet seasons were 2 and 8, representing 1-10% and 100% damage to the plant respectively (Fig. 3.11). Fig. 3.11 also shows that the proportional frequency of each of the eight damage scores was similar for bachelor groups and breeding groups, in both dry and wet seasons. Hence, bachelor groups and breeding groups showed no significant difference in the frequencies of damage scores recorded for utilised plants within seasons. However, bachelor groups alone exhibited a significant difference in damage score frequency for plants utilised in the dry season and in the wet season. No significant result was obtained for the breeding groups between seasons. The above results are for all utilised woody plants pooled, regardless of species. Average percentage damage was calculated for 14 woody species which were used more than five times by the elephants (plants within species used by both sexes were pooled) in the dry season (Fig. 3.12). These were *Burkea africana, Combretum zeyheri, Dichrostachys cinerea, Diplorhynchus condylocarpon, Dombeya rotundifolia, Elephantorrhiza burkei, Englerophytum magalismontanum, Grewia spp, Indigophera spp, Lannea discolor, Pterocarpus rotundifolius, Rhus leptodictya, Strychnos pungens* and *Terminalia sericea*. Six of those species were utilised to an average degree of more than 50% damage to the plants (*Burkea africana* 65%, *Combretum zeyheri* 51%, *Elephantorrhiza burkei* 81%, *Indigophera spp* 79%, *Lannea discolor* 87% and *Strychnos pungens* 62%). Average percentage damage was calculated for nine species used more than five times by both bachelor groups and breeding groups in the wet season, these were (Fig. 3.13): *Burkea africana, Elephantorrhiza burkei, Englerophytum magalismontanum, Grewia spp, Lannea discolor,*

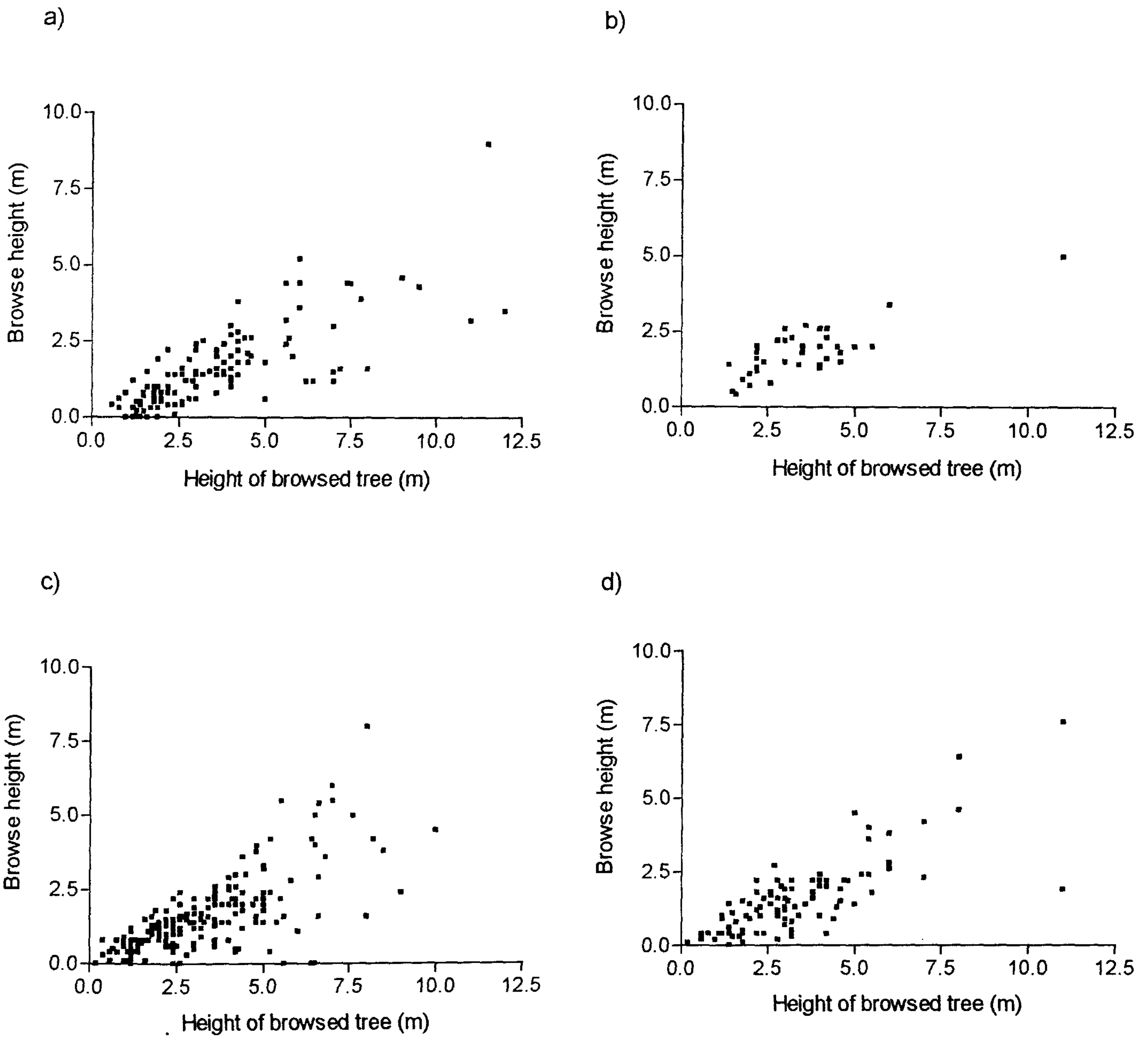


Fig. 3.10. Correlation between browse height (m) and height of browsed tree (m) was positive for a) bachelor groups in dry season ($r_s = 0.65$, $P < 0.0001$, n = 122), b) bachelor groups in wet season ($r_s = 0.64$, $P < 0.0001$, n = 36), c) breeding groups in dry season ($r_s = 0.49$, $P < 0.0001$, n = 215) and d) breeding groups in wet season ($r_s = 0.53$, $P < 0.0001$, n = 99).

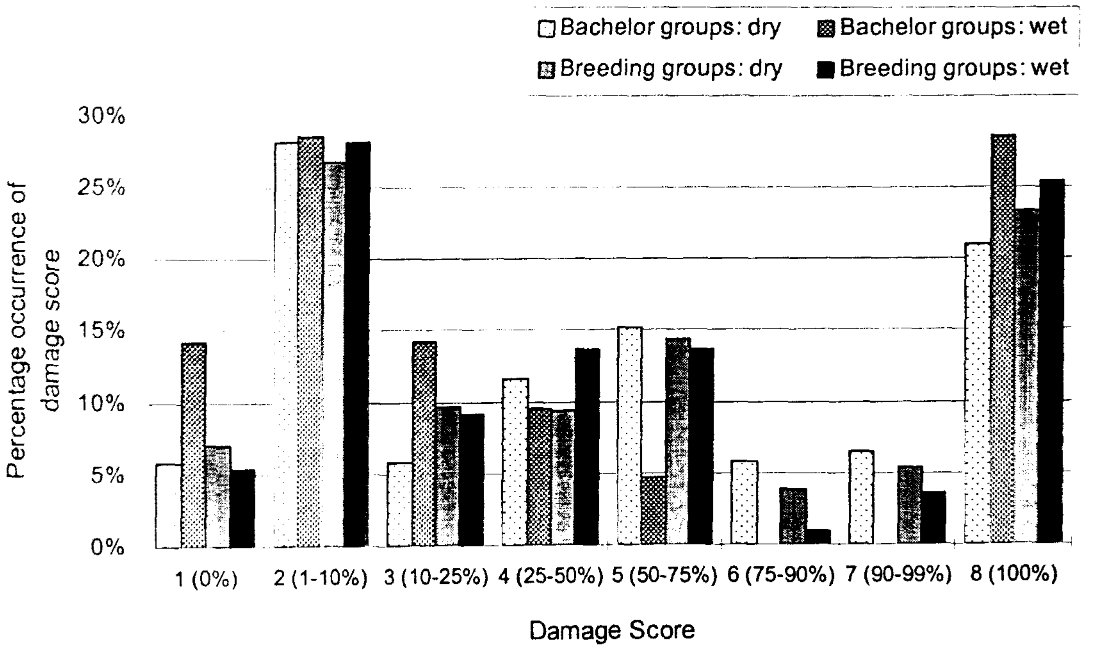


Fig. 3.11. Proportions of each damage score for bachelor groups and breeding groups in dry and wet seasons. Only bachelor groups exhibited a significant difference in frequency of damage score between dry and wet seasons ($\chi^2 = 14.8$, d.f. = 7, $P < 0.05$).

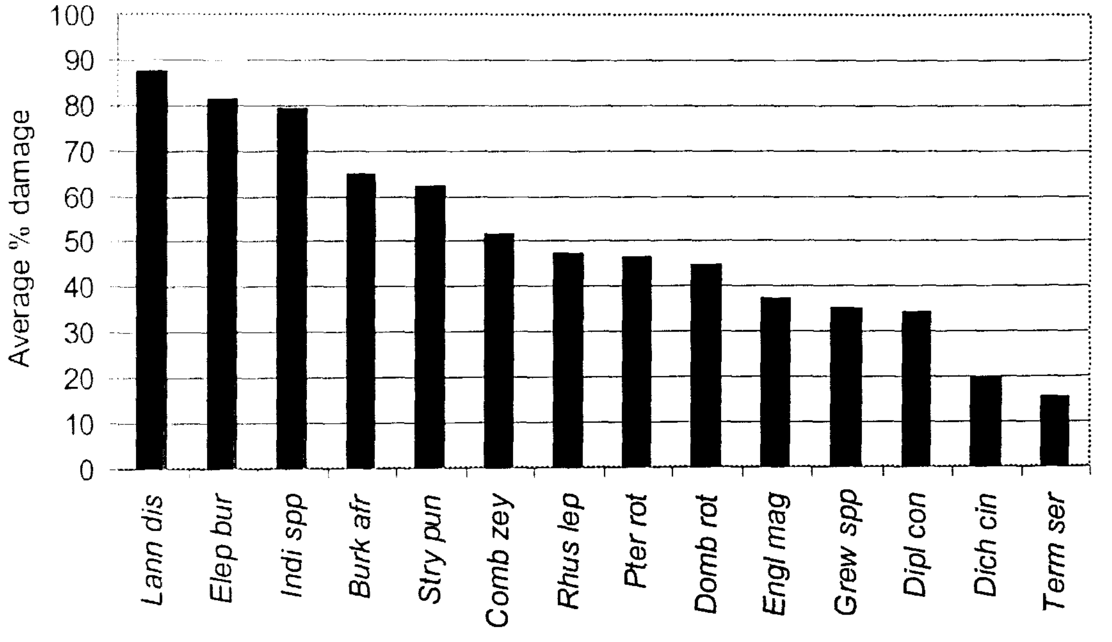


Fig. 3.12. Average percentage damage to 14 woody species used more than 5 times by the elephants (data pooled over sexes) in the dry season.

Species abbreviation	Species name
Burk afr	*Burkea africana*
Comb zey	*Combretum zeyheri*
Dich cin	*Dichrostachys cinerea*
Dipl con	*Diplorhynchus condylocarpon*
Domb rot	*Dombeya rotundifolia*
Elep bur	*Elephantorrhiza burkei*
Engl mag	*Englerophytum magalismontanum*
Grew spp	*Grewia spp.*
Indi spp	*Indigophera spp.*
Lann dis	*Lannea discolor*
Pter rot	*Pterocarpus rotundifolius*
Rhus lep	*Rhus leptodictya*
Stry pun	*Strychnos pungens*
Term ser	*Terminalia sericea*

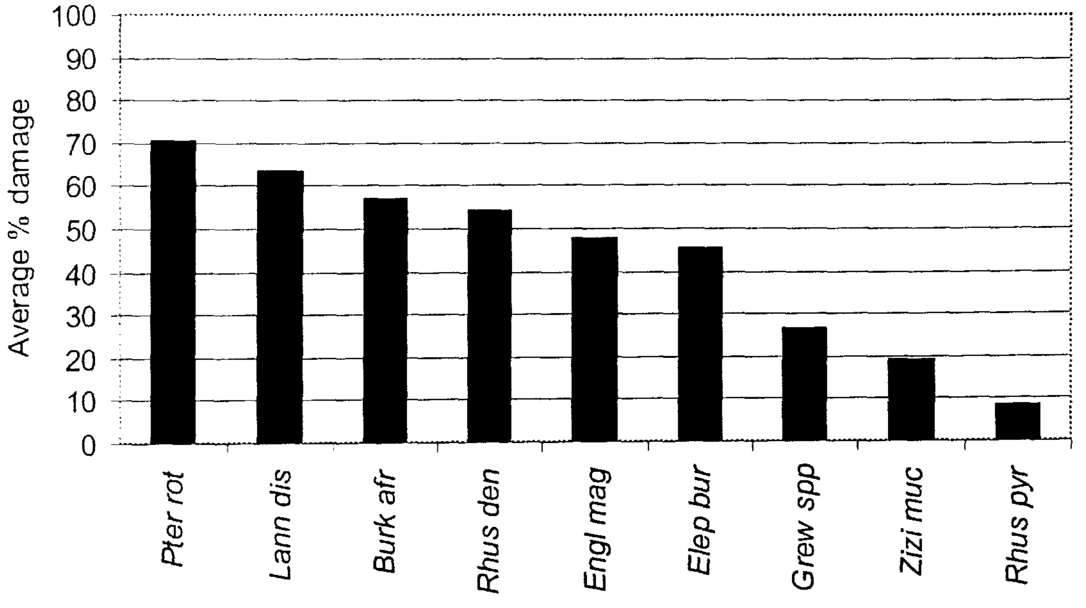


Fig. 3.13. Average percentage damage to nine woody species used more than 5 times by the elephants (data pooled over sexes) in the wet season.

Species abbreviation	Species name
Burk afr	*Burkea africana*
Elep bur	*Elephantorrhiza burkei*
Engl mag	*Englerophytum magalismontanum*
Grew spp	*Grewia spp.*
Lann dis	*Lannea discolor*
Pter rot	*Pterocarpus rotundifolius*
Rhus lep	*Rhus leptodictya*
Rhus pyr	*Rhus pyroides*
Zizi muc	*Ziziphus mucronata*

Pterocarpus rotundifolius, *Rhus dentata*, *Rhus pyroides* and *Ziziphus mucronata*. Only four of these species were utilised to a degree of more than 50% damage to the individual plants (*Burkea africana* 57%, *Lannea discolor* 64%, *Pterocarpus rotundifolius* 70% and *Rhus dentata* 54%).

3.5 Discussion

Although some significant differences were found in the comparisons of feeding habits between bachelor and breeding groups, the majority of the results were not significantly different. The hypothesis that an elephant population can be divided into two functional groups on the basis of their utilisation of the vegetation is therefore rejected. As discussed in the main introduction (chapter1), the elephant population does segregate into social units, but these did not appear to have markedly different patterns of vegetation use. Differences did exist in the elephant's choice of feeding patch where bachelor groups chose feeding patches with a higher species richness and number of woody plants, than breeding groups. Bachelor groups spent more time in valley bottom habitat than breeding groups (chapter 4). Since it is assumed that the soils in valley bottom are more nutrient rich than in other habitats [due to leaching of nutrients from dystrophic hillslope soils (Land type survey staff 1988)] and water availability is more permanent, it may be reasonable to assume that a higher diversity of species would be found in the valley bottom compared with in the other two habitat types. This assumption was supported by the results where a significant difference in species diversity of the three habitats types was found. However, no significant difference in species diversity was found between food plots of bachelor groups and of breeding groups. Both bachelor groups and breeding groups chose feeding patches with a significantly higher species diversity than the surrounding vegetation, when compared with the corresponding control plots. This suggests that bachelor groups and breeding groups feed non-randomly and therefore choose specific foraging paths while moving across the landscape.

Generally, the results of this study are inconsistent with those of Stokke (2000) for research done on sexual segregation in an elephant population in Chobe, because his results showed distinct sex differences in vegetation use and these differences supported the Body Size Hypothesis (BSH). The results of this study (on WPGR) showed few differences between the elephant sexes and therefore do not support the BSH, or any of the other current hypotheses explaining the concept of sexual segregation (see chapter 1 for brief overview).

The deviation in the results on WPGR from the results of the study in Botswana (Stokke 2000) may be explained by the differing elephant population densities between the two study sites, which, for WPGR is 0.2 elephants per km^2 and in Chobe is most likely over 25 elephants per km^2 (Gibson *et al.* 1998). The lower density of elephants on WPGR suggests that there are unlikely to be density-related pressures on resource availability and hence little intersexual competition, so that both bachelor groups and breeding groups can afford to select higher quality vegetation. This type of competition may arise in the future as the population density increases, as found by Clutton-brock *et al.* (1987) in red deer populations in Scotland. According to the BSH, in sexually dimorphic species, females select for higher quality vegetation due to higher nutritional demands because of their higher mass-specific metabolic requirements (Mysterud 2000) in comparison with males, as well as the increased physiological demands in pregnant and lactating females (Main *et al.* 1996). Larger-bodied animals are more tolerant of lower quality diet because gut capacity increases in direct proportion with body size (Parra 1978). Larger-bodied males will therefore be more tolerant of lower quality food but would require proportionately greater quantities thereof (Conradt *et al.* 1999). Males, however, may not necessarily utilise these lower quality resources if they are not competitively displaced from higher quality vegetation by females. This may be the case in the absence of intersexual competition, at low population densities. In such cases, as on WPGR, although bachelor groups preferentially utilised particular species which differed from those selected by breeding groups, both group types selected similar woody species. Bachelor groups also fed on the same plant parts as breeding groups (as assumed from the equivalent proportions of impact types between the sexes) and hence were not forced to utilise species of lower nutritional content, nor to browse at a different level in the canopy in times of limited resources i.e. the dry season. Apart from low population density, this pattern of no sex-difference in component utilisation could also be explained by the fact that data were collected for this study included a wet season in which double the average annual rainfall was recorded, with a consequent abundance of food resources well into the dry season.

Differences in the use of vegetation by elephant group types were found, where bachelor groups felled trees with significantly greater stem diameters than breeding groups in the dry season. One possible explanation for this is that due to their larger body size, bachelor groups are proportionately stronger than breeding groups, and therefore push over larger trees simply because they are able to. Results from this study showed that all of the woody plants felled by bachelor groups belonged to the same species as were felled by breeding groups, although breeding groups felled an additional six woody species which the bachelor groups did not use in this way.

In the dry season, bachelor groups browsed from significantly taller trees (mean = 3.62 m) than breeding groups. Therefore, in this season where foliage becomes limited when deciduous trees loose their leaves, bachelor groups may choose trees with a wider range of feeding levels available to them even if they do not use those additional levels, as shown by this research. Both elephant bachelor groups and breeding groups on WPGR browsed most frequently within a narrow height interval (2.0 - 2.4 m) in both dry and wet seasons. These results were consistent with the findings of Tchamba and Mahamat (1992) but were slightly higher than results obtained from other studies (Guy 1976, Stokke & du Toit 2000).

Bachelor groups were not found to have a significantly greater impact on the woody vegetation than breeding groups, therefore the hypothesis tested in this study pertaining this concept, is rejected. Since the elephant group types do not differ with respect to their damage to woody vegetation, data for bachelor groups and breeding groups were pooled and will be referred to collectively as "damage by elephants". Six species were utilised by the elephants to an average of over 50% damage to the individual plants in the dry season, and four in the wet season. Two of those species are common to both seasons (*Burkea africana* and *Lannea discolor*).

In conclusion, the lack of differences between bachelor groups and breeding groups in most aspects of their impact on the woody vegetation in the dry season may suggest that there is little intersexual competition for resources and hence would suggest that the elephant population on WPGR is currently below carrying capacity. Nonetheless, bachelor groups and breeding groups showed relatively high preference for almost half of the species that were available to both groups, in both seasons. Over all the woody plants utilised by the elephants, the most frequently occurring categories of percentage damage to the plants were less than 10% and 100% (completely destroyed). The significance of this is, however, best investigated on a species-specific basis. Woody species which are highly preferred and are severely damaged (50 to 100% of plant damaged) should be monitored in terms of their ability to regenerate after utilisation by the elephants, as well as their seedling survival rate and their age class distribution throughout the reserve.

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APPENDIX 3.1. List of the 113 woody species recorded in food plots and control plots on Welgevonden Private Game Reserve, their utilisation status by bachelor or breeding groups and the percentage frequency of occurrence of each species in each plot type.

- Unutilised species have no symbol
- Utilised species are indicated as: Used by bachelor groups *
  Used by breeding groups °

Species name	% Frequency of occurrence in: Food plots	Control plots
Acacia burkei °	100 %	0 %
Acacia caffra °	0 %	0 %
Acacia galpinii * °	38 %	62 %
Acacia karroo °	100 %	0 %
Acacia spp	50 %	50 %
Albizia tanganyicensis	100 %	0 %
Aloe marlothii	100 %	0 %
Aloe spp	100 %	0 %
Bauhinia galpinii	100 %	0 %
Bauhinia petersiana	0 %	0 %
Berchemia zeyheri	17 %	83 %
Brachylaena rotundata °	86 %	14 %
Bridelia mollis *	78 %	22 %
Burkea africana * °	52 %	48 %
Canthium gilfillanii	100 %	0 %
Canthium spp	100 %	0 %
Chrysanthemoides monilifera subsp.	100 %	0 %
Clerodendrum glabrum * °	76 %	24 %
Clerodendrum glabrum?	100 %	0 %
Combretum apiculatum	53 %	47 %
Combretum molle * °	58 %	42 %
Combretum nelsonii	0 %	0 %
Combretum zeyheri * °	67 %	33 %
Commiphora africana	100 %	0 %
Croton gratissimus	17 %	83 %
Cussonia spicata *	92 %	8 %
Dichrostachys cinerea *	68 %	32 %
Diospyros lycioides	91 %	9 %
Diplorhynchus condylocarpon * °	54 %	46 %
Dombeya rotundifolia * °	71 %	29 %
Ehretia rigida	48 %	52 %
Elephantorrhiza burkei * °	91 %	9 %
Englerophytum magalismontanum * °	56 %	44 %
Erythrina lysistemon	0 %	0 %
Euclea crispa * °	79 %	21 %
Euclea natalensis °	81 %	19 %

APPENDIX 3.1. Continued

Species name	% Frequency of occurrence in: Food plots	Control plots
Faurea saligna * °	65 %	35 %
Ficus abutifolia	0 %	0 %
Ficus glumosa	50 %	50 %
Ficus thonningii * °	90 %	10 %
Gardenia volkensii °	88 %	12 %
Grewia bicolor		
Grewia flava		
Grewia flavescens		
Grewia monticola		
Grewia occidentalis		
Note: All five *Grewia spp* * ° were pooled for data analyses	81 %	19 %
Gymnosporia buxifolia		
Gymnosporia senegalensis		
Note: Both *Gymnosporia spp* * ° were pooled for data analyses	64 %	36 %
Heteropyxis natalensis	84 %	16 %
Hexalobus monopetalus	34 %	66 %
Indigophera melanadenia		
Indigophera species		
Note: Both *Indigophera spp* * ° were pooled for data analyses	46 %	54 %
• *Jacaranda mimosifolia*	100 %	0 %
Jamesbrittenia burkeana	0 %	100 %
Kigelia africana	0 %	0 %
Kirkia acuminata	0 %	0 %
Lannea discolor * °	70 %	30 %
• *Lantana camara*	100 %	0 %
Leonotis spp	75 %	25 %
Leucosidea sericea	0 %	0 %
Leucospermum spp	100 %	0 %
Lippia spp	68 %	32 %
Mimusops zeyheri *	100 %	0 %
Mundulea sericea	100 %	0 %
Myrothamnus flabellifolia	40 %	60 %
Myrsine africana	100 %	0 %
Ochna natalitia	100 %	0 %
Ochna pulchra *	39 %	61 %
Osyris quadripartita	0 %	0 %
Ozoroa paniculosa * °	56 %	44 %
Pappea capensis * °	95 %	5 %
Pavetta zeyheri	89 %	11 %
Peltophorum africanum *	100 %	0 %
Plumbago zeylanica	100 %	0 %

APPENDIX 3.1. Continued

Species name	% Frequency of occurrence in: Food plots	Control plots
Podocarpus latifolius	0 %	0 %
Protasparagus setaceus	100 %	0 %
Protea caffra	36 %	64 %
• *Psidium guajava*	100 %	0 %
Pseudolachnostylis maprouneifolia * °	43 %	57 %
Pterocarpus rotundifolius * °	94 %	6 %
Rhoicissus dentata	100 %	0 %
Rhoicissus digitata	0 %	100 %
Rhoicissus revoilii * °	68 %	32 %
Rhoicissus tridentata	50 %	50 %
Rhus dentata * °	72 %	28 %
Rhus lancea	46 %	54 %
Rhus leptodictya * °	83 %	17 %
Rhus magalismontana	72 %	28 %
Rhus pyroides * °	79 %	21 %
Rhus spp	100 %	0 %
Rhyncosia nitens	57 %	43 %
Rothmannia capensis	0 %	0 %
Schrebera alata °	67 %	33 %
• *Sclerocarya birrea* *	100 %	0 %
Scolopia zeyheri	94 %	6 %
Solanum giganteum	0 %	0 %
• *Solanum mauritianum*	0 %	0 %
Strychnos pungens * °	65 %	35 %
Strychnos spinosa	28 %	72 %
Syzygium cordatum	100 %	0 %
Tapiphyllum parvifolium	39 %	61 %
Tecomaria capensis	0 %	0 %
Tephrosia longipes		
Tephrosia spp		
Note: Both *Tephrosia spp* were pooled for data analyses	63 %	37 %
Terminalia brachystemma °	70 %	30 %
Terminalia sericea * °	55 %	45 %
Tree 1	20 %	80 %
Vangueria infausta	63 %	37 %
Vitex pooara * °	51 %	49 %
Vitex rehmannii * °	51 %	49 %
Waltheria indica	50 %	50 %
Ximenia caffra	58 %	42 %
Ziziphus mucronata * °	68 %	32 %

Plant species were identified from Coates Palgrave (1997) and Van Wyk & Van Wyk (1997).

CHAPTER 4

SEXUAL SEGREGATION AT THE HABITAT SCALE: AFRICAN ELEPHANTS (*LOXODONTA AFRICANA*), REINTRODUCED TO WATERBERG WOODLAND

Abstract

Differences in habitat utilisation between two elephant group types (bachelor groups and breeding groups) were examined on Welgevonden Private Game Reserve, South Africa. Data were collected over one dry season and one wet season in three habitat types: plateau, hillslope and valley bottom, where 28, 52 and 81 elephant sightings were recorded in each habitat respectively. A significant difference in pattems of habitat utilisation between bull and breeding groups was found in the dry season, when bachelor groups were observed more than expected in valley bottom, and breeding groups more so in hillslope. A possible explanation for this pattern of habitat utilisation is that the breeding groups could be displaced from the preferred valley bottom by disturbance from vehicles because the highest proportion of roads per habitat area are in that habitat. Habitat utilisation by bull and breeding groups within sex, within season, was disproportionate to habitat availability. Both bachelor groups and breeding groups were observed in plateau and hillslope significantly less than expected, but significantly more than expected in valley bottom, in both seasons. Valley bottom has the smallest surface area of the three habitat types, therefore this has important implications for management.

4.1 Introduction

In chapter three, the relative impact of elephant bachelor groups and breeding groups at the feeding patch scale was investigated on Welgevonden Private Game Reserve (WPGR). I now move to the ecological scale and investigate the distribution of these two elephant group types across habitats, in the dry and wet seasons. This was examined to find out whether the elephants display any sexual segregation with regard to their patterns of habitat use between two distinct seasons (dry and wet seasons). The term sexual segregation is used to describe the phenomenon whereby some species segregate into single sex groups outside the breeding season. This is most likely influenced by social, spatial and temporal factors such as the periodicity of mating opportunities, population densities, resource distribution and environmental conditions (Main *et al.*1996). Proposed hypotheses explaining sexual segregation in ungulates are briefly reviewed in chapter one. Elephant social organisation is matriarchal and the population forms bachelor and breeding groups (Douglas-Hamilton 1972; Poole 1996). It is therefore possible that these two group types are not only socially segregated, but also use their environment in different ways.

It is important to consider the scale of habitat available to animals, especially on managed game reserves since boundaries of a fenced-in range often delineate a landscape system, while the annual range of migration of wild herbivores can define a regional system (Senft *et al.* 1987). Results of the research done at the feeding patch scale in chapter three showed no difference in patterns of utilisation of woody vegetation between the elephant bachelor groups and breeding groups.

Two hypotheses which were tested in this chapter are:

1. Bachelor groups and breeding groups do not differ in their relative utilisation of habitat types during each season.
2. Habitat utilisation within each sex is proportional to habitat availability.

Key questions to be addressed for habitat use in the Waterberg, therefore include the following :

1. What are the main habitat types available to the elephants on WPGR?
2. Which habitat types are preferred by bull and breeding groups?
3. Do habitat preferences differ between group types, in each season?

4.2 Study Area

See chapter 2 for details.

4.3 Methods

4.3.1 Data collection

Data were collected from July 1999 to November 2000, including one complete dry season, and wet season. A vegetation survey for WPGR is presently in the analysis stage, hence an official vegetation map defining available habitat types is not yet complete. Therefore, for the purpose of this study, habitat types were defined on the basis of terrain as well as known vegetation composition. There are six, clearly definable, habitat types available to the elephants, namely plateau, hillslope, terrace, valley bottom, riverine and old lands. Both bull and breeding groups were observed and recorded in all of these habitat types, but too few observations were recorded in terrace, riverine, and old lands (the three smaller habitat types) to satisfy the assumptions of the chi-square test. Therefore, for the purposes of data analysis, terrace was pooled with hillslope, riverine with valley bottom, and old lands were divided and pooled with valley bottom or plateau, depending on their location in relation to these other two habitats.
Fig. 4.1 represents these habitat types, and indicates the distribution of the sightings used in the data analysis. As in Stokke and du Toit (In press), the habitat types were distinguished in the field on the basis of terrain, species composition and vegetation structure (Table 4.1).

Most elephant sightings were observed from vehicles on the road, with a small proportion done on foot. I did not make use of fixed routes when locating elephants because the reserve is too large to cover a sufficiently effective proportion of the entire road network everyday. Elephant locations were therefore based largely on radio reports from lodge guides, which were then followed up independently. There were usually more than two game drive vehicles out each morning or evening. Lodges are evenly distributed throughout the reserve and the game drives always originated from different lodges. The focus of the game drives was to locate any members of the "big five" or other species, and did not concentrate on finding the elephants, thus were more likely to encounter them randomly. Therefore, although a certain bias may exist, it was assumed that this bias was minimal and that the method provided equal chances that any elephant(s) would be sighted in any one habitat. If no elephant movements had been reported for the day, roads were driven either where elephants were last seen, in search of fresh tracks, or at random in order to search for other animals possibly unseen by game drives.

Once elephant(s) were sighted, date, time, group type (bull group or breeding group), total number of individuals observed, activity, habitat type and location, both by description and GPS (Global Positioning System) were noted. Group types were categorised as either bachelor groups if a family unit was present, even if there were bachelor groups associated with it. A total of 146 elephant sightings were recorded during the course of this study.

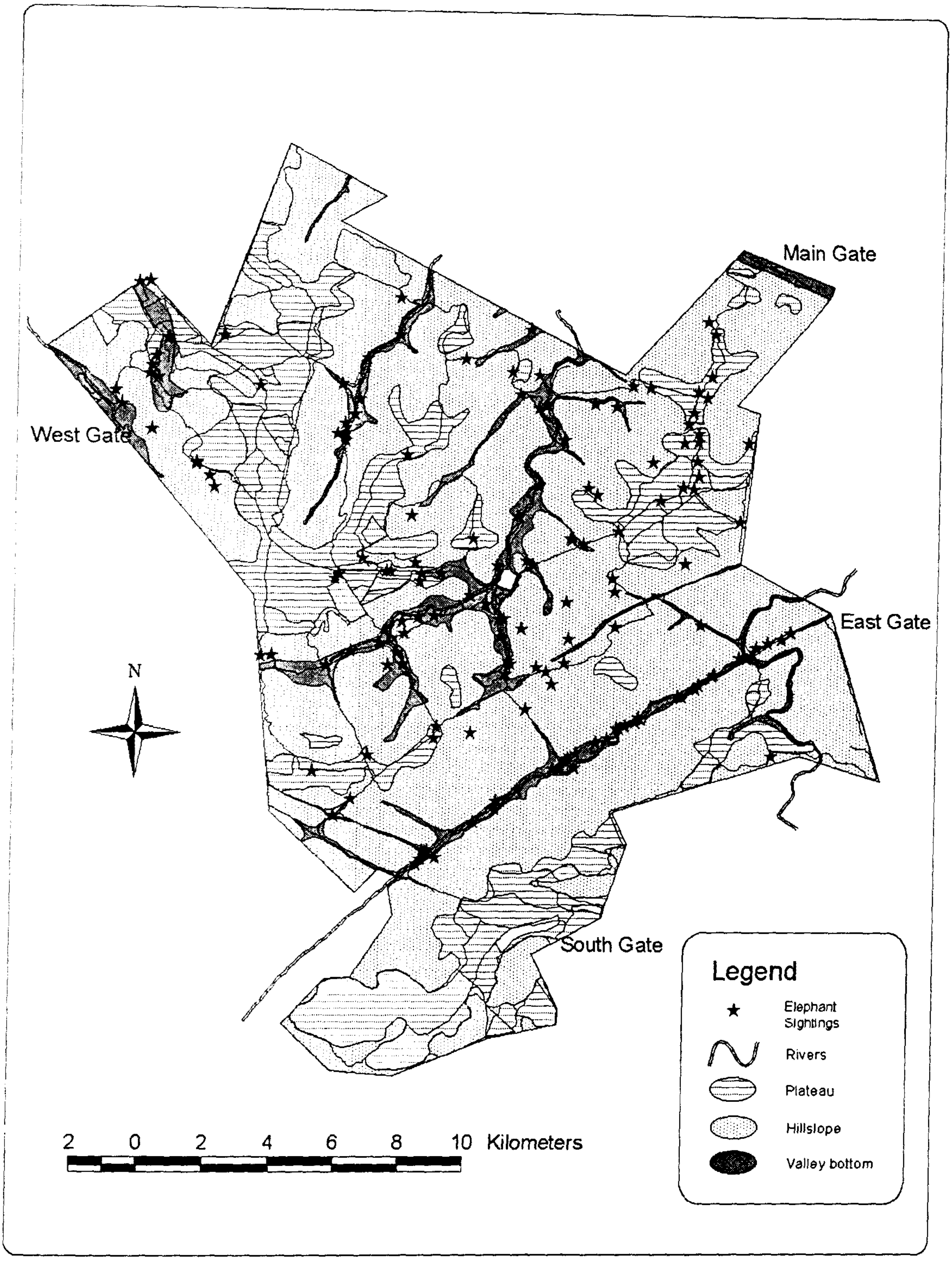

Fig. 4.1. Map of Welgevonden Private Game Reserve showing habitat types, rivers and the distribution of the 161 elephant sightings.

Table 4.1. Characteristics used to define each of the three main habitat types

Habitat type	Landscape	Vegetation structure	Distinguishing species
Plateau	Higher lying areas, relatively flat, moderate to few rocks, deep soils	Grassland or open woodland	*Lannea discolor, Terminalia sericea, Combretum zeyheri*
Hillslope	Moderate to steep slopes, very rocky, shallow soils	Small trees and shrubs, high percentage of unpalatable grasses	*Englerophytum magalismontanum, Ochna pulcra, Protea caffra, Diplorhynchus condylocarpon*
Valley bottom	Lower than neighbouring areas, temporary or permanent water source, deep soils	High density of woody species, tall trees, combination of woody species and riverine vegetation (reeds etc.) and/or tall grass	*Faurea saligna, Syzygium cordatum, Ficus thonningii*

Table 4.2. Habitat areas, road distances in each habitat and road distance per habitat

Habitat type	Area of each habitat (km^2)	Length of road in each habitat (km)	Roads per habitat (km/ km^2)
Plateau	72.5	147.2	2.03
Hillslope	238.1	112.6	0.47
Valley Bottom	23.7	80.8	3.41
SUM	334.3	340.6	

4.3.2 Data analysis

Although 146 elephant sightings were recorded, nine were excluded from the data analysis because they did not qualify as independent sightings as only one sighting per individual or herd, per day was included in data analyses. This left a total of 137 independent sightings which were used for analysis. In addition, the habitat location data from 24 "inferred group type" food plots was incorporated into the sighting data set, making a total of 161 elephant sightings. These food plots were recorded under an "inferred group type" because no elephant groups were actually sighted, but feeding activity was fresh and obvious, so I was 100% sure that the elephants were there. "Inferred group type" food plots were only made if the group type could be positively identified from evidence such as foot print size and number and/or dung bolus size [calves and juveniles in breeding groups would have small dung boli whereas bachelor groups would have very large dung boli (Jachmann & Bell 1984)]. Of the 161 total sightings, 76 (47% of total sightings) were of bachelor groups and 85 (53% of total sightings) were of breeding groups. Habitat types were pooled from six to three distinct types (plateau, hillslope and valley bottom) as explained in section 4.3.1, so that sample sizes were sufficiently large to satisfy the assumptions for the chi-square test (Roscoe & Byars 1971).

A chi-square test for independence was used to test the null hypothesis that bachelor groups and breeding groups exhibit no significant difference in their utilisation of habitats during dry and wet seasons. Another chi-square test for independence was used to determine if there was a significant difference in the habitat utilisation by each elephant group type separately, between dry and wet seasons.

Habitat availability was measured using both habitat area and road distance proportions in each habitat (Table 4.2). Habitat utilisation and availability was first investigated using the chi-square test for independence, and where significant results were obtained, the Bonferroni multiple comparison procedure (Neu *et al.* 1974) was used to find significant differences. Most elephant sightings were from a road. Where habitat availability was based on habitat area (the proportion of the total reserve area contributed by each habitat), the null hypothesis was that elephants use their habitats in proportion to habitat availability. The assumption was that the roads cover the habitats more or less evenly. The chi-square test for independence was used to determine whether the proportional use of habitats (based on sighting frequencies) by bachelor groups and breeding groups (separately), was significantly different from the proportional availability of the habitats (based on habitat areas), during dry and wet seasons (separately). To eliminate possible bias created by an uneven distribution of roads across habitats, another chi-square test for independence was run using the proportion of road in each habitat instead of the habitat area. New expected frequencies were then calculated for these data, by multiplying the total number of sightings for either bachelor groups or breeding groups by the proportion of road distance contributed by each habitat. Habitat areas and proportions of road in each habitat are shown in Table 4.2.

Where chi-square tests had significant results, Bonferroni confidence intervals (Neu *et al.*1974; Byers *et al.* 1984) were used to determine whether certain habitat types were utilised significantly differently to expected. The Bonferroni test is a good compromise between two other multiple comparison procedures, the Fisher and Scheffé tests (Howell 1995). Bonferroni confidence intervals were calculated for each of the three habitat types, for each elephant group type, for each season, using the following formula from Neu *et al.* (1974):

$p_i - z_{[1-(\alpha/2k)]} \sqrt{(p_i)(1-p_i)/n} \leq p_i \leq p_i + z_{[1-(\alpha/2k)]} \sqrt{(p_i)(1-p_i)/n}$

where: p_i is the observed proportion of usage (proportion of elephant sightings)

As in Neu *et al.* (1974), the appropriate tabulated probability for the *z* statistic is calculated using the following formula: $z_{[1-(\alpha/2k)]}$

where: α is the level of significance and k is the number of habitat types tested

Individual confidence intervals were calculated for all the habitat utilisation-availability data, using α =0.05 (95 % significance level). The corresponding *z* statistic was obtained from the tables in Rosner (1995).

4.4 Results

4.4.1 Elephant habitats

There are three main habitats types (plateau, hillslope and valley bottom) available to the elephants on WPGR. Twenty eight of the 161 sightings (17%) were recorded in plateau, 52 (32% of sightings) in hillslope and 81 (50% of sightings) in valley bottom.

4.4.2 Seasonal utilisation of habitats by bachelor groups and breeding groups

Bachelor groups and breeding groups differed significantly in their relative utilisation of habitats in the dry season (Fig. 4.2). Bachelor groups were observed in valley bottom more than expected, and in plateau and hillslope less than expected. Breeding groups, however, were observed in hillslope and plateau more than expected and in the valley bottom less than expected. Where expected frequencies were calculated from the observed frequencies using chi-square contingency tables.

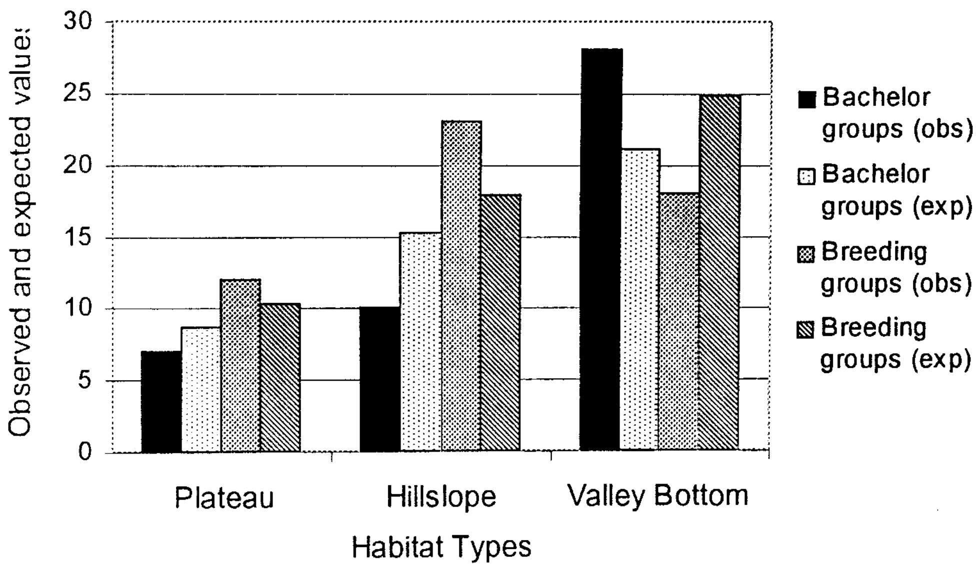

Fig. 4.2. Observed (obs) and expected (exp) values of sightings for habitat utilisation by elephant bachelor groups and breeding groups were significantly different in the dry season ($\chi^2 = 8.01$, d.f. = 2, $P < 0.05$).

No significance difference in habitat utilisation was found between bachelor groups and breeding groups in the wet season. No seasonal shift in patterns of habitat use by bachelor groups was found between dry and wet seasons. The same results were found for breeding groups between dry and wet seasons.

4.4.3 Seasonal habitat utilisation by bachelor groups and breeding groups in relation to habitat availability

Where availability was based on habitat area, bachelor groups utilised significantly different habitats than expected in the dry season (χ^2 = 208.9, d.f. = 2, $P < 0.05$). Results from wet season data for bachelor groups also showed a difference in pattern of habitat utilisation (χ^2 = 139.2, d.f. = 2, $P < 0.05$). Bachelor groups used the valley bottom habitat far more than expected, and the other two habitats were utilised less than expected, in both seasons (Table 4.3). Breeding groups also showed a significant difference in their utilisation of habitats in comparison with availability in both the dry season (χ^2 = 59.8, d.f. = 2, $P < 0.05$) and the wet season (χ^2 = 89.5, d.f. = 2, $P < 0.05$). In the dry season, plateau was observed to be used slightly more than expected, hillslope considerably less than expected and valley bottom more than expected. Utilisation of habitats in the wet season followed the same pattern (Table 4.3).

Where habitat availability was based on proportional contributions of road distances in each habitat (Table 4.3), utilisation of habitats by bachelor groups was significantly different than expected in both the dry season (χ^2 = 37.7, d.f. = 2, $P < 0.05$) and the case in the wet season (χ^2 = 24.8, d.f. = 2, $P < 0.05$). In both seasons plateau and hillslope were utilised less than expected, while valley bottom was utilised more than expected. Breeding groups also displayed a significant difference in habitat utilisation in the dry (χ^2 = 9.26, d.f. = 2, $P < 0.05$) and wet seasons (χ^2 = 16.5, d.f. = 2, $P < 0.05$). Breeding groups were observed in plateau less than expected, but in hillslope and valley bottom more than expected, in both seasons.

These results were tested for significance using Bonferroni confidence intervals which were calculated from observed proportions of usage (proportions of elephant sightings). Expected proportions of usage for habitat availability based on habitat area (Table 4.4) and proportional contribution of roads to each habitat (Table 4.5) were evaluated against these intervals. See Appendix 4.1 for calculation of expected proportions of usage (p_{io}). Byers *et al.* (1984) explain how the results of this test are evaluated (Appendix 4.2). The results of this Bonferroni multiple comparison procedure (Table 4.4; 4.5) show that the conclusions made by comparing differences between observed and expected frequencies in Fig. 4.2 were significant. Elephant

Table 4.3. Observed (Obs) and expected (Exp) values inputted into the chi-square test for independence for habitat utilisation by bull and breeding groups (separately) in comparison with habitat availability in each season, where expected values are calculated from habitat area (HA) as well as the proportional contribution of road distances to each habitat (RP)

	Plateau			Hillslope			Valley Bottom		
	Obs	Exp HA	Exp RP	Obs	Exp HA	Exp RP	Obs	Exp HA	Exp RP
Bachelor groups: dry season	7	9.76	19.5	10	32.1	14.9	28	3.19	10.7
Bachelor groups: wet season	5	6.72	13.4	7	22.1	10.3	19	2.19	7.35
Breeding groups: dry season	12	11.5	22.9	23	37.8	17.5	18	3.76	12.6
Breeding groups: wet season	4	6.94	13.8	12	22.8	10.6	16	2.27	7.59

Table 4.4. Observed (p_i) and expected proportions of usage (p_{io}) and Bonferroni confidence intervals for bachelor groups and breeding groups in dry and wet seasons are shown, where habitat availability (p_{io}) is based on habitat area.

Group type, season and habitat type		Proportion of elephant sightings (p_i)	Proportion of reserve area (p_{io})	Bonferroni confidence intervals around sighting proportions	Significance of habitat use
Bachelor	Pl	0.156	0.217	$0.026 \leq p_1 \leq 0.285$	0
groups:	Hs	0.222	0.712	$0.074 \leq p_2 \leq 0.370$	-
dry	VB	0.622	0.071	$0.450 \leq p_3 \leq 0.795$	+
Bachelor	Pl	0.161	0.217	$0.003 \leq p_1 \leq 0.319$	0
groups:	Hs	0.226	0.712	$0.046 \leq p_2 \leq 0.405$	-
wet	VB	0.613	0.071	$0.404 \leq p_3 \leq 0.822$	+
Breeding	Pl	0.226	0.217	$0.089 \leq p_1 \leq 0.364$	0
groups	Hs	0.434	0.712	$0.271 \leq p_2 \leq 0.597$	-
dry	VB	0.340	0.071	$0.184 \leq p_3 \leq 0.495$	+
Breeding	Pl	0.125	0.217	$0.015 \leq p_1 \leq 0.265$	0
groups	Hs	0.375	0.712	$0.171 \leq p_2 \leq 0.580$	-
wet	VB	0.500	0.071	$0.289 \leq p_3 \leq 0.711$	+

NOTE: Abbreviations for habitat types are as follows: Pl = Plateau; Hs = Hillslope; VB = Valley Bottom. Symbols for significance of habitat use indicate whether the use is significantly more (+) or less (-), or not significantly different (0) than expected.

Table 4.5. Observed (p_i) and expected proportions of usage (p_{io}) and Bonferroni confidence intervals for bachelor groups and breeding groups in dry and wet seasons are shown, where habitat availability (p_{io}) is based on proportional contributions of road distances in each habitat.

Group type, season and habitat type		Proportion of elephant sightings (p_i)	Proportion of reserve area (p_{io})	Bonferroni confidence intervals around sighting proportions	Significance of habitat use
Bachelor	Pl	0.156	0.432	$0.026 \leq p_1 \leq 0.285$	-
groups:	Hs	0.222	0.331	$0.074 \leq p_2 \leq 0.370$	0
dry	VB	0.622	0.237	$0.450 \leq p_3 \leq 0.795$	+
Bachelor	Pl	0.161	0.432	$0.003 \leq p_1 \leq 0.319$	-
groups:	Hs	0.226	0.331	$0.046 \leq p_2 \leq 0.405$	0
wet	VB	0.613	0.237	$0.404 \leq p_3 \leq 0.822$	+
Breeding	Pl	0.226	0.432	$0.089 \leq p_1 \leq 0.364$	-
groups	Hs	0.434	0.331	$0.271 \leq p_2 \leq 0.597$	0
dry	VB	0.340	0.237	$0.184 \leq p_3 \leq 0.495$	0
Breeding	Pl	0.125	0.432	$0.015 \leq p_1 \leq 0.265$	-
groups	Hs	0.375	0.331	$0.171 \leq p_2 \leq 0.580$	0
wet	VB	0.500	0.237	$0.289 \leq p_3 \leq 0.711$	+

NOTE: Abbreviations for habitat types are as follows: Pl = Plateau; Hs = Hillslope; VB = Valley Bottom. Symbols for significance of habitat use indicate whether the use is significantly more (+) or less (-), or not significantly different (0) than expected.

bachelor groups and breeding groups display patterns of habitat utilisation which are disproportionate to habitat availability in both seasons, where both plateau and hillslope are utilised significantly less than expected, but valley bottom more than expected.

These two sets of results for elephant utilisation of habitats in comparison with availability (based on a) habitat area and b) proportional contribution of roads to each habitat) are similar in terms of which habitats were used significantly (or not) compared with expected use thereof. Therefore I conclude that the roads created no bias in the collection of data. These results also suggest that the bachelor groups and breeding groups utilise their habitats disproportionately to the habitat availability where the larger plateau and hillslope are generally used less than expected, whereas the smaller valley bottom was used more than expected. This pattern of habitat utilisation was found in both dry and wet seasons.

4.5 Discussion

4.5.1 Habitat utilisation by elephant bachelor and breeding groups

Three main habitat types (plateau, hillslope and valley bottom) are available to the elephants on WPGR. In comparison with availability, elephant bachelor groups and breeding groups (separately) were observed to utilise the larger habitats (plateau and hillslope) significantly less than expected, but valley bottom (with the smallest surface area) significantly more so. This was true for both dry and wet seasons. Due to leaching of nutrients from dystrophic hillslope soils (Land type survey staff 1988) into valley bottom, it follows that more nutritious plant species would be found in the valley bottom. This may explain why, in conjunction with the water availability in that habitat, both elephant group types utilise valley bottom habitat proportionately more than expected in comparison with habitat availability. When the sexes were compared within seasons, elephant bull and breeding groups displayed a difference in pattern of habitat utilisation, but only in the dry season. From these results, it appears that bachelor groups used the valley bottom more, and breeding groups used hillslopes more. This does not necessarily mean that they prefer these habitats but only that they were observed there more than expected.

One possible explanation for the dry season pattern of habitat use by bachelor groups and breeding groups is human disturbance avoidance by breeding groups. Breeding groups were relatively more nervous than bachelor groups, especially when they had young calves with them, and readily moved off a road and into thicker vegetation when approached by a vehicle(s) (pers. obs.). The highest proportion of roads per unit area of habitat occurs in valley bottom, and bachelor groups did not appear to be distressed by vehicles (pers. obs.). Therefore valley bottoms may provide bachelor groups with access to more nutritious vegetation as well as to permanent water in rivers. Dry season home ranges cover only about 10 % of the area of wet season ranges, and are based on the availability of permanent water sources (Owen-Smith 1988). Breeding groups, however may be displaying a trade-off between nutritious vegetation or water availability in the preferred valley bottoms, for the cover provided by the denser hillslope vegetation. The amount of cover provided by plants can influence the distribution and abundance of mammals, usually by provision of protection from predation (Batzli 1994). Males and females may select habitats according to different criteria (Main & Coblentz 1990). In particular, females may seek habitats with more cover that are safer for their offspring, while males may select habitats on the basis of foraging opportunities (Main & Coblentz 1990). This hypothesis is known as the reproductive-strategy hypothesis (Main *et al.* 1996) or the predation risk hypothesis (Ruckstuhl & Neuhaus 2000). It is based on energetics and the relative differences in reproductive strategies employed by males and females of polygynous ungulates. Verified observations of predation on elephants are rare in the scientific literature (Ruggiero 1991), although very young calves are vulnerable to attacks by predators such as hyenas and lion (Sikes 1971; Poché 1974; Apps 1996). Animals respond to human disturbance in the same way they would to a risk of predation; they avoid areas of high risk either completely or by using them for limited periods of time (Gill *et al.* 1996). Studies have found that human disturbance can significantly alter animal behaviour (Poché 1974; Dorrance *et al.* 1975; Schultz & Bailey 1978; Pedevillano & Wright 1987; Del Thompson 1989). In addition to their reaction to vehicles, elephant breeding groups reacted with alarm and sometimes retreated to denser vegetation in response to helicopters flying nearby, or over them (pers. obs.). The same response was noted by Côté (1996) in mountain goats. Adult male elephants are not vulnerable to predators, and therefore would not feel threatened by human presence. Sukumar and Gadgil (1988) found that bull elephants take more risks, in terms of human threat, while foraging than breeding groups do, this is because bachelor groups do not have young to protect. The pattern of habitat utilisation shown in the results of my research was therefore not considered to be as a result of predation, but rather human disturbance, which can be considered equivalent to other predator disturbances. I therefore assume that the bachelor groups may use the valley bottom vegetation without concern of disturbance from vehicles but the breeding groups are displaced from preferred valley bottom by disturbance from vehicles, and hence seek the safety of hillslope vegetation, only utilising valley bottom resources in the absence of the vehicles, i.e. at night (pers. obs.). Consequently, the breeding groups may be displaying a variation on the predator avoidance hypothesis (Geist 1974; du Toit 1995; Ruckstuhl & Neuhaus 2000). A more detailed study is required to test this hypothesis.

The difference in habitat use by bachelor groups and breeding groups is possibly only found in the dry season, because there is little cover available in the valley bottom at that time of the year due to the abundance of deciduous trees. In the wet season, however, when a similarity in habitat utilisation by bull and breeding groups was observed, the vegetation would be expected to provide more cover in the form of leaf flush initiated by the rains and so the breeding groups may not find it necessary to retreat to the safety of the hillslopes as much.

This study into the habitat utilisation by elephant bachelor groups and breeding groups on WPGR was conducted on a short temporal scale (relative to the life-span of an elephant). The results should therefore not be extrapolated over long-term situations. The pattern of habitat utilisation between the sexes shown here is likely to change over time as the breeding groups become more habituated to vehicles and also as additional external factors influence them such as the availability of water between seasons. The seasonal cycles over which data were collected were unusually wet, where more than double the annual rainfall was recorded, and therefore availability of water in valley bottoms was not considered as a factor of habitat utilisation during this study. Water availability could, however, play a significant role in habitat utilisation by elephants in future, more distinct, dry and wet seasons.

4.5.2 Management implications

Valley bottom has the smallest surface area compared with the two other habitats. Since the elephants appear to prefer this habitat, it can be considered that they are utilising it habitat disproportionately to its availability. Possible consequences of this could be the accelerated modification of the structure of the woody vegetation in this habitat. Since the highest proportion of roads is in the valley bottom, such impacts by elephants will be more visible to landowners and tourists. Elephants are important to tourism, but the aesthetic value of the vegetation to tourism must also be considered. Elephant impact on woodland is a concern (Chapter 3, Chapter 5) and needs to be addressed in reserve management.

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APPENDIX 4.1. Calculation of expected proportion of usage (p_{io}): the proportion of habitat area (Table 4.4) / road distance (Table 4.5)

From Table 4.4: e.g. Plateau

- Area of plateau habitat: 72.47 km^2
- Total reserve area: 334.26 km^2
- Therefore proportion of plateau to reserve area: 72.47/334.26=0.2168
- Observed number of sightings in plateau: 7
- Total number of sightings in all habitats: 45
- Therefore expected usage: 0.2168*45=9.756
- And expected proportion of usage (p_{io}) (Proportion of reserve area): 9.756/45=0.2168
- Observed proportion of usage (p_i) (Proportion of elephant sightings): 7/45=0.15556
- Lower Bonferroni Confidence Interval = $p_i - z_{[1-(\alpha/2k)]} \sqrt{(p_i)(1-p_i)/n}$
- Upper Bonferroni Confidence Interval = $p_i + z_{[1-(\alpha/2k)]} \sqrt{(p_i)(1-p_i)/n}$

APPENDIX 4.2. Interpretation of results from Bonferroni Confidence Intervals (Byers *et al.* 1984)

The expected proportion of usage (proportion of reserve area) (p_{io}) is compared with the confidence intervals (which were calculated using the observed proportion of usage (the proportion of elephant sightings) (p_i)). If this figure (p_{io}) lies within the interval, we can conclude that the expected and observed utilisations are not significantly different (0). Conversely, if p_{io} lies outside of the interval, the expected and observed utilisation are said to be significantly different, whether the habitat is used significantly more (+), or less (-) than expected.

CHAPTER 5

FINAL DISCUSSION AND MANAGEMENT IMPLICATIONS

Abstract

Results of woody vegetation and habitat utilisation by the elephants on Welgevonden Private Game Reserve are discussed in terms of their implications to management. Over all, there was a distinct lack of differences in vegetation use between elephant bachelor and breeding groups on WPGR (chapter 3). This suggests that there is unlikely to be inter-sexual competition for resources, which suggests that the elephant population on WPGR is currently below carrying capacity. Particular woody species were preferred by bachelor groups and by breeding groups. Monitoring of those species is suggested. With reference to habitat utilisation (chapter 4), both group types selected valley bottom disproportionately to that habitat's availability, in both dry and wet seasons. This habitat has the smallest area of the three habitat types, and therefore may be proportionately more impacted. Comparisons between sexes, within seasons revealed that bachelor groups and breeding groups displayed different patterns of habitat use in the dry season. Bachelor groups were observed in valley bottom more than expected, and breeding groups more so in hillslope. An explanation of this is that breeding herds could be displaced from the preferred valley bottom by human disturbance in the form of vehicles in that habitat, in search of cover in the hillslope vegetation.

5.1 Elephant – vegetation interactions on WPGR

In many ways, man has a proportionately greater impact on the environment than any individual animal. One of the most important influences, as a result of human population growth, is a reduction in space available for conservation purposes, which results in populations of large-bodied animals such as elephants becoming concentrated on small pockets of land (Novellie *et al.* 1991; Cumming *et al.* 1997). During the time of farming activities in the region, vegetation on WPGR was protected from feeding habits by large herbivores, with the result that once the area was proclaimed as a reserve (1993) and elephants were introduced (1994), changes to the structure of the vegetation became noticeable. Changes such as felled or uprooted trees (by elephants), although aesthetically unpleasing, are not necessarily detrimental to the vegetation, indeed some degree of vegetation disturbance is probably beneficial to habitat diversity as well as its productivity (Owen-Smith 1988). Such changes are inevitable where elephants are concerned, but limits surrounding the degree of change should be decided on. If the decision is made that elephants are the main priority in terms of tourist attractions, then some change in vegetative structure must be accepted. However, if the aesthetic appeal of the vegetation is also considered to be important, then damage to that vegetation by elephants should be restricted. In order to limit changes to vegetation where elephants are involved, objectives must be defined which set levels of permissible change, and determine options for management once those levels are reached. When managing increasing megaherbivore populations (with special reference to elephants), reserve managers are generally most concerned with the following points with respect to changes to vegetation (Owen-Smith 1988):

(i) radical modification of certain habitat types (and hence, possibly changes in behaviour of, or loss of, species dependant on them);
(ii) elimination of certain sensitive plant species;
(iii) reduced vegetation cover causing accelerated soil erosion and hence a decline in the overall productivity of the system;
(iv) depression of the resource base for megaherbivore populations themselves;
(v) loss of aesthetic features of the landscape such as large trees or grasslands.

Tree destruction is often attributed to elephant activity. Wind, lightning and fire also have a profound effect (Spinage & Guiness 1971; Eckhardt *et al.* 2000). Both wind and lightning are prevalent on WPGR, where August winds are known to break branches and fell trees, and lightning from dry storms causes many fires towards the end of the dry season. Besides elephants, other animals also have a certain impact on the vegetation. Giraffe (*Giraffa camelopardalis*) have been known to break branches from trees and kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasii*) and rhino (*Ceratotherium simum*) have been observed scratching their horns on young trees, thereby causing damage to the bark, sometimes extensively (pers. obs.). Such utilisation of woody species by elephants and other animals can damage trees and allow fires to burn exposed areas of wood (Yeaton 1988). Therefore, damage to woody plant species is often a combination of factors including elephant impact, feeding activities of other browsers and insects, and fire. Smaller herbivores may also have an impact on the survival of the seedlings of woody species most highly utilised by larger browsers. Elephants themselves may also influence woody species survival by searching for, and utilising seedlings thereof, as found by Dublin (1984) in the Serengeti-Mara ecosystem .

Although noticeable at times, damage to woody vegetation by the elephants on WPGR is not presently considered to be destructive on a large scale. Results from this research (at the present elephant density) show that the elephants (bachelor groups and breeding groups together) utilised only 7% of the 7 579 individual woody plants recorded as available to them. All height classes are utilised, the elephants do not appear to be selecting for tall trees. This is important since it suggests that over all species, the elephants are using what is available. If the elephants utilise woody species which have an abundance of seedlings (which fall into the smaller height classes), this may suggest that these species regenerate more readily than those species which have relatively few seedlings, and therefore that they would have a better chance of survival. The percentage of all feeding activities comprised of felling, uprooting, barkstripping and branch breaking by both bachelor groups and breeding groups in both seasons was consistently lowest for tree felling and highest for branch breaking (7% felling; 9% uprooting; 30% barkstripping and 54% branch breaking). Average percentage plants utilised to unutilised in each food plot was 26% in the dry season and 18% in the wet season. This means that bachelor groups and breeding groups are utilising more woody plants per food plot in the dry season than in the wet season, and they are using less than a third of the resources available to them within each of the patches at which they choose to feed, in either of the seasons.

The elephant population density on WPGR is presently at 0.21 elephants/km^2. When elephant populations are at densities approaching 0.5 elephants/km^2 for periods of ten years and more, it has been observed that savanna woodlands begin to convert to shrublands or grasslands (Fowler 1973; Cumming *et al.* 1997). For the elephant population to equal this density on WPGR, there would have to be 167 elephants on the present property size. Selective use of resources by the elephants can, however, cause localised woodland damage and loss of certain tree species at elephant densities of less than 0.2 elephant/km^2 in a wide range of woodlands (Cumming *et al.* 1997). Therefore it is important that elephant impact on woody species which are utilised by both bachelor groups and breeding groups, in both dry and wet seasons, be monitored.

5.2 Management suggestions

1. Particular woody species were preferred by bachelor groups and by breeding groups. These species should be carefully monitored in the future for changes in abundance as well as height-age class distribution on WPGR. Recovery mechanisms of these species in response to impact by elephants should also be monitored.

2. Exclusion plots may be erected in the different habitat types which, if regularly monitored, would provide valuable information in the long term. Such exclusion plots would have to be surrounded by electric fencing (powered by solar panels), and the number of electrified strands of wire can be manipulated depending on which animals are intended to be excluded from the area. This will provide baseline data on the level and type of impact that elephants are having on woody species where, for example, a) all large browsers (including elephant and giraffe) are excluded, and b) where smaller ungulates are excluded. The results can then be compared to provide information on which factors most influence the recruitment of seedlings of species preferred by the elephants.

3. Tree species of aesthetic importance to landowners may be identified, tagged and monitored for elephant damage over the long term. In conjunction with data from these trees, other factors such as edaphic and climatic effects which would influence growth rates apart from the influence that elephants may have, should be also recorded.

4. Since few significant differences were found in the utilisation of vegetation between bachelor and breeding groups, it may be suggested that little intersexual competition exists and that the population may currently be below carrying capacity, and therefore adjusting the sex ratio is no longer recommended as a management option. Vegetation utilisation can therefore be monitored collectively for both elephant sexes while elephant densities are low and summer rainfall figures are above average. The results obtained and conclusions made from this study will undoubtedly need to be re-assessed after the removal of the fence (E. Leibnitz, pers. comm.) which currently separates WPGR and Marakele National Park.

5.3 Directions for future elephant research on WPGR

Our tendency as scientists is to generalise about systems from the limited scope of our own research, this is necessary so that we can use these results to make informed management recommendations for the near future (Dublin 1984). This provides a starting block in finding the pieces for the "bigger picture", and as more research is conducted over a larger temporal scale, those pieces begin to fall into place. It is the role of the scientist to provide the technical information and set out the management alternatives. It is then the role of the manager to choose the most appropriate management policy for the park (Bell 1983). The state of a park in 10 or 20 year's time depends upon the events of today. In order to understand tomorrow's ecological and management problems we must study those that exist today (Barnes 1983). Woodland – herbivore interactions are both complex and dynamic. Due to the life expectancy of African elephants, the impact they can have over long periods of time is cumulative. Therefore, understanding the ecology of systems which include elephants is a long term project of continuous data collection and interpretation. The following points are suggestions for future research on WPGR which are considered important to supplement the research done in this study.

- Monitor the recovery of woody species impacted by the elephants in terms of their resprouting capabilities in combination with various degrees of damage, and whether or not the elephants (or other animals) ustilise the coppice.
- Analyse chemical composition (nutrient content, tannin content) of woody species preferred by the elephants on WPGR (see chapter 3). This should be done on a seasonal basis to highlight any changes in species utilisation by the elephants in conjunction with changes in plant chemistry. This will provide information which may be important in predicting which species may be targeted by the elephants at a particular time of year.
- Investigate influence of fire and insects on survival of woody species after impact by elephants e.g. barkstripping which exposes underlying tissues vulnerable to these factors.

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SUMMARY

Overpopulation of elephants in confined conservation areas is a concern in South Africa. As elephant populations increase, so too does their impact on the vegetation. In May 1994 a successful relocation of 50 elephants from the Kruger National Park (KNP) to Welgevonden Private Game Reserve (WPGR) in the Northern Province, South Africa took place. Impact by the elephants on the vegetation of this reserve has since become a concern. The aims of this study were to quantify this impact by determining whether differences in patterns of vegetation or habitat use existed between bachelor and breeding groups. Data were collected at two ecological scales: the first at the local feeding patch scale and the second at the environmental habitat scale. Data were analysed by comparing resource use between sexes within seasons, and within sexes between seasons. Feeding data collected from 202 food plots were used to test two hypotheses concerning feeding patch utilisation by elephant bull and breeding groups on WPGR. The first hypothesis stated that an elephant population can be divided into two functional groups on the basis of their relative utilisation of the vegetation: a) bachelor groups and b) breeding groups. The second hypothesis tested stated that bachelor groups have a greater impact on the woody vegetation than breeding groups. Both of these hypotheses were rejected for this research in the Waterberg. Results show that elephant bachelor and breeding groups on WPGR exhibit few differences in resource use at the feeding patch level in the dry season. In this season, when resources undoubtedly become limited, no difference in feeding patch use between bachelor groups and breeding groups suggests a lack of inter-sexual competition and hence that the population is currently below carrying capacity. The results also showed that bachelor groups and breeding groups do not differ in the intensity or frequency of impact they have on the woody vegetation. Nevertheless, the continued monitoring of woody species preferred by the group types is imperative. Three habitat types are available to the elephants: plateau, hillslope and valley bottom. Both bachelor and breeding groups preferred valley bottom disproportionately more than habitat availability, in both seasons. Plateau and hillslope were utilised disproportionately less than availability. Habitat availability was calculated

using two methods: using habitat area and using the proportional contribution of roads to habitat area. Preference of valley bottom by both elephant sexes is important for management purposes since this habitat has the smallest surface area in comparison with the other two habitats, and therefore structural modification could be more visible in that habitat. Damage to vegetation will also be more obvious to both landowners and tourists since the highest proportion of roads per habitat area are in the valley bottom. When sexes were compared within seasons, in the dry season, bachelor groups used valley bottom more and breeding groups used hillslope more. One explanation for this differential pattem of habitat utilisation is that the breeding groups may be displaced from preferred valley bottom by disturbance from vehicles in that habitat.