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.

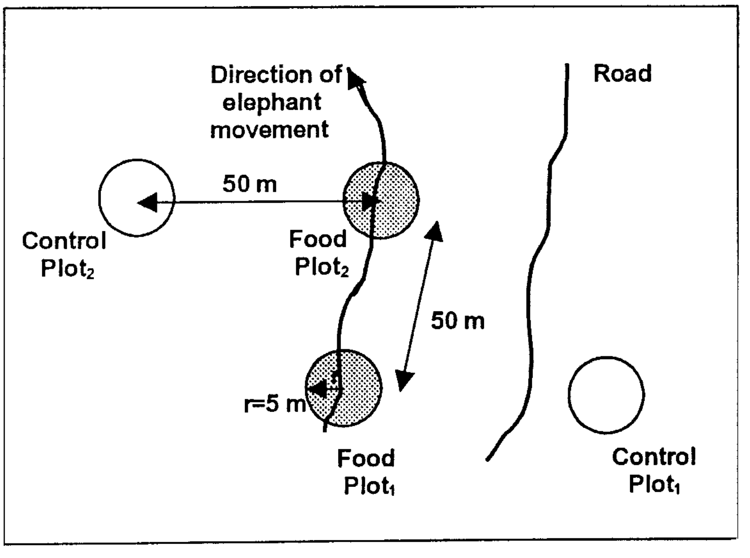


Fig. 3.1. Representation of the method used to locate plots. Not to scale. Modified from Stokke (1999).

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.

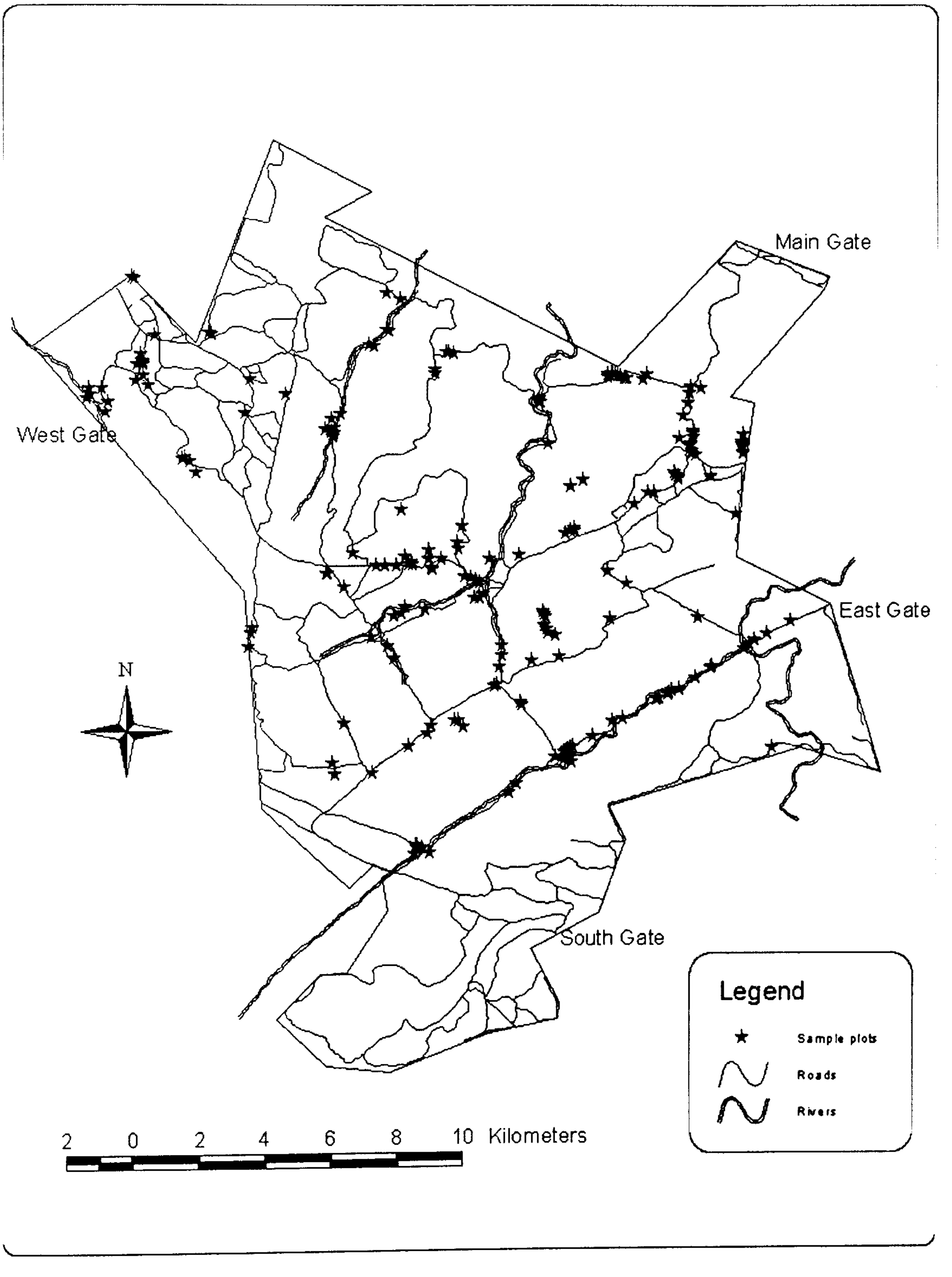


Fig. 3.2. Map of WPGR showing distribution of 203 food plots from which feeding data were collected.

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

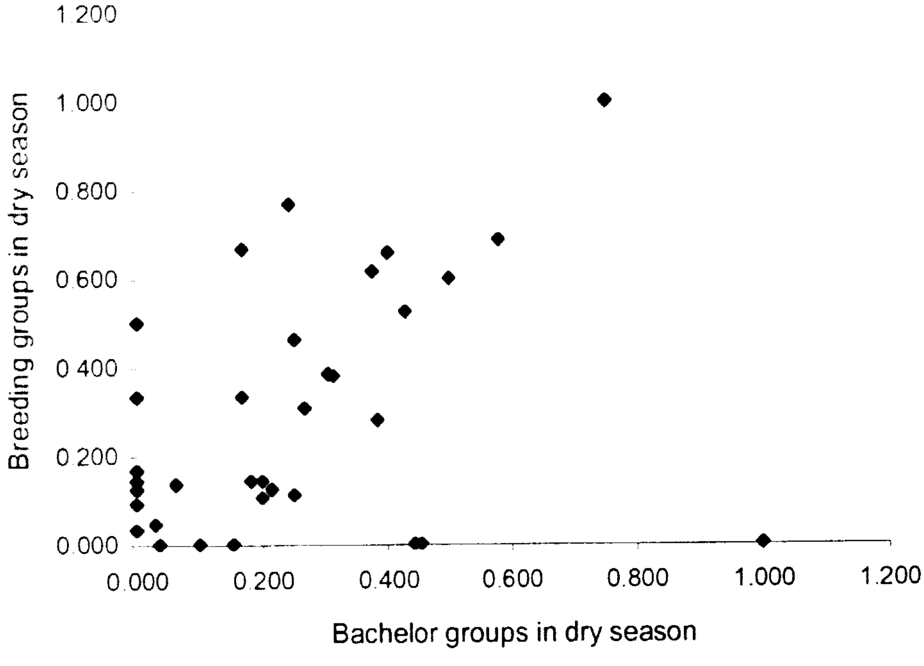


Fig. 3.3 Scatterplot of the correlation between preference ratios for 37 woody species used at least once by bachelor groups or breeding groups in the dry season, but available to both groups in that season. The relationship was not significant (r_s = 0.28, P = 0.10).

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

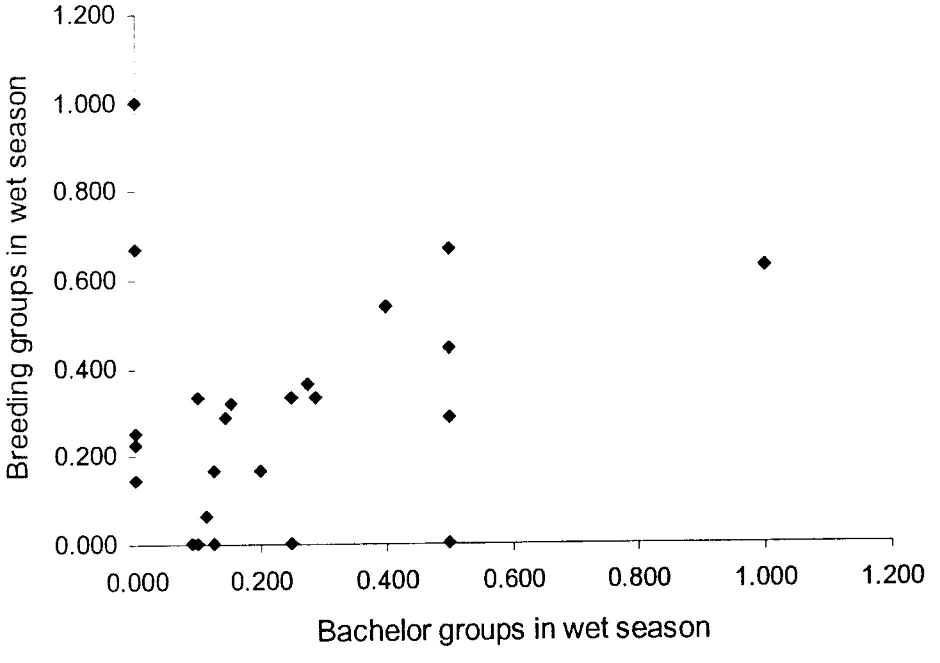


Fig. 3.4 Scatterplot of the correlation between preference ratios for 25 woody species used at least once by bachelor groups or breeding groups in the wet season, but available to both groups in that season. The relationship was not significant ($r_s = 0.23$, $P = 0.29$).

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.

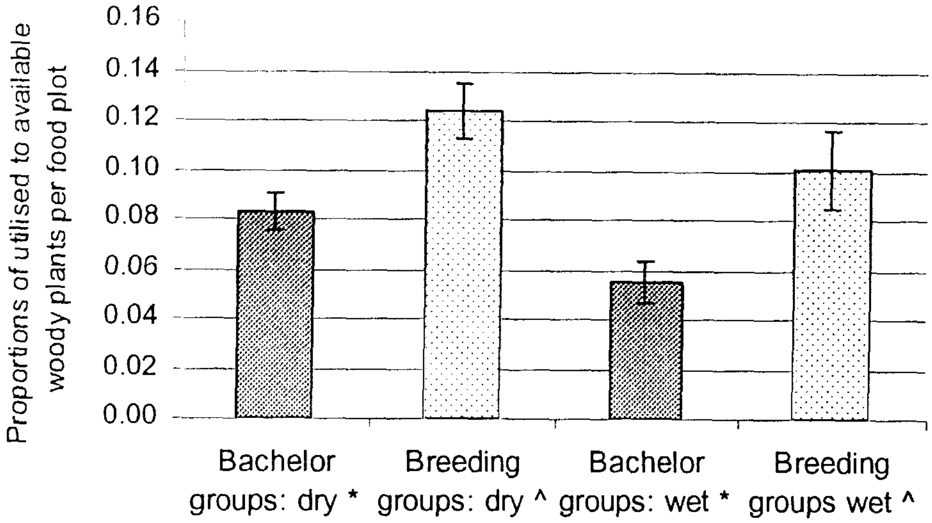


Fig. 3.5. Mean (and standard error bars) of the proportions of utilised woody plants to those available in food plots for each elephant group type, in each season. Bachelor groups and breeding groups utilised significantly different proportions of woody plants to those available in their respective food 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.

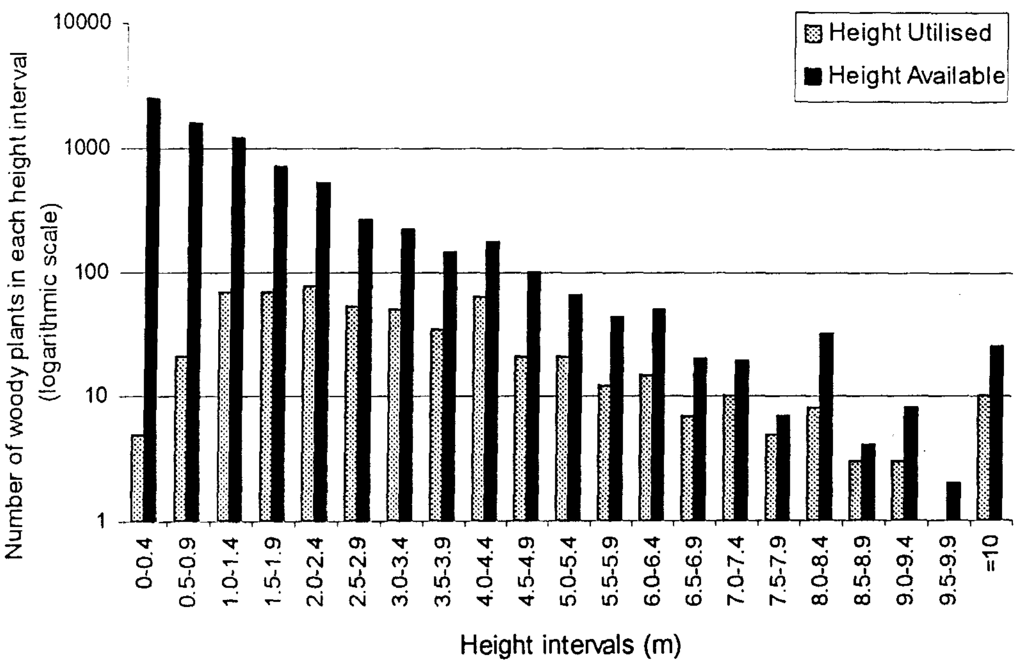


Fig. 3.6. A comparison of heights of woody plants utilised by both elephant group types, with the heights of woody plants available to them in food plots, over both seasons.

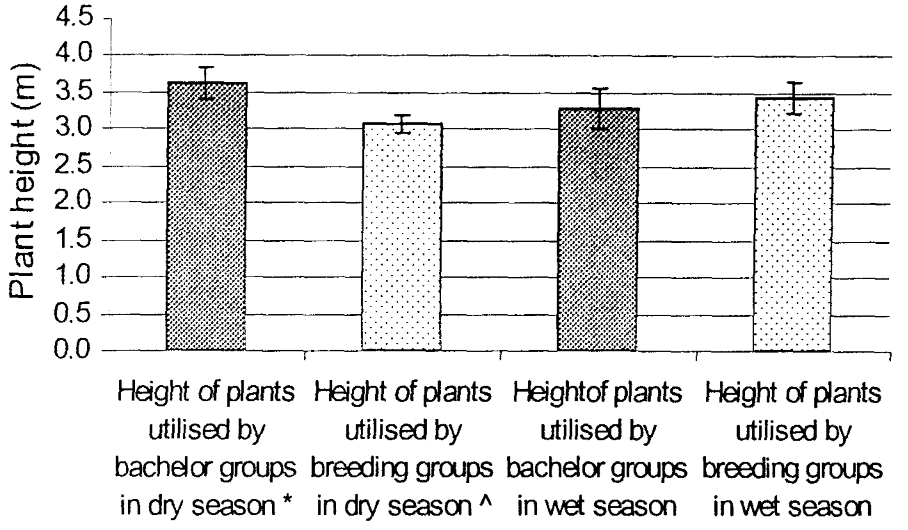


Fig. 3.7. Mean (± standard error) height of woody plants utilised by bachelor groups and breeding groups in each season are shown. Different symbols indicate that bachelor groups browsed from significantly taller woody plants (3.62 ± 0.20 m) than breeding groups (3.08 ± 0.12 m) in the dry season (Mann-Whitney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

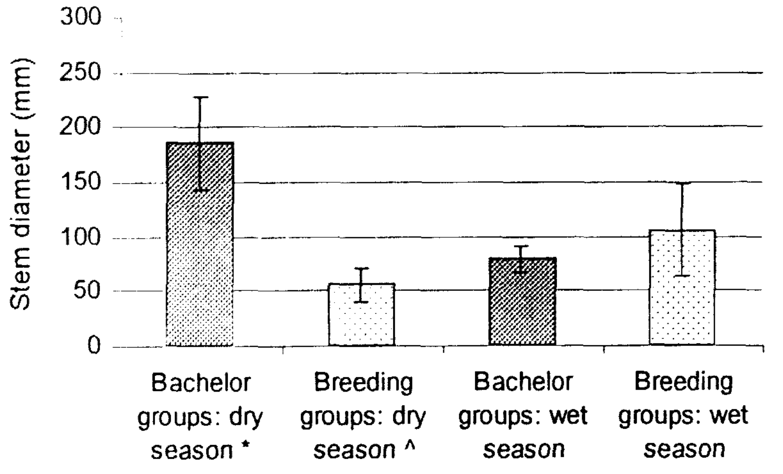
Stem diameter of woody plants that had been uprooted did not differ between bachelor groups and breeding groups in the dry season or the wet season. Bachelor groups did not exhibit any difference in the stem diameter of the plants that they uprooted between dry and wet seasons. The same results were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

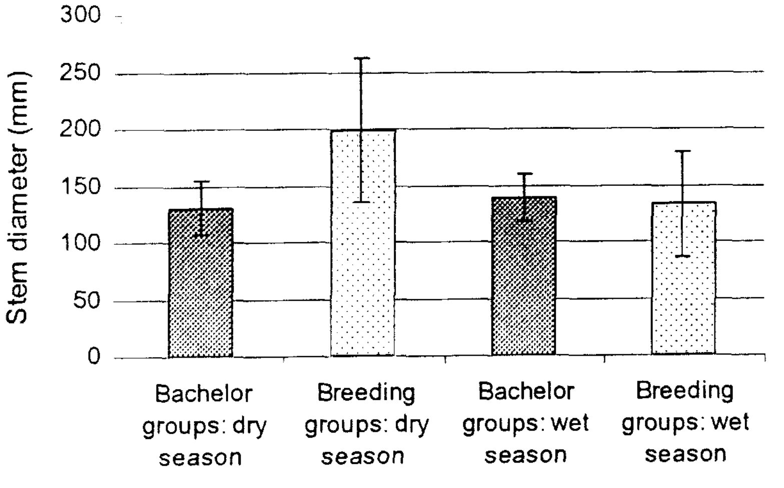
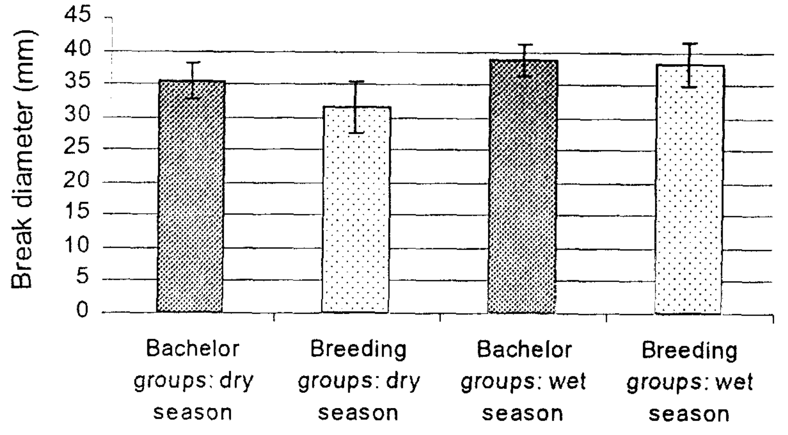


Fig. 3.8. Comparisons between bachelor groups and breeding groups, between seasons, of a) stem diameter of felled plants where main stem was broken-off and b) stem diameter of uprooted plants. Different symbols indicate significant differences between group types or seasons. In the dry season bachelor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

a)



b)

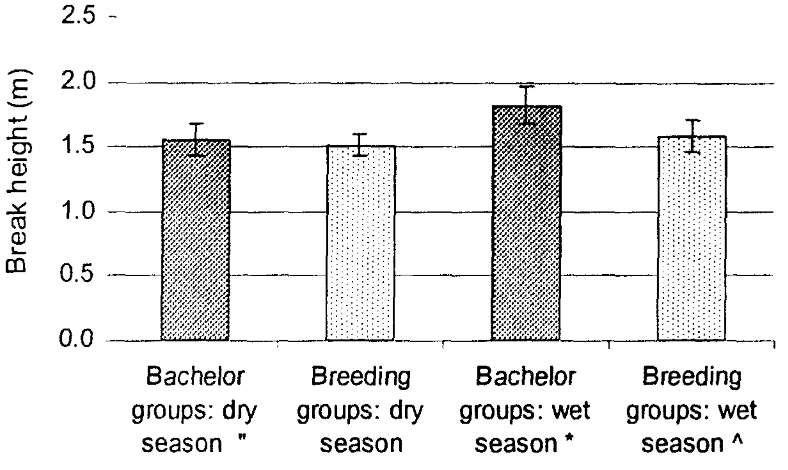


Fig. 3.9. Comparisons between bachelor groups and breeding groups, between seasons, of a) break diameter and b) break height of branches. Different symbols indicate significant differences between group types or seasons. Break height by bull elephants was significantly higher (Mann-Whitney U = 1362,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

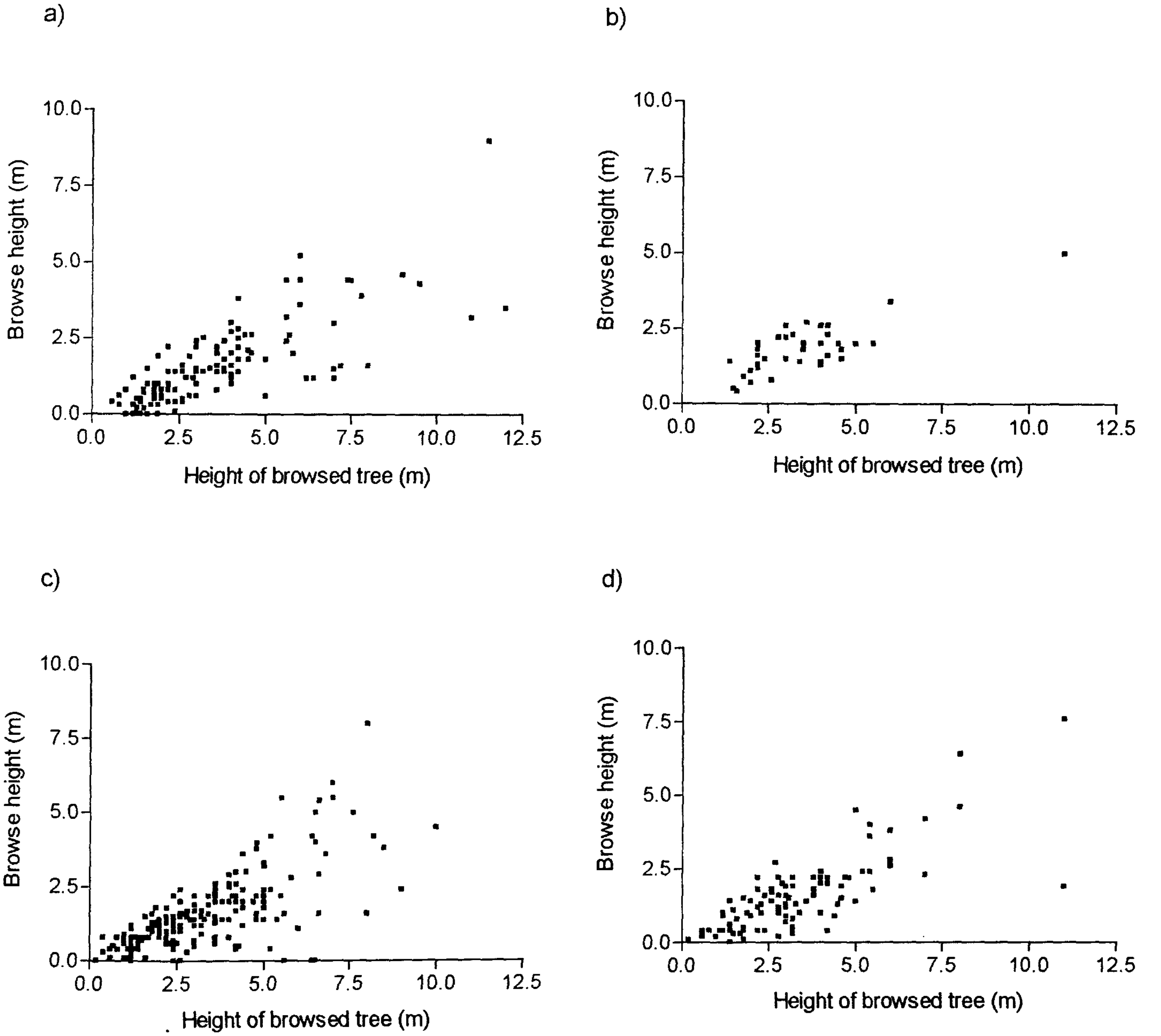


Fig. 3.10. Correlation between browse height (m) and height of browsed tree (m) was positive for a) bachelor groups in dry season (r_s = 0.65, P < 0.0001, n = 122), b) bachelor groups in wet season (r_s = 0.64, P < 0.0001, n = 36), c) breeding groups in dry season (r_s = 0.49, P < 0.0001, n = 215) and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

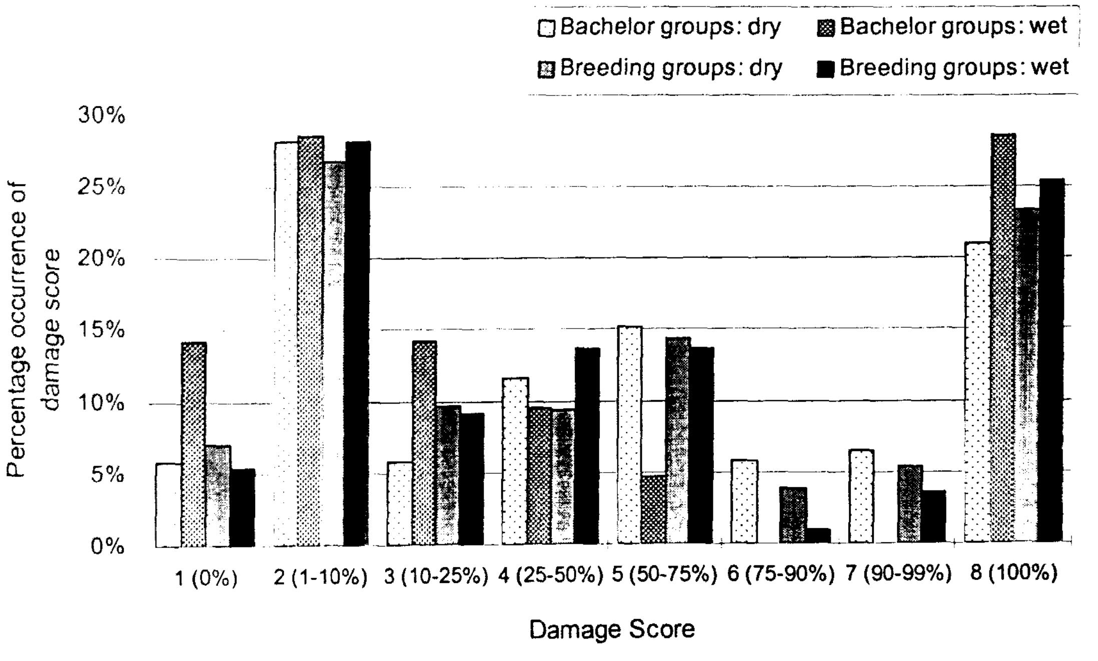


Fig. 3.11. Proportions of each damage score for bachelor groups and breeding groups in dry and wet seasons. Only bachelor groups exhibited a significant difference in frequency of damage score between dry and wet seasons (χ^2 = 14.8, d.f. = 7, P < 0.05).

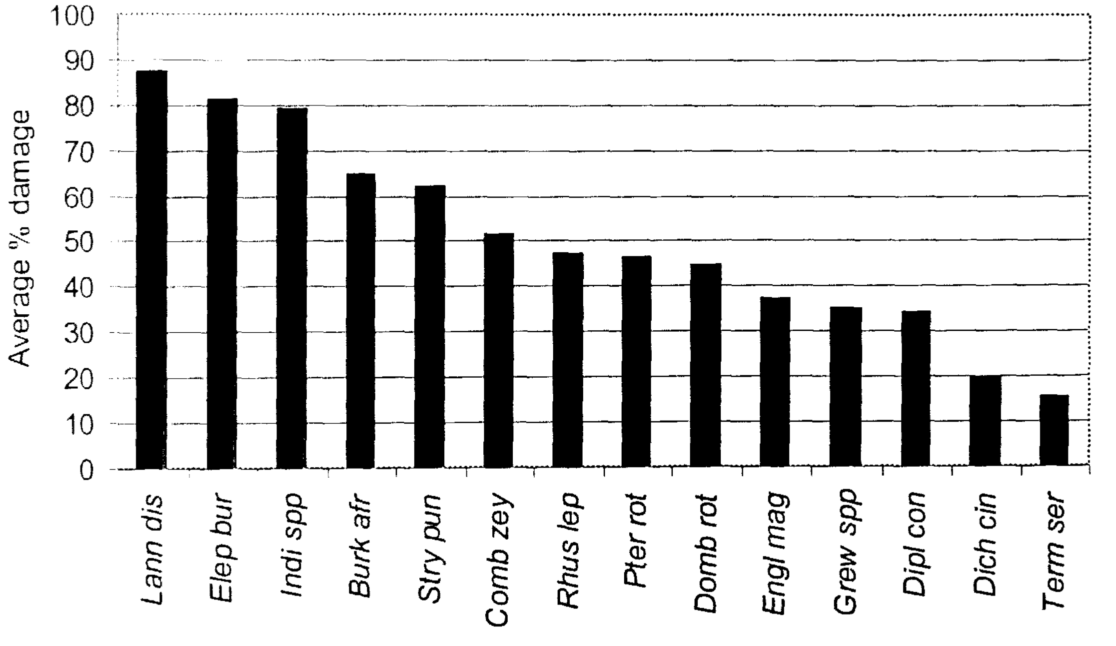


Fig. 3.12. Average percentage damage to 14 woody species used more than 5 times by the elephants (data pooled over sexes) in the dry season.

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*

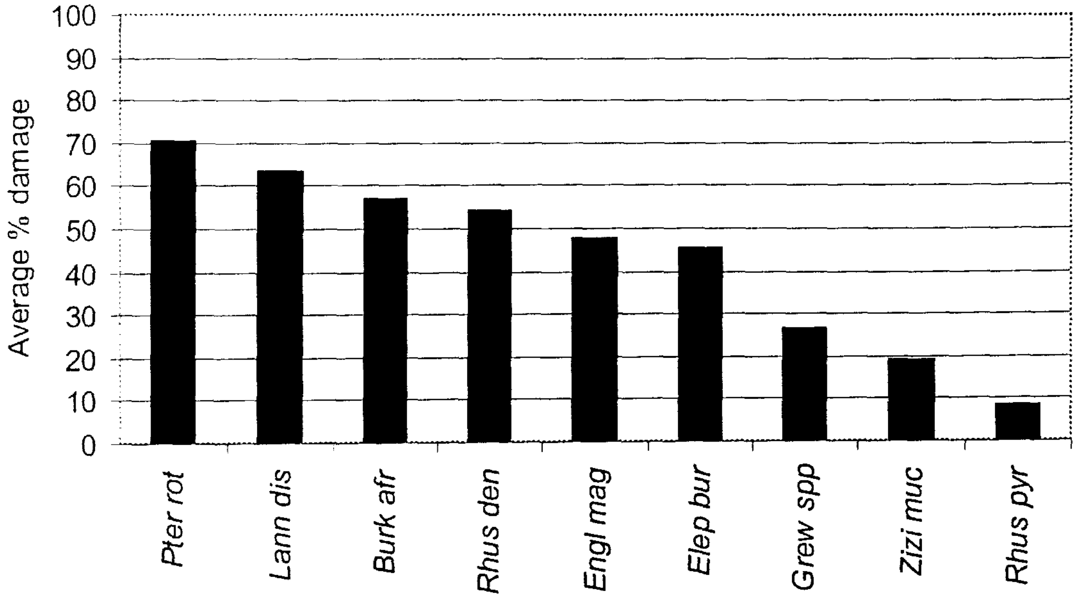


Fig. 3.13. Average percentage damage to nine woody species used more than 5 times by the elephants (data pooled over sexes) in the wet season.

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.

3.6 References

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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).