

The consequences of body size dimorphism: are African elephants sexually segregated at the habitat scale?

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Summary

Sexual segregation is a commonly observed phenomenon in dimorphic ungulates, which has been categorised into two distinct components: social segregation and habitat segregation. In this study we investigated whether elephants were sexually segregated at the habitat scale. The locations of 12 family groups and 16 males, in three distinct populations were recorded over a period of 2.5 years. Selection ratios were calculated for each habitat type and a Kendall's coefficient of concordance was used for the analyses. The habitat and foraging preferences were firstly tested for concordance within sex, and then between the sexes. Female habitat preferences showed significant concordance across all reserves and they also exhibited strong concordance in their summer foraging preferences. Their weakest association with habitat and foraging preference was during winter, which may be related to resource scarcity. Males exhibited significant concordance in their habitat preferences in two out of the three reserves. They had their weakest associations in the summer months and this may be linked to avoidance of other males in musth and the abundance of forage. There were no significant differences in habitat preference between males and females and it is likely that individual preferences vary as much within sex as between sexes. Differential habitat utilisation does not appear to be driving sexual segregation in elephants and it is postulated that sociality, divergent reproductive strategies and foraging behaviour at the plant scale play a more significant role. The results of this study highlight the importance of scale in elucidating the mechanisms involved in sexual segregation.

Keywords: *Loxodonta africana*, ungulate, habitat utilisation, foraging behaviour.

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Introduction

Sexual segregation occurs when males and females live apart outside of the breeding season and is commonly associated with body size dimorphism in large ungulates (Conradt, 1998; Ruckstuhl, 1998; Barboza & Bower, 2000). Sexual segregation, which has also been recorded in primates, cetaceans and a number of bird species is not just an interesting biological phenomenon but has important implications for the management and conservation of dimorphic species (Conradt & Roper, 2000; Bowyer, 2004; Ruckstuhl & Neuhaus, 2005). This is due to the direct influence that sexual segregation has on spatial use, reproductive performance and survival (Owen-Smith, 1993; Conradt & Roper, 2000; Mysterud, 2000). As a result, extensive research into sexual segregation has taken place over the past 10 years. Despite this, the underlying mechanisms remain poorly understood. (Ruckstuhl, 1998; Conradt, 1999; Ruckstuhl & Neuhaus 2000, 2002; Bowyer, 2004). It has also been suggested that the extent and causes of sexual segregation will vary depending upon the ecological conditions that the animal is exposed to and the different spatial and temporal scales at which they are studied (Conradt, 1998; Kie & Bowyer, 1999; Bonenfant et al., 2004; Bowyer, 2004). In this study we deal solely with segregation at the habitat scale.

Conradt (1998) was the first to separate and quantify sexual segregation, using two distinct categories, habitat segregation (the differential use of habitats by the two sexes) and social segregation (distinct male and female groups within the same habitat). Initially social segregation was believed to be a result of habitat segregation (Main et al., 1996). However, recent studies have demonstrated that segregation can occur within homogeneous habitats due to social factors or differing activity patterns (Ruckstuhl, 1998; Conradt, 1999; Ruckstuhl & Kokko, 2002; Pérez-Barbería et al., 2005). Therefore, social segregation and habitat segregation need to be treated as two separate components when investigating the mechanisms driving sexual segregation (Conradt, 1999; Ruckstuhl & Neuhaus, 2005).

Habitat segregation has been observed in a number of large herbivores including the red deer (*Cervus elaphus*) (Conradt, 1999; Bonenfant et al., 2004), alpine ibex (*Capra ibex ibex*) (Bon et al., 2001), white-tailed deer (*Odocoileus virginianus*) (Kie & Bowyer, 1999) and feral soay sheep (*Ovis aries*) (Conradt, 1999). Outside of the mating season, these animals separate into same sex groups, use different areas of their range and effectively exist

as two distinct 'ecological species' (Demment, 1983; Ginnett & Demment, 1997; Bowyer, 2004). Elucidating the factors responsible for this segregation is important for understanding how herbivores are spatially and temporally distributed, how their resources are partitioned and the resulting influence on habitat structure and ecosystem function (Bowyer, 2004). There are three main hypotheses that have been proposed to explain habitat segregation; these include the forage selection hypothesis (Ruckstuhl, 1998, Ruckstuhl & Neuhaus, 2000, Stokke & du Toit, 2000) the predation risk hypothesis (Kie & Bower, 1999; Ruckstuhl & Neuhaus, 2000; Corti & Shackleton, 2002) and the indirect competition hypothesis (Clutton-Brock et al., 1987; Conradt, 1999).

The key assumption of the forage selection hypothesis is that body size has a significant influence on the energy requirements of an individual due to the allometric scaling of metabolic rate (body mass^{0.75}) (Mysterud, 1998; Ruckstuhl & Neuhaus, 2000; Stokke & du Toit, 2000) resulting in larger individuals having reduced energy requirements per kg body mass (Demment, 1983; Demment & Van Soest, 1985). This relationship is coupled with an isometric scaling of gut size resulting in greater capacity and increased retention time proportional to body size (Demment & Van Soest, 1985; McNaughton & Georgiadis, 1986; Owen-Smith, 1992). Larger bodied individuals, can therefore digest low quality fibrous food for longer and derive greater nutritional benefit. It is therefore suggested that large herbivores should concentrate their foraging approach on lower quality food which is abundant in the environment rather than searching out rarer, higher quality food sources (Stokke & du Toit, 2000).

The predation risk hypothesis states that larger males are less susceptible to predation when compared with females and their offspring (Bleich et al., 1997; Ruckstuhl & Neuhaus, 2000; Corti & Shackleton, 2002). Therefore, males are predicted to select habitats primarily on the basis of foraging opportunities, in order to maximize growth and their reproductive potential, which is limited by competitive access to receptive mates (Clutton-Brock & Harvey, 1978; McElligott et al., 2001). In contrast, females invest disproportionately more energy and time into reproduction and the weaning of their offspring (Clutton-Brock & Harvey, 1978; Krebs & Davies, 1993). This alternative reproductive strategy and greater parental investment, coupled with increased risk of predation is believed to result in females selecting habitats

that are primarily safe, with forage quality and availability being a secondary consideration (Corti & Shackleton, 2002).

The indirect competition hypothesis predicts that females will out-compete males in the harvesting of resources and will therefore force them into utilising sub-optimal habitats (Clutton-Brock et al., 1987). The rationale being, that due to their larger body size males have greater metabolic demands than females and these need to be met by increasing intake (Demment, 1983; Demment & Van Soest, 1985). The intake rate of an individual herbivore is correlated to standing biomass and bite size. As bite size does not increase to the same extent as energetic demands with increasing body size, males require a greater quantity of standing biomass than females (Illius & Gordon, 1987). During periods of resource scarcity it is predicted that competition will lead to females reducing the standing biomass to such an extent that males can no longer forage efficiently (Conradt, 1999). Ultimately, this will lead to males utilising areas of lower forage quality but with greater available biomass.

The frequency of sexual segregation has been shown to increase with greater body size dimorphism (Mysterud, 2000). Therefore elephants provide an ideal study animal, with adult males weighing up to 6000 kg, twice the weight of an adult female (Owen-Smith, 1992; Poole, 1994). The aim of this study was to establish if the sexual segregation observed in elephant was being driven at the habitat scale. The objectives were: (1) Determine if the habitat use of male and female elephants is non-random throughout both the year and season. (2) Establish whether there is significant concordance in the habitat use of each sex. (3) Compare the habitat use of males and females to determine if there is concordance of behaviour between the sexes. (4) Explore the habitat use of males and females with regard to foraging behaviour. (5) Discuss the results of this study in context of the three main habitat segregation hypotheses.

Methods

Study sites

The Pongola Game Reserve (PGR) was established in 1993 and is situated in Northern Zululand, South Africa with a total extent of 82 km² (27°54'-27°35'S; 32°01'-31°86'E). The climate is hot and arid with an annual rainfall

of 400-700 mm. The vegetation falls into three of Acocks (1988) veld types: Zululand Thornveld, Lowveld and Arid Lowveld. Seven habitat types were recognized (Figure 1a). PGR has three distinct elephant groups, a small orphan family ($N = 7$), three adult males and a large herd ($N = 38$) (elephant population size as of October 2004). The herd utilise only the eastern section of the reserve (40 km^2) as they do not cross the railway line which effectively bisects the reserve in two. The three males and the orphan group range across the entire reserve.

Phinda Private Game Reserve (PPGR) is 180 km^2 in extent ($27^\circ 92' - 27^\circ 68'S$; $32^\circ 44' - 32^\circ 20'E$) and is located in Northern Zululand, South Africa. The reserve has a diverse range of habitat types from the endemic sand forest through to the sweet lowveld bushveld, Natal low bushveld and the coastal bushveld of the savanna biome (Low & Rebelo, 1996). Nine distinct habitats were distinguished (Figure 1b). The reserve has an average rainfall of approximately 750 mm (averaged over a 10 year period) with a maximum temperature of 35°C and a minimum of approximately 10°C . There is one river that runs through the southern section of the reserve and 6 dams that are fed with water from boreholes during the dry season. The total elephant population in 2004 was 75, comprising 18 adult males and 21 adult females in five family groups.

Pilansberg National Park (PNP) is a 500 km^2 reserve situated in the North West province of South Africa. It was established in 1979 and is approximately circular in shape ($25^\circ 8' - 25^\circ 22'S$; $26^\circ 57' - 27^\circ 13'E$). It occupies the crater of an extinct volcano and as such has hilly savanna relief. Acocks (1988) distinguishes the vegetation types as sour bushveld. Seven broad habitat types were used in this analysis (Figure 1c). The average yearly rainfall is 630 mm, which mainly falls in the summer (November-April) (Slotow & Van Dyk, 2001). The total population in early 2004 was 158 comprising 34 adult males and 124 females and juveniles in 16 family groups.

Location data

The data used in these analyses were collected over a 3 year period, from April 2002 to May 2005. The elephants were located using either radio telemetry or by traditional methods (following dung and tracks). On sighting an elephant, a GPS position of the observer was taken, along with date, time, habitat type and behavioural observations. The elephant's precise location was then calculated by estimating the distance and bearing from the

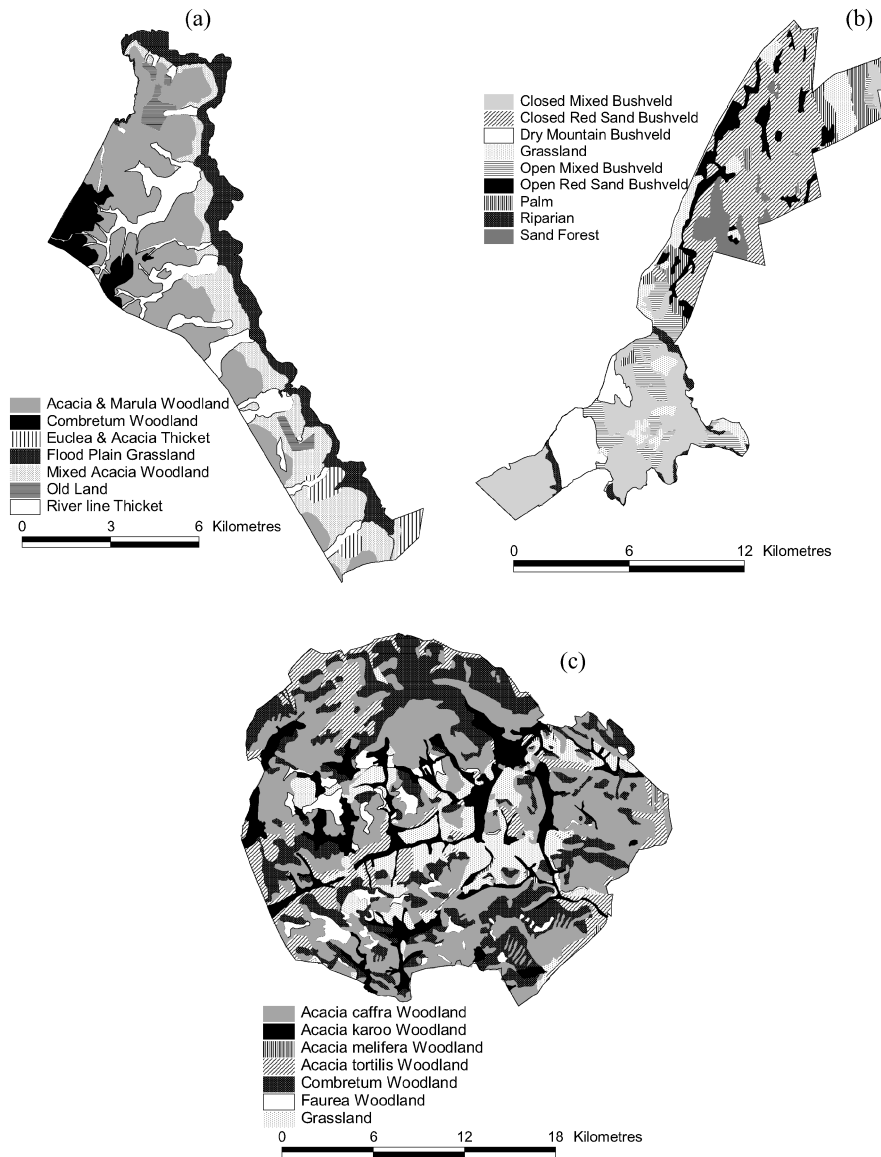


Figure 1. Habitat maps of the (a) Pongola Game Reserve, (b) Phinda Private Game Reserve and (c) Pilanesberg National Park.

observer to the individual elephant or the centre of the group. The elephants were then followed at a discrete distance until they moved out of sight, or the

observation period ended. During this time, location points were taken at approximately 20-minute intervals. Satellite GPS collars and GPS/GSM collars automatically recorded positional data throughout the day at pre-determined times.

Habitat mapping

Geographically referenced habitat maps were developed for each of the reserves. The habitat map of PGR was produced using satellite images, aerial photos and vegetation transect data (Figure 1a). The transect data, collected at 47 different sites throughout the reserve provided information on the vegetation composition within different areas. Seven broad habitat types were derived from these data using a TWIN SPAN analysis. The borders of the major habitats were digitised in ArcView[®] 3.2 from the aerial photos and satellite images using physiognomic features. The map was then assessed for reliability using a GPS to record the actual positions of vegetation boundaries, river lines and other physical features of the landscape.

The habitat map of PPGR was developed by Hunter (1998). The map was created by first mapping the boundaries and major features of the reserve, including water points, roads and buildings. From this basic outline, the vegetation was surveyed in different areas of the reserve and a GPS used to delineate the boundaries of distinct vegetation types. The classification of the original vegetation types was done according to the species present, the overall habitat structure and a broad substrate classification. Aerial photos of the region were also used to distinguish habitat types and their boundaries. As with the other reserves, the vegetation map was checked for reliability using ground surveys. Nine habitat types were distinguished (Figure 1b).

The habitat map in PNP was created using an extensive ground surveying technique, which involved separating the reserve into distinct 250 m² blocks. Each of these blocks was then assigned a vegetation type on the basis of a previous analysis. A GPS was used to map distinct features of the reserve including the boundaries, roads and drainage lines, this enabled the vegetation blocks within the reserve to be spatially referenced. The map was checked for reliability using further field surveys. For the analyses in this study, similar vegetation types were combined on the basis of shared attributes to create distinct physiognomic habitat types in the same way that had been done for PGR. These habitats were classified not just on the basis of vegetation

composition but also terrain, aspect and slope. Contour maps and additional vegetation data from Moolman (unpublished data) were utilised for this aspect of the mapping. The final habitat map of PNP consisted of 7 broad types (Figure 1c).

Statistical analysis

Data were used from 12 female groups (PGR = 2, PPGR = 3 and PNP = 7) and 16 adult males (PGR = 3, PPGR = 7 and PNP = 6). Adult males were distinguished as individuals ≥ 15 years old, which ranged independently from the female groups and are therefore, theoretically, reproductively active. Due to the limited sample size of males we did not classify the elephants into sub-adults and adults, despite significant size dimorphism. The elephants used in this study were selected on the basis that accurate location data were available for a minimum of 100 days throughout the study period. Microsoft Access was used to filter the data and select one location point for each individual/group per day. This ensured independence of the data and prevented errors associated with auto correlation (Swihart et al., 1988; de Solla et al., 1999; Ramsey & Usner, 2003). The data were then separated further on the basis of season (summer and winter) and three time periods, 5:00-10:00, 10:00-15:00 and 15:00-20:00. Finally, the behavioural codes were used to filter out locations when foraging was observed. This enabled an analysis of the habitats selected specifically for feeding to be carried out.

These positional data were imported into ArcView[®] 3.2 ensuring that each location was geographically referenced and in the correct format for spatial analysis. Using the Geo-Processing Wizard in ArcView[®] 3.2, each location point was assigned a habitat type in accordance with the reserve habitat maps (Figure 1). These data were then exported to Excel and the number of locations within each habitat type was determined. The X-tools extension in ArcView[®] 3.2 was used to calculate the area of each habitat within the reserve. Habitat utilisation ratios were calculated as: (the number of locations in a specified habitat / the total number of locations) / (the area of the specified habitat type / the total area).

If habitats were utilised in direct proportion to their occurrence, then a ratio of 1 would be expected, whilst ratios below 1 suggested below average utilisation and values above 1 indicated above average utilisation. Two of the

habitats (*Protea caffra* woodland and Tambothi) in PNP were removed from the analysis due to their limited size (less than 1% of the area), and because there were no elephant sightings within them. The habitat selection ratios were calculated for the entire data set (both seasons combined), separately for summer and winter and for the three daily time periods, allowing the temporal aspect of habitat segregation to be explored. This analysis was repeated for each female group and all the adult males. A Chi-Squared test was used to ascertain whether male and female elephants were exhibiting distinct patterns of habitat selection throughout the two seasons, or using the available habitats at random. The mean habitat selection ratios for male and female elephants, in each reserve, were used for these analyses.

A Kendall's coefficient of concordance (Siegel & Castellan, 1988) was used to assess the ranking of habitats for each sex in the three different reserves. This non-parametric analysis tests the hypothesis that several related samples are drawn from the same population. In this study, the related samples were the ranked habitat selection ratios of the male and female elephants. The test returns a result of between 0 (no agreement) and 1 (total agreement). The data were initially tested for one sex at a time, females versus females and males, versus males to ascertain whether individuals of the same sex were ranking habitats in a significantly concordant manner. The male and female data were then combined and the analysis repeated. The idea being, that intra-sexual and inter-sexual differences in habitat ranking could be compared from the two sets of results. If males and females were found to exhibit significant concordance in their utilisation of habitats then we could conclude that segregation is not being driven at the habitat scale. Similarly, the variation exhibited within sex could be compared with the variation between sexes, and thus enable us to elucidate whether variation in habitat selection was due to the behavioural preferences of individuals, or whether it was driven by sex differences. The data were analysed separately for each reserve due to the differences in habitat types.

The data for the female groups in PGR were analysed using the Kendall's tau b test, as a sample size of two required the use of a bivariate correlation. The remaining data were analysed using the Kendall's coefficient of concordance as they consisted of sample sizes greater than three. The Kendall's tau-b test was also used to establish whether the mean habitat selection ratios for the sexes, within a particular reserve, were significantly correlated. This allowed the actual values to be compared as well as the ranks that were

calculated using the Kendall's coefficient of concordance. The results from these analyses were plotted with one standard error to account for variation within the male and female data sets.

A secondary analysis was performed to assess whether there was differential use of habitats selected for foraging by the sexes, as differences in feeding behaviour have been proposed to drive habitat segregation in sexually dimorphic herbivores (Main et al., 1996; Ruckstuhl & Neuhaus, 2005). The data were filtered to include only location points associated with foraging, compared to the previous analysis which included all behaviours. For individual males it was relatively easy to assign a behavioural code depending upon their activity, whilst for the female groups the dominant behaviour was established as the activity engaged in by $\geq 55\%$ of the individuals present. Both sexes were analysed using the Kendall's coefficient of concordance to establish whether female groups and individual males in the same reserve ranked habitats concordantly with regard to their foraging behaviour. Once the sexes were analysed individually, the data were combined and the analysis re-run to determine if males and females were segregating on the basis of their foraging behaviour. A final analysis of foraging behaviour involved using a *G*-test to compare the locations of 500 individual feeding bouts that were observed throughout the PGR and PPGR from 2002-2005. The location of each feeding bout was spatially assigned to a habitat type using the same method detailed above. The *G*-test was then used to establish if males and females targeted significantly different habitats during their foraging bouts.

Results

Elephant habitat selection and rankings

The chi-squared test confirmed that both male and female elephants exhibited pronounced habitat selection throughout the year (Table 1). The same result was repeated across the three data sets, with only the summer result for PGR males proving the exception. However, this result is in agreement with the 2000-2001 PGR habitat utilisation analysis (Shannon et al., 2006). The ranking of habitats by males and females (Figure 2) indicates a strong relationship and selection of certain habitats, whilst others appear to be avoided.

Table 1. Results of a chi-squared test showing that males and females are utilising habitats in a non-random manner. Mean habitat selection ratios for males and females in PGR, PPGR and PNP were used for the analysis.

	PGR		PPGR		PNP	
	χ^2_6	<i>p</i> -value	χ^2_8	<i>p</i> -value	χ^2_6	<i>p</i> -value
Summer female	21.34	<0.005	27.54	<0.005	106.23	<0.001
Winter female	72.7	<0.001	31.61	<0.001	80.01	<0.001
Summer male	3.4	>0.75	17.94	<0.025	79.11	<0.001
Winter male	23.13	<0.001	39.53	<0.001	71.53	<0.001

PGR female groups $N = 2$ and males $N = 3$, PPGR female groups $N = 3$ and males $N = 7$, PNP female groups $N = 7$ and males $N = 6$.

Habitat utilisation in PGR

There was a strong correlation (Kendall's tau b) in habitat selection for the two female groups throughout the year (Figure 2 & Table 2). The summer season exhibited the strongest relationship with both groups ranking the seven habitats in the same order, (Kendall's tau b = 1.00, $p = 0.00$, $N = 7$). The winter association had a weaker correlation but was still significant (Kendall's tau b = 0.71, $p = 0.02$, $N = 7$). There was also a correlation between the temporal utilisation of habitats throughout the day, except in the third period (15:00-20:00). The three males in PGR did not exhibit concordance in the use of their habitats during the different seasons (Figure 2 & Table 2). They had low Kendall's W values in both the summer and winter period. The three daily time periods are also non-significant.

The combination of the male and female data indicates a significant concordance in the ranking of habitats (Table 2). The summer season in PGR showed no concordance across male and female habitat selection (Table 2). The temporal use of habitats throughout the year was correlated for females and males, suggesting similar patterns in use at the 5 hr scale. The mean male and female selection ratios were plotted with one standard error to show the male and female habitat use in the two seasons. (Figure 3a & b). Males used all seven habitats during the summer, whilst the females only used five, thus creating a significant difference in habitat use (Kendall's tau b = 0.05, $p = 0.88$, $N = 7$). The winter utilisation showed a closer correlation between the two sexes but remains non-significant (Kendall's tau b = 0.43, $p = 0.18$, $N = 7$). The *Combretum* woodland was removed from the analysis as the herd do not access this habitat due to it occurring solely on the

Table 2. The results of a Kendall's coefficient of concordance analysis ($p < 0.05$ indicates concordance) to establish whether female groups and individual males exhibit concordance in their habitat selection (the first analysis uses all behaviours and the second specifically focuses on foraging behaviour).

	Habitat selection: all behaviours						Habitat selection: foraging					
	PGR		PPGR		PNP		PGR		PPGR		PNP	
	Kendall's W	p- value	Kendall's W	p- value	Kendall's W	p- value	Kendall's W	p- value	Kendall's W	p- value	Kendall's W	p- value
Female total	0.78	0.02	0.8	0.01	0.68	0	0.52	0.1	0.76	0.02	0.62	0
Female summer	1	0	0.84	0.01	0.94	0	0.8	0.01	0.9	0.01	0.79	0
Female winter	0.71	0.02	0.58	0.08	0.54	0	0.29	0.29	0.35	0.4	0.49	0
Male total	0.63	0.08	0.7	0	0.95	0	0.65	0.07	0.52	0	0.85	0
Male summer	0.49	0.18	0.6	0	0.73	0	0.48	0.2	0.38	0.01	0.57	0.01
Male winter	0.56	0.12	0.67	0	0.91	0	0.73	0.04	0.63	0	0.88	0
Male & female total	0.5	0.02	0.65	0	0.72	0	0.43	0.05	0.52	0	0.68	0
Male & female summer	0.2	0.43	0.63	0	0.81	0	0.07	0.91	0.49	0	0.64	0
Male & female winter	0.52	0.02	0.58	0	0.6	0	0.54	0.01	0.43	0	0.63	0

PGR female groups $N = 2$ and males $N = 3$, PPGR female groups $N = 3$ and males $N = 7$, PNP female groups $N = 7$ and males $N = 6$.

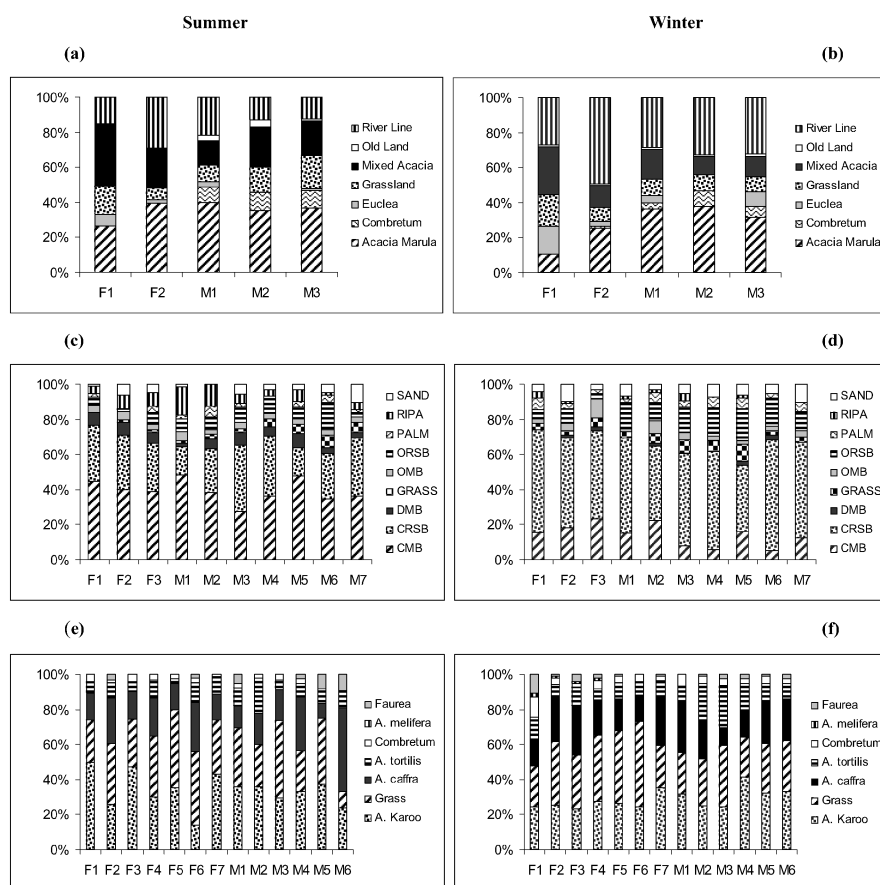


Figure 2. The ranking of habitat types by male and female elephants during the summer and winter seasons, in the (a & b) PGR, (c & d) PPGR and (e & f) PNP. (F = distinct female groups, M = individual males.) Refer to Figure 1 for habitat types.

western side of the railway line. The summer remained non-significant for the analysis of the means (Kendall's tau b = 0.28, $p = 0.44$, $N = 6$) but the mean winter habitat selection of the two sexes were significantly correlated (Kendall's tau b = 0.73, $p = 0.04$, $N = 6$).

Habitat utilisation in PPGR

The females in PPGR exhibited strong statistical concordance in their habitat selection during the summer months, this weakened during winter and the result was marginally non-significant (Figure 2 & Table 2). The three

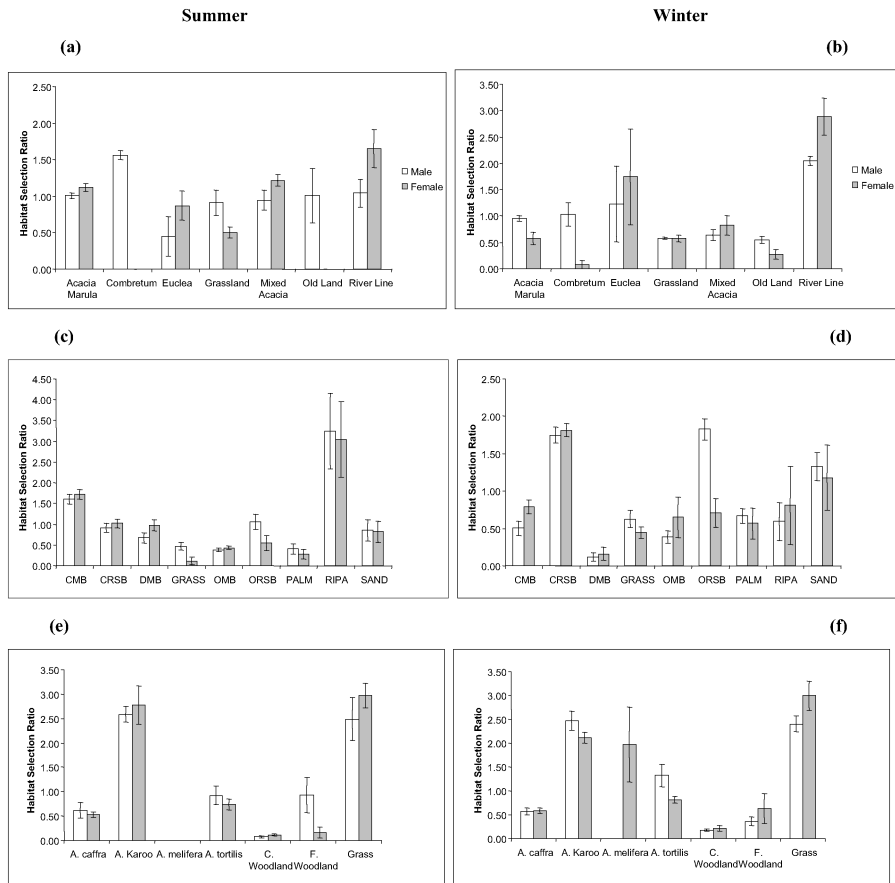


Figure 3. Comparing habitat utilisation of male (white) and female (grey) elephants using the mean selection ratios (all behaviours) for both summer and winter in (a & b) PGR, (c & d) PPGR and (e & f) PNP (Data are mean \pm 1 standard error).

family groups also exhibited concordance during the three time periods. The males showed concordance in their habitat selection through all the different analyses and all the daily time periods (Figure 2 & Table 2). The combined data indicates concordance in habitat choices by males and females (Table 2). The mean preference ratios for both sexes exhibited a similar pattern throughout the year (Figure 3c & d). The largest discrepancy was in the winter period when males target the open red sand bushveld to a much greater extent than the females. The mean habitat selection of males and females were significantly correlated in the summer (Kendall's tau $b = 0.611$,

$p = 0.02$, $N = 10$) but not in winter (Kendall's tau b = 0.44, $p = 0.1$, $N = 10$).

Habitat utilisation in PNP

The females and males both exhibited significant concordance in their habitat selection across all analyses (Figure 2 & Table 2). The combined data showed significant concordance in habitat selection for male and female elephants in PNP, across all analyses (Table 2). The mean habitat selection of female and male elephants was correlated in the summer season (Kendall's tau b = 0.015, $p = 0.78$, $N = 13$), whilst winter was non-significant (Kendall's tau b = 0.43, $p = 0.18$, $N = 13$). The use of *A. melifera* woodland by the females may well account for a significant level of variation (whilst males completely avoided the habitat).

Foraging behaviour

The data were further analysed to establish whether different habitats were used for foraging by the two sexes (Figure 4). Female groups in all three reserves exhibited strong statistical concordance with regard to feeding preference during the summer months, whereas during the winter the concordance was much weaker, with non-significant results for both PGR and PPGR (Table 2). The males exhibited the opposite relationship, with weaker concordance during the summer months, including non-significant results for PGR and stronger concordance in the winter (Table 2).

The three time periods showed varied results for both sexes, but all of them were statistically significant, except for the males in PGR during the second time period (10:00-15:00) (Kendall's $W = 0.50$, $p = 0.18$, $N = 7$). The males in PPGR exhibited concordance throughout all of the time periods. However, the Kendall's values were below 0.5 for each result and this suggests a substantial variation in preference between individual elephants. PNP showed a consistently ($W \geq 0.6$) high concordance throughout the day as did the female groups in all three of the reserves.

Male and female seasonal foraging selection showed concordance throughout the data set except for one non-significant result the PGR summer data (Table 2). Despite the concordance there was a high level of variation with Kendall's values ranging from 0.42-0.68 (Table 2). Male and female elephants in PNP showed the highest concordance in foraging preference. The

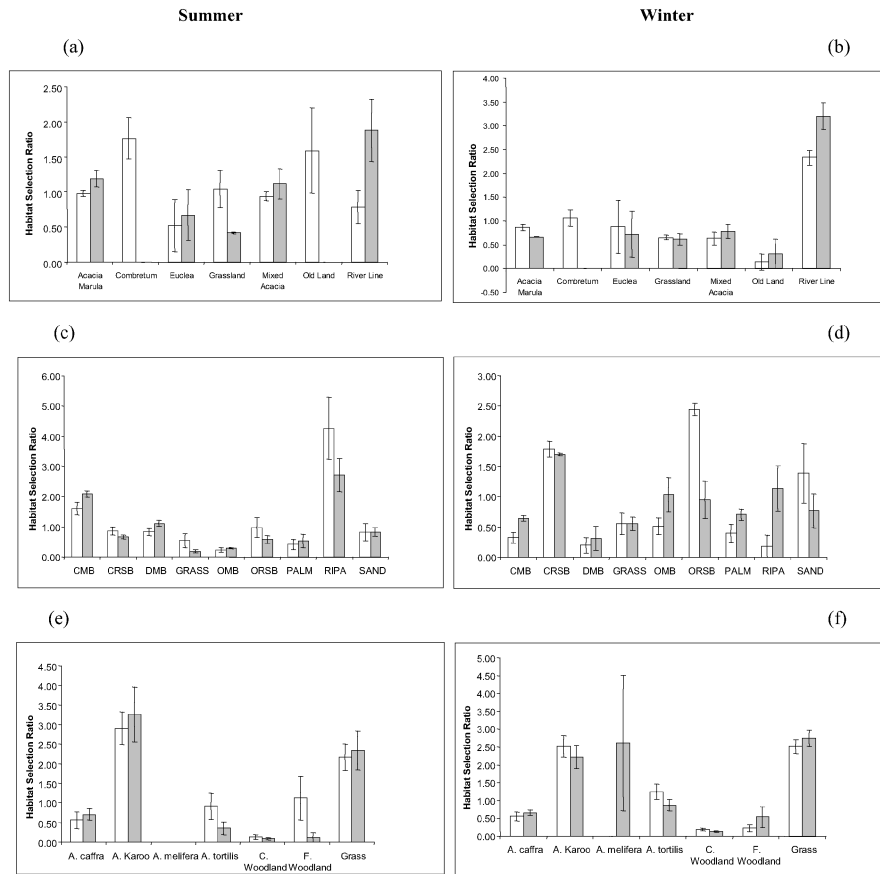


Figure 4. Comparing habitat utilisation of male (white) and female (grey) elephants using the selection ratios (foraging behaviour) for both summer and winter in (a & b) PGR, (c & d) PPGR and (e & f) PNP (Data are mean \pm 1 standard error).

three time periods were significantly concorded throughout all of the data sets, suggesting a similar pattern of temporal use throughout the day for both males and females. The means were calculated and the values plotted for each sex in all three reserves and a Kendall's tau b correlation was used to test whether there was a significant relationship between mean habitat preference for females and males (Figure 4).

The G -test comparing the locations of observed male and female feeding bouts in the PGR returned a significant result when all the habitats were analysed ($\chi^2_7 = 15.6$, $p < 0.05$), suggesting differential habitat use. A

non-significant result was returned however, when the combretum woodland (habitat not accessed by the large herd) was excluded from the analysis ($\chi^2_6 = 6.5$, $p > 0.25$). The analysis of the PPGR data indicated that there was no significant difference in the locations of foraging bouts for male and female elephants, when they were compared at the habitat scale ($\chi^2_6 = 4.9$, $p > 0.5$).

In summary females and males exhibited concordance across their results and are therefore not selecting habitats significantly differently from each other. However, there were distinct patterns exhibited by each sex throughout the three data sets. The females had their weakest concordance values throughout the winter periods for both habitat and foraging selection, whilst the males showed the opposite relationship with their weakest concordance values occurring in the summer period.

Discussion

Male and female elephants exhibited distinct habitat selection and do not use their available range in a random manner. This concurs with the findings of Shannon et al. (2006) and previous studies on elephant (Viljoen, 1989; Babassa, 2000). Despite this, the analyses suggest that sexual segregation of elephants is not being driven at the habitat scale, as males and females appear to be responding in a similar manner with regard to their overall habitat selection, throughout the reserves and on the basis of both season and time. In fact the variation in habitat selection is as broad between the sexes as it is within groups and individuals of the same sex. A similar result was also found for the analyses of habitats used by the sexes for foraging, with only PGR showing any significant differences. However, this is likely to be explained by the railway line that bisects the reserve in two and acts as a barrier to the large female herd from accessing the west of the reserve. Stokke & du Toit (2002) investigated habitat segregation of elephants in the Chobe National Park, Botswana and found that the proximity of water rather than vegetation quality had the most significant effect in determining habitat preference because females and their offspring had higher rates of water turn over and lower mobility compared to males. In this study, access to water is factored out of the analysis due to the relatively small size of the reserves (<500 km²) and the abundance of permanent water points. This may be a

contributory factor in explaining why habitat segregation was not observed, yet it allowed us to test for the occurrence of habitat segregation solely on the basis of vegetation types.

Habitat segregation has been exhibited in a number of dimorphic species, including bighorn sheep (*Ovis canadensis*) (Ruckstuhl, 1998), red deer (*Cervus elaphus*) (Conradt, 1999), and soay sheep (*Ovis aries*) (Bonenfant et al., 2004). However these species are all temperate ruminants, which are smaller and more selective in their foraging approach than the elephant, which is a large generalist herbivore with the ability to digest significant quantities of low quality fibrous forage. The diversity of habitats occupied by the African elephant is further evidence to its generalist habits (Owen-Smith, 1992; Spinage, 1994). Therefore, despite body size differences, females and males will be able to utilise most habitats for foraging as they can target a wide range of species from grasses to browse (Owen-Smith, 1992).

It is indeed more likely that the feeding approach at the patch and plant scale may provide the catalyst for segregation in resource use (Stokke, 1999; Stokke & du Toit, 2000). Similar results were found for the giraffe, with both males and females using similar habitats yet exhibiting significant differences in their use of forage resources at the patch and plant level (Ginnet & Demment, 1997). This highlights the importance of investigating different spatial and temporal scales in studies on sexual segregation (Conradt & Roper, 2000; Bonenfant et al., 2004). Shannon et al. (in press) and Stokke & du Toit (2000) confirm the importance of foraging behaviour to the sexual segregation of elephants, with males exhibiting a significantly different foraging approach to females. These differences include male elephants targeting larger trees, ingesting greater quantities of low quality forage, having feeding bouts of longer duration and exhibiting more destructive feeding behaviour. Grazers are less likely to be influenced at the plant scale due to the relatively homogenous nature of grasses, which may explain their pronounced segregation at the habitat scale.

The predation risk hypothesis predicts that females should choose 'safer' habitats as their offspring are vulnerable to predation (Ruckstuhl & Neuhaus, 2000; Corti & Shackleton, 2002). Natural predation of elephants in the three study sites chosen for this research is almost non-existent and even in large open systems, the predation of elephant is generally minimal and opportunistic (Ruggiero, 1991), although in Botswana, certain lion prides have been observed to specifically target elephants (Joubert, 2006). Despite this, predator

response has evolved over millions of years and it is likely that there will be a perceived risk whether predators are present or not (Ruckstuhl & Neuhaus, 2000). Human predation must also be considered as it has been a very significant factor in the mortality of elephants over the past 500 years (Spinage, 1994). Therefore elephants in the small reserves are expected to show similar fear responses and risk aversion behaviour as elephants in larger more open systems. In this study female elephants utilised habitats in a similar manner to males and there does not appear to be avoidance of certain habitats due to 'predation risk'. Female elephants are however disturbed and stressed with greater frequency than male elephants leading them to seek out dense habitat for safety (Burke, 2005), yet this appears to be a fairly short-term response and feeding will often resume within the previous habitat once the threat has passed. Male elephants on the other hand have been recorded to exhibit greater risk tolerance in order to maximize nutritional return (Sukumar & Gadgil, 1988). It is suggested that this is reason that the majority of crop raiding is perpetrated by male elephants (Hoare, 1999). This behaviour appears to be opportunistic however and varies from one individual to another and is unlikely to be a causal role in the segregation of the sexes.

Of the three theories explaining habitat segregation in ungulates, the indirect competition hypothesis has garnered the least support. Conradt et al. (1999) concluded that it was not a causal factor in the segregation of red deer, despite Clutton-Brock et al. (1987) initially proposing the theory after observations on the same population. Theoretically grazers are the most likely to be affected by indirect competition, due to the homogenous structure and distribution of grass, which is likely to be reduced to a lower standing crop and sward height during resource scarcity, creating a situation where individuals with larger energy requirements may be out competed by smaller individuals (Illius & Gordon, 1987; Conradt et al., 1999). The catholic diets of elephants, coupled with their mixed foraging approach (being able to target both grass and browse) and large body size would suggest that they are unlikely to be influenced by indirect competition, even during the relative resource scarcity of the dry season (Stokke & du Toit, 2000). Despite the lack of an empirical test at the habitat scale, it is likely that this theory can be rejected on the basis of limited evidence of its role in the segregation of other herbivore species, coupled with the lack of habitat segregation observed in this study.

Both male and female elephants demonstrated seasonal patterns of variation in the concordance of habitat and foraging selection. The female groups

exhibited the greatest variation (i.e., lowest Kendall's values) in concordance during the winter periods, whilst in summer the values were much greater. This may well be a function of resource abundance which enables family groups to forage in close proximity to each other. Such aggregations serve a social purpose, as female groups exhibit a complex societal structure which is often reaffirmed when resources permit and groups can interact (Wittemyer et al., 2005). In PGR for example, the summer period accounted for 64% of the recorded associations between the two female groups. In winter however, resource scarcity may force family groups to segregate in an attempt to reduce potential competition. The group dynamics of impala have been shown to reduce individual foraging efficiency and cause significant intraspecific competition (Fritz & De Garine-Whichatitsky, 1996). This may also be a factor that influences the association of female elephants during the winter season or drought periods (Wittemyer et al., 2005).

Males show the opposite relationship to females. During winter they exhibited high values of concordance for both habitat and foraging selection. This may be associated with their large size and independent nature, which allows them to target remaining abundant low quality forage with little if any competitive exclusion (Shannon et al., in press). Indeed, Shannon (2005) found that male elephants focus their ranges and their movements during resource scarcity. Throughout the summer months, males have their lowest values of concordance suggesting higher levels of variation in habitat selection from one elephant to the next. This may be explained either due to the greater availability of resources which provide increased flexibility with regard to foraging and/or by the presence of musth males which have heightened levels of testosterone and display aggressive behaviour towards would be competitors (Poole, 1989; Slotow & van Dyk, 2001). In all three of our study sites, musth was most commonly observed during the summer, when resources are abundant (pers. obs.). It is important to note however, that it is a year-round phenomenon (Poole, 1994; Owen-Smith, 1992). Elephants in musth are avoided by other males and this tends to indicate that reproductive strategies can play a significant role in habitat utilisation and selection. This was also postulated as a reason for habitat segregation in a study on elephant habitat use in the Chobe National Park (Stokke & du Toit, 2002). Male elephants were found to range widely during the dry season, despite the paucity of water sources and it was suggested that this response is driven by conflict avoidance, with dominant musth males associating with family groups in regions close to water (Stokke & du Toit, 2002).

Conclusions

Elephants exhibit distinct patterns of habitat utilisation, but the differences that occur are as pronounced for individuals of the same sex as they are when males and females are compared. This was confirmed across all three reserves, despite their diversity in vegetation, size differences, populations and history. Large generalist herbivores such as the elephant are able to target a wide diversity of habitats and food sources within the African savanna and we suggest that it is unlikely that the pronounced segregation observed in elephant is being driven at the habitat level by the foraging selection or indirect competition hypotheses. Instead, the actual foraging approach adopted by males and females is expected to be significantly different at the patch and plant level where decisions on how to feed, and for how long, occur (Shannon et al., in press). Male elephants appear to show greater tolerance to disturbance than females and therefore may use more 'risky' habitats, but this has been difficult to assess and is generally an occasional event, rather than a distinct strategy. However, further investigation is necessary for predation risk to be ruled out completely as a factor in the segregation of elephant. On the basis of our results, we conclude that, differential habitat selection by the sexes is unlikely to be the mechanism by which elephants are segregated.

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