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.

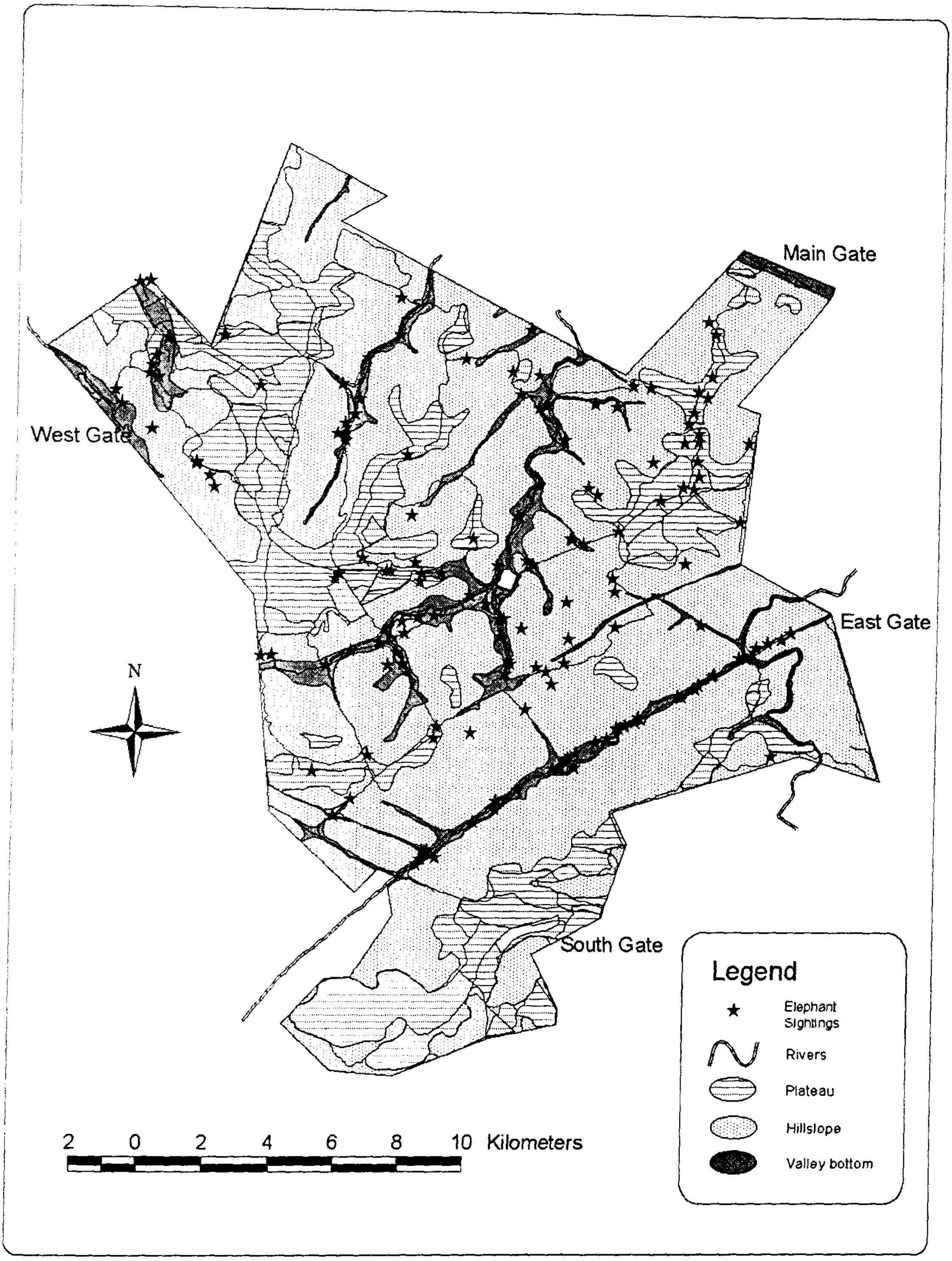

Fig. 4.1. Map of Welgevonden Private Game Reserve showing habitat types, rivers and the distribution of the 161 elephant sightings.

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.

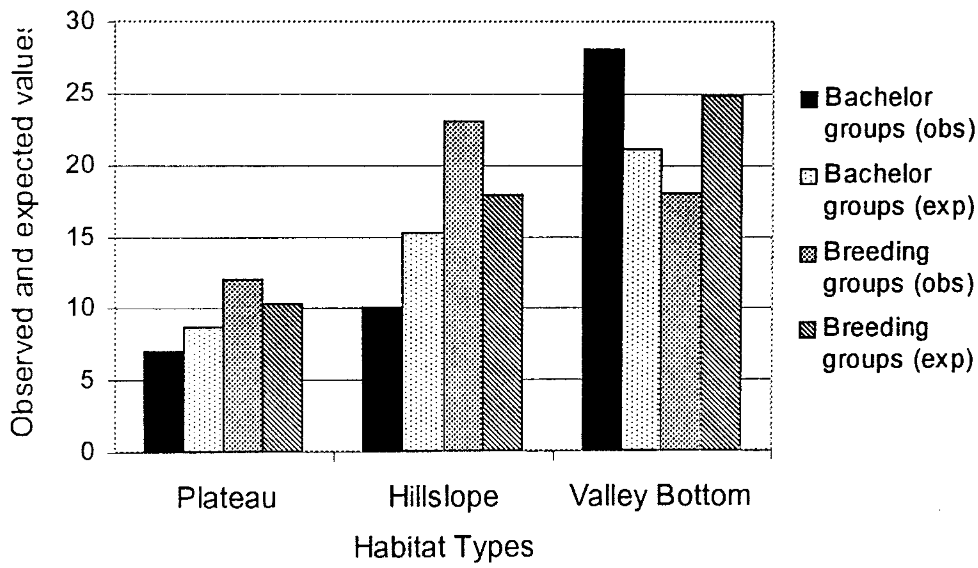

Fig. 4.2. Observed (obs) and expected (exp) values of sightings for habitat utilisation by elephant bachelor groups and breeding groups were significantly different in the dry season (χ^2 = 8.01, d.f. = 2, P < 0.05).

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.

4.6 References

APPS, P. (Ed). 1996. Elephants. In: *Smither's Mammals of Southern Africa. A Field Guide.* Southern Book Publishers (Pty) Ltd. South Africa.

BATZLI, G. 1994. Mammal-plant interactions. Special Feature. *Journal of Mammalogy* **75**: 813-815.

BYERS, C.R., STEINHORST, R.K. & KRAUSMAN, P.R. 1984. Clarification of a technique for analysis of utilisation-availability data. *Journal of Wildlife Management* **48**: 1050-1053.

CÔTÉ, S.D. 1996. Mountain goat responses to helicopter disturbance. *Wildlife Society Bulletin* **24**: 681-685.

DORRANCE, M.J., SAVAGE, P.J. & HUFF, D.E. 1975. Effects of snowmobiles on white-tailed deer. *Journal of Wildlife Management* **39**: 563-569.

DOUGLAS-HAMILTON, I. 1972. On the ecology and behaviour of the African elephant. "The Elephants of Lake Manyara". PhD Thesis, University of Oxford, Oxford.

DU TOIT, J.T. 1995. Sexual segregation in kudu: sex differences in competitive ability, predation risks of nutritional needs? *South African Journal of Wildlife Research* **25**: 127-132.

GEIST, V. 1974. On the relationship of social evolution and ecology in ungulates. *American Zoology* **14**: 205-220.

GILL, J.A., SUTHERLAND, W.J. & WATKINSON, A.R. 1996. A method to quantify the effects of human disturbance on animal populations. *Journal of Applied Ecology* **33**: 786-792.

HOWELL, D.C. 1995. *Fundamental Statistics for the Behavioural Sciences*. Third Edition. Duxbury Press, U.S.A.

JACHMANN, H. & BELL, R.H.V. 1984. The use of elephant droppings in assessing numbers, occupance and age structure: a refinement of the method. *African Journal of Ecology* **22**: 127-141.

LAND TYPE SURVEY STAFF 1988. Land type of the maps 2426 Thabazimbi and 2428 Nylstroom. Mem. Agric. Nat. Resour. S. Afr. No. 10.

MAIN, M.B. & COBLENTZ, B.E. 1990. Sexual segregation among ungulates: a critique. *Wildlife Society Bulletin* **18**: 204-210.

MAIN, M.B., WECKERLY, F.W. & BLEICH, V.C. 1996. Sexual segregation in ungulates: new directions for research. *Journal of Mammalogy* **77**: 449-461.

NEU, C.W., BYERS, C.R. & PEEK, J.M. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* **38**: 541-545.

OWEN-SMITH, R.N. 1988. *Megaherbivores. The influence of very large body size on ecology*. Cambridge University Press.

PEDEVILLANO, C. & WRIGHT, R.G. 1987. The influence of visitors on mountain goat activities in Glacier National Park, Montana. *Biological Conservation* **39**: 1-11.

POCHÉ, R.M. 1974. Ecology of the African elephant (*Loxodonta a. africana*) in Niger, West Africa. *Mammalia* **38**:567-580.

POOLE, J. 1996. The African Elephant. Pp 1-8. In: Studying Elephants. AWF Technical Handbook Series 7. Kangwana, K. (Ed.) African Wildlife Foundation. Nairobi, Kenya.

ROSCOE, J.T. & BYARS, J.A. 1971. An investigation of the restraints with respect to sample size commonly imposed on the use of the Chi–Square Statistic. *Journal of the American Statistical Association* **66**: 755-759.

ROSNER, B. 1995. *Fundamentals of Biostatistics*. Fourth Edition. Duxbury Press, U.S.A.

RUCKSTUHL, K.E. & NEUHAUS, P. 2000. Sexual segregation in ungulates: a new approach. *Behaviour* **137**: 361-377.

RUGGIERO, R.G. 1991. Opportunistic predation on elephant calves. *African Journal of Ecology* **29**: 86-89.

SCHULTZ, R.D. & BAILEY, J.A. 1978. Responses of national park elk to human activity. *Journal of Wildlife Management* **42**: 91-100.

SENFT, R.L., COUGHENOUR, M.B., BAILEY, D.W., RITTENHOUSE, L.R., SALA, O.E. & SWIFT, D.M.. 1987. Large herbivore foraging and ecological hierarchies. *Bioscience* **37**: 789-799.

SIKES, S. 1971. *The Natural History of the African Elephant*. Weidenfeld and Nicholson, London.

STOKKE, S. & DU TOIT, J.T. In Press. Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *J. Trop. Ecol.*

STOKKE, S. & DU TOIT, J.T. 2000. Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park Botswana. *Ecography* **23**: 70-80.

SUKUMAR, R. AND M. GADGIL. 1988. Male-female differences in foraging crops by Asian elephants. *Animal Behaviour* **36**: 1233-1235.

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.