African elephant home range and habitat selection in Pongola Game Reserve, South Africa

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The ranging behaviour and habitat occupancy by three elephant groups (cow herd, bulls, and an orphan group) were studied over a two-year period in a small, fenced reserve. No summer dispersal was observed. Distinct seasonal home ranges were exhibited for all groups, with the summer (wet season) ranges being smaller than the winter (dry season) ranges. Home range size was much smaller than in other locations. The dam and surrounding high density of patches of vegetation of high nutritional quality are thought to be the reasons. Habitat selection was strongly evident with all of the elephant groups selecting River Line habitats in the dry season. In the wet season the cow herd and orphans selected the more open *Acacia* habitats and the bulls exhibited no significant habitat preference.

Key words: elephant, seasonal range, habitat selection, range use.

INTRODUCTION

The non-random use of space and differential habitat selection is a longstanding basic tenet of ecology (Rosenzweig 1981). Energetic constraints, social factors and the abundance and distribution of resources influence the size, shape and location of seasonal ranges. These constraints and the resource distribution at the end of the dry season determine which resources are limiting, and their influence on demographic parameters. Understanding seasonal range dynamics and what drives them is therefore of critical importance in understanding how populations are limited.

It is generally accepted that in semi-arid environments, an expansion of the distribution range occurs at the beginning of summer that results in the entire elephant population of a region being spread over a wider area than during the dry winter season when sub-populations, sometimes referred to as clans or bond groups, are restricted to much smaller areas close to rivers and waterholes (e.g. Jarman 1972; Norton-Griffiths 1975; Williamson 1975; Leuthold 1977; Western & Lindsay 1984; Merz 1986; Ottichilo 1986; Lindeque & Lindeque 1991; Chase 2003). This summer dispersal gives rise to distinct summer and winter ranges for the sub-populations.

Precisely how this sub-population level summer range expansion is linked to changes in the area of the seasonal home range of individual males or family units, is not clear. The literature provides contradictory data. Jachmann (1983) suggested that dry season ranges for females were larger than wet season ranges. The results were, however, based on a small sample. Viljoen (1988) showed that of the four female herds studied, two had larger dry season core areas, and two had smaller core areas. Similarly, one of two bulls had a larger dry season core area and the other the reverse. De Villiers & Kok (1997) stated that the wet season ranges that they identified for seven elephants were larger than the dry season ranges. However, closer examination of the data in their Table 3 indicates that the statement is not as clear-cut as suggested. Seasonal home range size was examined in their study in three different phenological seasons: a wet season when both trees and grasses had green leaves (about November to March), a transitional season when the trees had green leaves but the grasses were senescent (about April to August), and a dry season when trees had lost their leaves and the grasses were senescent (August/September to October/November). For five of the six home ranges the intermediate season (mid to late winter) home range was larger than the summer range, and thereafter decreased to an area smaller than during the wet season. However, their dry season was shorter so it is likely that this resulted in fewer sightings, which may have affected their results. The single bull monitored in their study showed a consistent decrease in the size of the home range from the wet to dry period. Osborn (2003), working with bull elephants in the Sengwa Wildlife Research area in Zimbabwe, showed precisely the same pattern as observed by De Villiers

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& Kok (1997). Ntumi (2003) found that the dry season ranges of four female groups were smaller than the wet season ranges, but the single male had a larger dry season range. Similarly, Chase (2003), in an unpublished report, describing the results of an analysis of movement of six female elephants, indicated that the wet season ranges were larger. Clearly more detailed data on elephant movement and the factors affecting it are required to properly understand how and why these discrepancies arise.

Relatively few studies have quantified habitat occupancy and use by elephants, particularly on a seasonal basis. Viljoen (1989), Babassa (2000), De Boer *et al.* (2000), Stokke & du Toit (2002), and Osborn & Parker (2003) have found strong selection for some habitats and avoidance of others. Particularly in the dry season, riparian and low-lying habitats on relatively nutrient-rich soils are selected for.

This study had three main objectives, namely to determine: (1) if the elephants in the Pongola Game Reserve dispersed away from water in summer; (2) if they used distinct home ranges and if these were different in different seasons and for males and females; and (3) habitat preferences and whether these were different in summer and winter.

MATERIALS & METHODS

Study site

The Pongola Game Reserve (PGR), established in 1993, covers an area of approximately 73.6 km^2, on the western shore of the Jozini Dam. The dam occurs along the entire eastern and northern boundary. A railway line bisects the reserve from the southern border to the northwest (Fig. 1). The climate is hot and arid with rainfall of 400–600 mm per annum. The annual rainfall for the two years of this study was, however, well above average with 1220 mm in 2000 and 780 mm in 2001. The vegetation falls into three of Acocks' (1988) veld types; Zululand Thornveld, Lowveld and Arid Lowveld. The last two cover the southern and central portions of the Kruger National Park and adjoining reserves, making these results of interest in the management of these areas. Canonical correspondence analysis and 'two-way indicator species analysis' of woody species densities in randomly located transects identifies seven vegetation types (Page & Duffy, unpubl. data), the limits of which can be identified on orthophotos of the area (Fig. 1; Table 1).

Seventeen elephants in two family groups were translocated from Kruger National Park to PGR during June 1997. Six bulls were introduced: three in 1998 (one of which died and one was shot); and three in 2002 (one of which died). The population in 2000/1 consisted of two permanently associated family units in a group of 28–30 individuals, and four adult bulls. Five orphan elephants*, all approximately ten years old, broke into PGR from a nearby reserve in July of 2000 and remained together as a separate group of four females and one male.

Data collection

Elephants were located from March 2000 to February 2002, two or three times a week. Locations were aided by radio collars on one adult female and an adult bull. On sighting a Global Positioning System (GPS) was used to record the position of the group from a vehicle. Observations were made from the reserve's extensive road and track network, and off-road from a position that did not influence the direction or rate of movement of the elephants.

Data analysis

The first location for the period between 06:00 and 10:00 each day was used for this analysis in order to avoid the possible effects of elephants using different habitat types at different times of the day. The seasons were based on rainfall data (Fig. 1c) and defined as summer between 1 November and 30 April and winter between 1 May and 31 October.

Distributions were overlayed using ArcView® 3.2a on the habitat type map (Fig. 1) and each location assigned to a habitat type. Elephant home ranges based on minimum convex polygons have been shown to be strongly dependent on the number of points used (Whyte 2001) and therefore kernel analysis was used in this study (Hooge & Eichenlaub 1997) and 50% kernels and 95% kernels calculated (Worton 1989) using distance units of 500 m. Separate analyses were run for each of the three groups of elephants in each season in each year.

While preference ratios lack statistical precision, they nevertheless provide a crude but easily understood comparison of selection and avoid-

*The term 'orphan elephants' refers to young elephants between the ages of five and ten years that were captured during culling operations and translocated in small groups to reserves without elephants for the purpose of restocking. The practice has been discontinued.

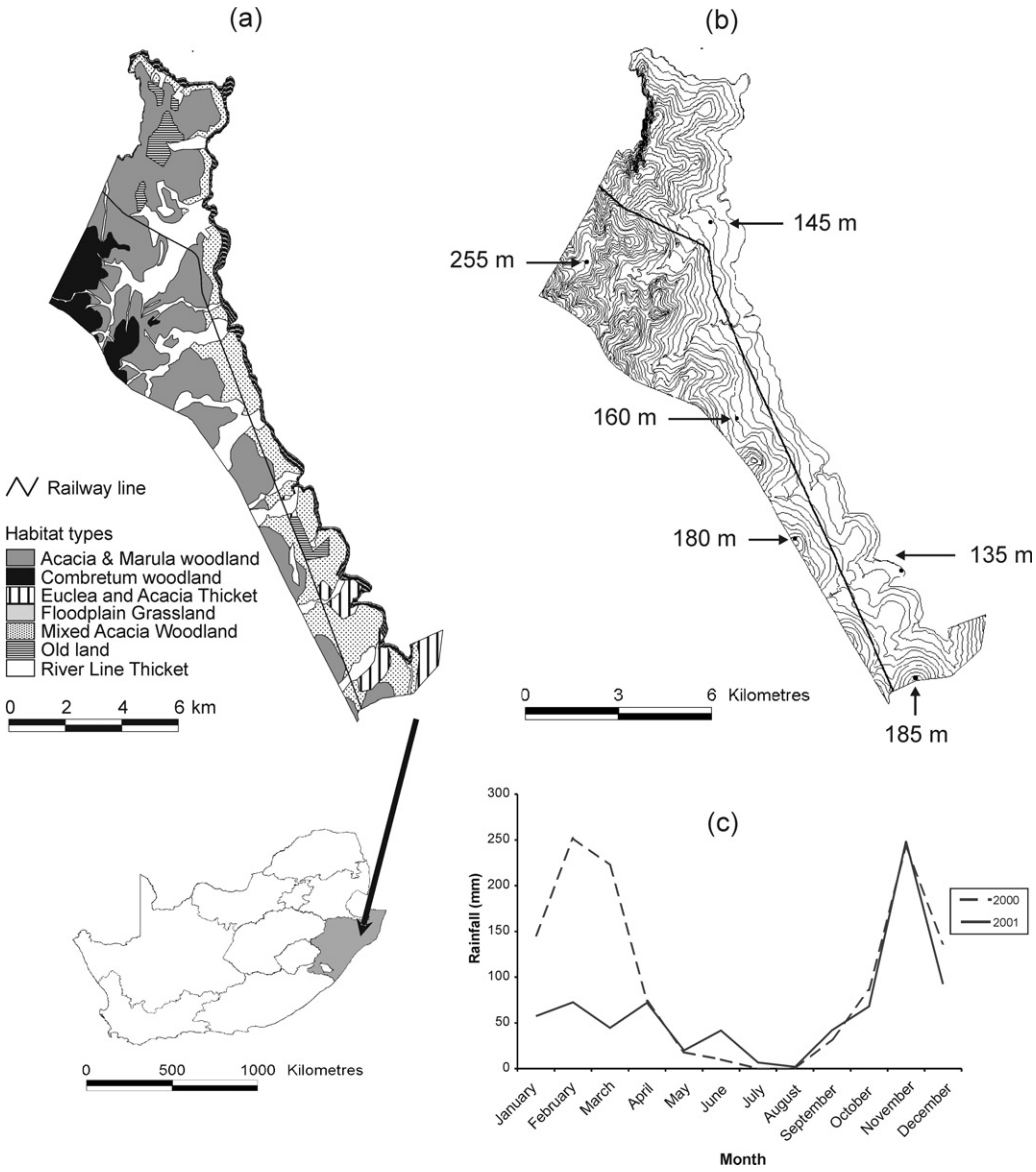

Fig 1. **a**, Habitat map of the Pongola Game Reserve with an arrow indicating the geographic position of the reserve in South Africa (KwaZulu Natal is highlighted). **b**, Contour map of the reserve, exhibiting the hillier relief of the northern section. Altitude and relief are directly linked to the spatial distribution of the habitat types within the reserve. **c**, Rainfall figures for 2000 and 2001, clearly showing the seasonality in precipitation. The black line down the centre of the reserve indicates the route of the railway line. Josini Dam forms the entire eastern boundary of the reserve.

ance for particular habitat types. Preference ratios were therefore calculated for different habitat types as the proportion of locations in a particular habitat type as a ratio of the proportional area of that habitat type, that is: (number of locations in a specified habitat/the total number of locations)/(the area of the specified habitat type/the total area).

Chi-square tests were used establish statistical differences in the occurrence of elephants in the different habitats. The railway acts as a functional barrier for the cow herd (see Results below). Analyses were therefore performed using different area values, 36.8 km^2 for the cow herd, and the total extent of the reserve, 73.6 km^2 for the bulls and orphan group which traversed the entire reserve.

Table 1. Link between habitat types, topography, soils and dominant woody species of the Pongola Game Reserve. Numbers in brackets indicate the number of woody species recorded in the type.

Habitat type	Topographic position and soils	Dominant species
Combretum Woodland	Rocky, well drained soils of upper slopes and tops of highest hills	*Combretum apiculatum, Acacia nigrescens, Ozoroa engleri, Gymnosporia buxifolia, Grewia villosa, Grewia hexamita, Grewia caffra, Sclerocarya birrea, Ziziphus mucronata* (17)
River Line Thickets	Clay rich deep soils of drainage lines	*Ehretia rigida, Capparis tomentosa, Salvadora australis, Gymnosporia senegalensis, Acacia nilotica, Acacia tortilis, Schotia brachypetala, Rhus guenzii, Acacia luederitzii, Acacia senegal, Gymnosporia buxifolia, Dichrostachys cinerea* (28)
Flood Plain Grassland	Deep alluvial clay soils of dam shore	Mixed grasses and forbs
Mixed *Acacia* Woodland	Higher nutrient soils on lower slopes	*Acacia nilotica, Acacia tortilis, Acacia luederitzii, Dichrostachys cinerea, Ehretia rigida, Capparris tomentosa, Rhus guenzi, Spirostachys africana* (25)
Acacia-Marula Woodland	Shallow soils of mid to upper slopes on higher hills.	*Acacia nigrescens, Sclerocarya birrea, Ziziphus mucronata, Acacia tortilis, Grewia flava, Gymnosporia buxifolia, Grewia villosa, Dichrostachys cinerea, Ozoroa englerii, Canthium inerme* (38)
Euclea Thickets	Alluvial soils on flat areas close to water at lower altitudes.	*Euclea racemosa, Euclea divinorum, Euclea natalensis, Pappea capensis, Gymnosporia nemorosa, Acacia nilotica, Capparis tomentosa, Salvadora australis, Acacia luederitzii, Ehretia rigida* (31)
Old Land	Soils and elevation correspond to adjacent habitat type	Mixed *Acacias* & *Dichrostachys cinerea*

RESULTS

Dispersal

No indication of dispersal away from water in summer or contraction of the range toward it in winter was noted.

Individual home range analysis

The cow herd utilized only the area east of the railway line despite the fact that it does not present a physical barrier. Both the orphan group and the bulls crossed it freely (Fig. 2; Table 2). Equivalent vegetation types are found for at least a kilometre away on either side of the railway line along its entire route (Fig. 1), and there is surface water on both sides of the line. No observations or signs of the cow herd were ever recorded to the west of the line. The herd was, however, observed on several occasions approaching the line and then turning away.

The home ranges of the bulls, cow herd and orphan group showed strong seasonal shifts

Table 2. The home ranges of elephant groups in the Pongola Game Reserve, 2000–2001.

Elephant group	Season	Year	Total home range (95% kernel) (km^2)	Core home range (50% kernel) (km^2)
Bulls	Summer	2000	40.0	10.8
	Summer	2001	33.6	19.4
	Winter	2000	71.5	31.5
	Winter	2001	61.2	18.7
Herd	Summer	2000	20.6	9.0
	Summer	2001	17.5	4.3
	Winter	2000	36.7	21.0
	Winter	2001	36.7	18.9
Orphan	Summer	2000	40.6	13.8
	Summer	2001	26.8	8.1
	Winter	2000	10.5	1.7
	Winter	2001	60.5	11.3

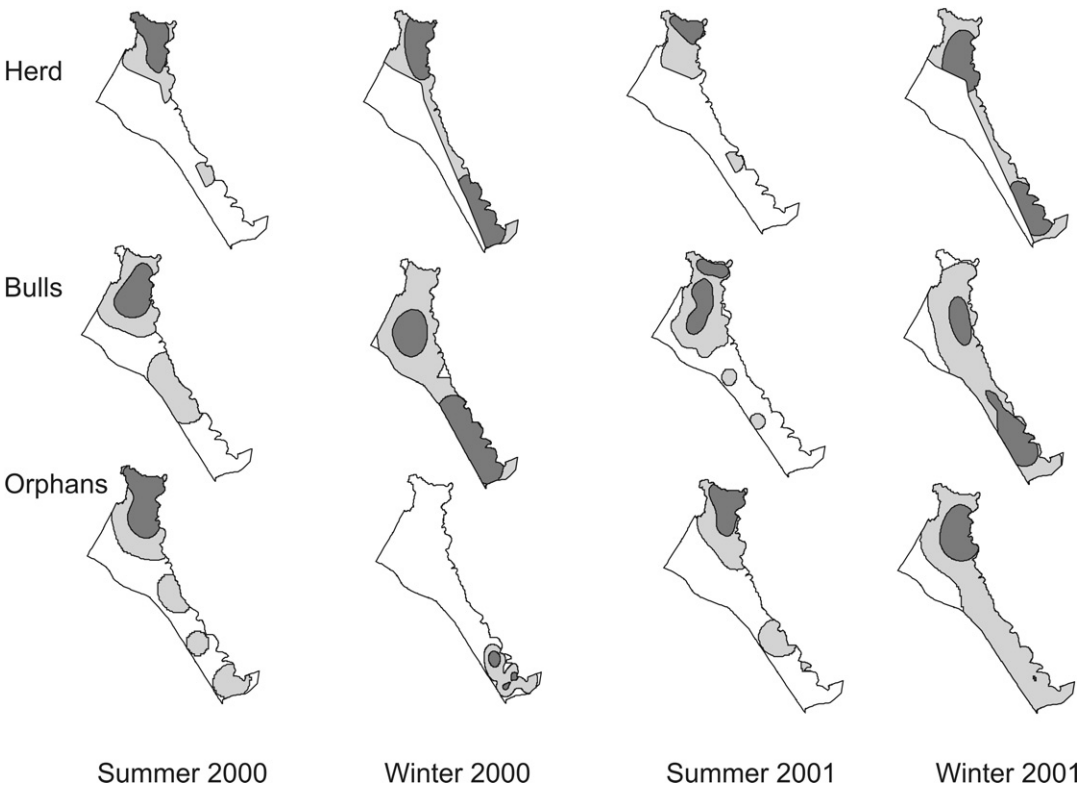

Fig. 2. Home ranges of the herd, bulls and orphans in different seasons and years. Dark shading indicates core home range (50% kernel) and light shading indicates total range (95% kernel).

(Fig. 2). In both years, the summer home range of all three elephant groups, had the core home range (50% kernel) locatedover the northern dam shore and the surrounding *Acacia*-Marula Woodland (Fig. 1a). The bulls and orphan group occupied a larger range than the females. In winter there are two core ranges for all three groups, in the north and south of the reserve, in both years, with the northern core shifting slightly south.

Larger areas were used in the winter than in summer (Table 2). In 2000, the winter total range for the herd was 1.78 of the summer range and the winter core home range was 2.33 of the summer range. In 2001, the winter range was 2.10 of the summer total range and 4.40 of the summer core range. In 2000, the winter total home range of the bulls increased to 1.79 of the summer range and the winter core home range increased to 2.92 of the summer range. The orphans only entered the reserve in July 2000 so their Winter 2000 range is not comparable to the other distributions. In 2001 the winter total home range was 2.26 of the summer range and a winter core range 1.40 of the summer range. The cow herd and bulls had smaller seasonal ranges in 2001 compared to 2000 (Table 2).

Habitat occupancy

All three elephant groups used different habitats with varying intensity from one season to the next (Table 3). In summer the bulls used the habitats in proportion to their area ($\chi^2_6 = 9.776$, $P > 0.1$) but in the winter there was a significant difference ($\chi^2_6 = 44.498$, $P < 0.001$). The herd strongly selected for particular habitats in both seasons (summer-$\chi^2_6 = 11.603$, $P < 0.05$ and winter-$\chi^2_6 = 31.808$, $P < 0.001$). The orphans also exhibited heterogeneous habitat use throughout the year (summer-$\chi^2_6 = 28.205$, $P < 0.001$ and winter-$\chi^2_6 = 33.376$, $P < 0.001$).

Acacia-Marula Woodland was selected for by both the cow herd and bulls in the summer and avoided in the winter. In the winter a strong preference for River Line Thickets was indicated.

All three groups showed a positive preference for *Euclea* Thicket during winter. The mixed *Acacia* Woodland was selected for by the orphans in both seasons, and by the bulls in winter.

Table 3. Habitat selection of the cow herd, bulls and orphans.

Vegetation	% of total area	Summer		Winter	
		% of total sighting No. (= *n*)	Preference ratio	% of total sighting No. (= *n*)	Preference ratio
Cow herd					
Acacia-Marula Woodland	26.5	37 (45)	1.40	14 (17)	0.53
Mixed *Acacia* Woodland	32.8	31 (38)	0.95	36 (45)	1.10
River Line Thicket	13.7	16 (20)	1.17	29 (36)	2.12
Combretum Woodland	0	0 (0)	0	0 (0)	0
Flood Plain Grassland	11.9	11 (13)	0.92	6 (7)	0.50
Euclea and *Acacia* Thicket	8.5	2 (3)	0.24	13 (16)	1.53
Old land	6.6	3 (4)	0.45	2 (3)	0.30
Bulls					
Acacia-Marula Woodland	39.8	50 (57)	1.26	24 (26)	0.60
Mixed *Acacia* Woodland	21.9	19 (22)	0.87	30 (32)	1.37
River Line Thicket	17.8	17 (19)	0.96	37 (40)	2.08
Combretum Woodland	7.0	6 (7)	0.86	0 (0)	0
Flood Plain Grassland	6.0	3 (3)	0.50	2 (2)	0.33
Euclea and *Acacia* Thicket	4.2	0 (0)	0.00	7 (7)	1.67
Old land	3.3	5 (6)	1.52	0 (0)	0.00
Orphans					
Acacia-Marula Woodland	39.8	32 (31)	0.80	16 (14)	0.40
Mixed *Acacia* Woodland	21.9	34 (33)	1.55	33 (28)	1.51
River Line Thicket	17.8	15 (15)	0.84	27 (23)	1.52
Combretum Woodland	7.0	0 (0)	0	0 (0)	0
Flood Plain Grassland	6.0	16 (16)	2.67	6 (5)	1.00
Euclea and *Acacia* Thicket	4.2	1 (1)	0.24	15 (13)	3.57
Old land	3.3	2 (2)	0.61	3 (2)	0.91

DISCUSSION & CONCLUSIONS

Dispersal

There are two possible explanations for the lack of dispersal in this small reserve, either the size prevents it, or the permanent availability of water and forage on the dam shore make it unnecessary.

Home ranges

The results from several studies indicate that boundaries to home ranges often lie along rivers or roads that can easily be crossed (Leuthold 1977; Thouless 1996; Whyte 2001). The ability of elephants to recognize features in the landscape and respond to them in terms of defining home range boundaries has not previously been mentioned in the literature, and other features that might be recognized have not been identified. In this regard it is worth noting that it is unlikely that every elephant in the group responds in the same way to these features, which suggests that the size and configuration of the home range may be strongly determined by the matriarch.

The size of home ranges reported in the literature for cow herds vary widely from 240 km^2 in the Kruger National Park, South Africa, to 1800 km^2 in Tsavo East National Park, Kenya (Owen-Smith 1988). The maximum area of the range for the cow herds reported here (36.7 for 95 % kernel) is therefore considerably smaller. The 95% ranges of bulls in this study are slightly larger than those described at Addo Elephant National Park (100% range based on minimum convex polygon = 52.8 km^2; reserve area = 103 km^2) (Whitehouse & Schoeman 2003), but smaller than those described for bulls in Pilanesberg National Park (95% range based on kernel analysis = 99.7 km^2; reserve area = 500 km^2) (Slotow & van Dyk 2004).

The distribution of water is known to affect home range size (Osborn 2004). The permanent widespread supply of drinking water, and the abundance and clustering of relatively high nutritional quality forage in small patches of different vegetation types (Fig. 1), probably account for the relatively small range observed in PGR.

The larger winter range could be explained in

either of two ways. Food availability may be limited, thus forcing animals to move over a wider area. Alternatively the spatial distribution of habitat types of higher nutritional quality may result in a wider area being traversed in winter. In the dry season, dam levels drop and a narrow band of comparatively good quality grazing becomes available on the dam edge. At the same time away from the dam there is a reduction in the quality and availability of forage. The River Line and *Euclea* Thickets that are the preferred habitats in winter (Table 3) lie perpendicularly to the dam edge, and are widely separated (Fig. 1). These three factors together appear to result in the elephants covering a greater area to satisfy their nutritional demands during winter.

Naturally occurring lakes are rare in Africa. However, there are very many man-made dams in conservation areas, along which subpopulations of elephants occur. The effect of these water bodies on the movement of elephants has not been established, but it appears from this study that there may be negative impacts on vegetation because of reduced home range size around water bodies. Where there is no shift in the seasonal range impact is likely to be higher than where movement occurs. The similarity in position of the core home ranges in both seasons in both years (Fig. 2) indicates that this may be cause for concern.

Habitat occupancy

As water availability in PGR is not limiting it is likely that nutritional demand and social factors drive elephant ranging behaviour. Over the period of this study, rainfall in both wet seasons were well above average, so it is likely that resources were very abundant. Dam levels were high in summer, so a large proportion of the Flood Plain Grasslands were covered. *Acacia*-Marula woodland which is dominated by a wide range of highly palatable species (Table 1), was strongly selected for in both summers (Table 3; Fig. 2). The Mixed *Acacia* woodlands have fewer palatable species. In addition, the lower-lying areas in the Mixed *Acacia* woodlands and Drainage Line Thickets were also probably avoided because they were relatively muddy, compared to the *Acacia*-Marula woodlands that occur on steeper slopes (Fig. 1).

Habitat types selected for during the winter season are all located in lower-lying regions (Fig. 1). It is well established that soils in bottomlands have a higher nutrient status and moisture-holding capacity than soils at the top of hills (e.g. Schimel *et al.* 1985). Elephants are, therefore, probably selecting for nutritional quality during the winter period. Several studies in semi-arid environments have characterized elephants as riparian species and invoked both the availability of palatable plants and water as explanatory factors (Viljoen 1989; Ottichilo 1986; Sommerlatte 1976). This study suggests that nutritional quality is probably important.

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