

The role of foraging behaviour in the sexual segregation of the African elephant

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Abstract Elephants (*Loxodonta africana*) exhibit pronounced sexual dimorphism, and in this study we test the prediction that the differences in body size and sociality are significant enough to drive divergent foraging strategies and ultimately sexual segregation. Body size influences the foraging behaviour of herbivores through the differential scaling coefficients of metabolism and gut size, with larger bodied individuals being able to tolerate greater quantities of low-quality, fibrous vegetation, whilst having lower mass-specific energy requirements. We test two distinct theories: the scramble competition hypothesis (SCH) and the forage selection hypothesis (FSH). Comprehensive behavioural data were collected from the Pongola Game Reserve and the Phinda Private Game Reserve in South Africa over a 2.5-year period. The data were analysed using sex as the independent variable. Adult females targeted a wider range of species, adopted a more selective foraging approach and exhibited greater bite rates as predicted by the body size hypothesis and the increased demands of reproductive investment (lactation and pregnancy). Males

had longer feeding bouts, displayed significantly more destructive behaviour (31% of observations, 11% for females) and ingested greater quantities of forage during each feeding bout. The independent ranging behaviour of adult males enables them to have longer foraging bouts as they experience fewer social constraints than females. The SCH was rejected as a cause of sexual segregation due to the relative abundance of low quality forage, and the fact that feeding heights were similar for both males and females. However, we conclude that the differences in the foraging strategies of the sexes are sufficient to cause spatial segregation as postulated by the FSH. Sexual dimorphism and the associated behavioural differences have important implications for the management and conservation of elephant and other dimorphic species, with the sexes effectively acting as distinct “ecological species”.

Keywords *Loxodonta africana* · Body size dimorphism · Allometric relationships · Ecological segregation

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Introduction

Body size influences the foraging behaviour of mammalian herbivores in three distinct ways. Firstly, metabolic rate scales with a coefficient of approximately 0.75 as body size increases (Kleiber 1961; Peters 1983; Demment 1983; Owen-Smith 1992), resulting in larger individuals requiring less energy per kg of mass, due to greater efficiency and reduced heat loss. Secondly, larger body size is coupled with a directly proportional increase in gut capacity (Demment 1983; Demment

and Van Soest 1985; Stokke and du Toit 2000). Increased gut size allows larger quantities of forage to be retained for longer periods and thus greater levels of digestion are achieved (Owen-Smith 1992; Van Soest 1996; Clauss et al. 2003). The relationship between decreasing metabolic rate, increased gut size and longer retention time enables larger bodied herbivores to consume and digest greater quantities of low-quality forage than smaller individuals; this correlation is known as the Jarman-Bell principle (Bell 1971; Jarman 1974; Mysterud 1998). Finally, forage quality varies dramatically across a range of scales in terrestrial biomes, from the different plant parts and chemical constituents (e.g. tannins) to the diversity of different species at the habitat and landscape scales (McNaughton and Georgiadis 1986; Seagle and McNaughton 1992; Skarpe et al. 2000). Therefore, unlike mammalian carnivores where protein availability and energetic return per kg is relatively constant, herbivores need to make a complex series of decisions in order to maximize their nutritional intake (Stephens and Krebs 1986; Brown 2000). This is dependent on body size and the scale of spatial resolution (Senft et al. 1987; Jetz et al. 2004).

Large herbivores are predicted to trade-off quality against quantity, as the benefits of abundance outweigh the costs of searching for forage opportunities of high nutritional return, which are generally rare in the environment (Demment and Van Soest 1985; McNaughton and Georgiadis 1986). In contrast, smaller herbivores, which have greater relative energetic demands and reduced gut efficiency, will forage selectively for higher quality food sources (Demment and Van Soest 1985). Therefore, as the body size of herbivores increases, the relationship between the organism and the environment changes, especially with regard to the scale of resolution (Demment 1983). This relationship is also predicted to play a significant role in the foraging behaviour of species that exhibit pronounced sexual dimorphism (Owen-Smith 1992; Ginnet and Demment 1999; Stokke and du Toit 2000).

Sexual dimorphism in ungulates is believed to result from two contrasting reproductive strategies. Adult males gain an advantage through larger body size, as it enables them to dominate smaller individuals and achieve greater mating success (Darwin 1871; Jarman 1974; Loison et al. 1999). The reproductive investment for the male ends after successful copulation and is only limited by the availability of females in oestrus (Clutton-Brock and Harvey 1978; Krebs and Davies 1993). Females, on the other hand, exhibit much higher levels of investment in reproduction and select mates on the basis of size and fitness (Anderson 1994;

McElligott et al. 2001). They are limited by the number of offspring they can produce (Clutton-Brock and Harvey 1978; Le Blanc et al. 2001), and subsequently no significant advantage is gained from larger body size.

In addition to smaller body size, female ungulates experience elevated energy demands during pregnancy and lactation, with peak lactation costs increasing the energy requirements of an individual by as much as 150% (Loudon 1985; Clutton-Brock et al. 1989; Blanchard 2005). This is especially pronounced in elephant, with adult females often being in a state of pregnancy (gestation of 22 months), lactation (weaning takes approximately two years) or both (Spinage 1994). Such a considerable reproductive investment results in female elephants attaining their full height around 20–25 years old, whilst males continue to divert energy into growth throughout their lives (Poole 1994; Lee and Moss 1995). Male and female elephants have similar body sizes and comparable energy demands until their mid-teens, but after this age they begin to exhibit pronounced dimorphism and behavioural differences (Poole 1994; Lee and Moss 1995).

Sociality in elephants is also strongly dependent on sex, with adult females and their offspring remaining together in tightly bonded groups (Moss and Poole 1983; McComb et al. 2001; Charif et al. 2005). It is believed that this complex and highly developed sociality has developed in response to predation pressure (Wittermeyer et al. 2005). Young males are forced out of the family group between the ages of 10–15 and either establish bachelor groups or range independently. The social ties between male elephants are much weaker than the ones between related females, and as such they make decisions on an individual basis as opposed to the group decisions made in elephant herds (Barnes 1979; Poole 1994; Spinage 1994; Rands et al. 2003). Elephants are sexually segregated for the majority of the year, with adult males and females only associating for the purpose of reproduction (Poole 1994).

The forage selection hypothesis (FSH) is one of the main theories proposed to explain spatial segregation in sexually dimorphic species (Main et al. 1996; Ruckstuhl and Neuhaus 2000). It is based on the premise that differences in body size, energy budgets and efficiency of digestion result in distinct feeding strategies for both sexes (Main et al. 1996). Females are predicted to be more selective in their foraging approach, due to their higher relative energy demands and reduced digestive efficiency, whilst males consume greater quantities of fibrous, low-quality forage (Stokke and du Toit 2000; Ruckstuhl and Neuhaus 2000). These feeding differences are predicted to result in both spatial and temporal segregation (Ginnet and

Demment 1999; Ruckstuhl and Neuhaus 2000). The second theory tested in this study is the scramble competition hypothesis (SCH), which predicts that females will out-compete and therefore displace larger males (Clutton-Brock and Guinness 1987; Conradt 1999; Ruckstuhl and Neuhaus 2000). Females are predicted to be superior competitors due to their lower absolute energy requirements and narrower muzzles, which enables them to reduce the sward height to such an extent that it is no longer profitable for males (Illius and Gordon 1987; Clutton-Brock and Guinness 1987). This results in males being displaced into lower quality habitats which have greater overall biomass. In browsing herbivores, feeding height stratification would result, with males being out-competed at preferred heights, forcing them to compensate by feeding higher up the tree, out of the reach of females (du Toit 1990; Stokke and du Toit 2000).

The role of the FSH in the sexual segregation of elephant has previously been investigated by Stokke and du Toit (2000); their study was carried out during the dry season in the Chobe National Park, Botswana, using vegetation sampling methods to assess the foraging behaviour of elephants after they had fed at a particular location. In this study we use direct observations of elephant feeding bouts in both the summer and winter seasons. The data were collected from two populations, where repeat sightings of known individuals were possible. The objectives were to: (1) quantify the foraging approach of male and female elephants at the plant scale; (2) establish what influence age, body size and sociality have on the foraging behaviour of elephants; (3) compare our results with those of Stokke and du Toit (2000); (4) assess the forage selection hypothesis and scramble competition hypothesis as explanations for sexual segregation in elephant.

Methods

Study site

The Pongola game reserve (PGR) is 82 km² in extent and situated in Northern Zululand, South Africa (27°54′–27°35′ S; 32°01′–31°86′ E) on the western shoreline of the Jozini Dam. The climate is hot and arid, with an annual average rainfall of 650 mm and a range of 350–1,000 mm. The vegetation falls into three of Acocks (1988) veld types: zululand thornveld, lowveld and arid lowveld. Seven habitat types are recognized (Shannon et al. 2006). PGR has three distinct elephant groups, a herd of 38 individuals, consisting of two closely associated families, a small orphan group

totalling seven individuals and four adult males. The youngest male in PGR was approximately 17 years old, whilst the other three were older than 32. There were 13 adult females (distinguished as individuals with offspring) in the herd and a further four in the small orphan family group, all of which were used in the analyses. The four males and the orphan group range across the whole reserve, whilst the herd only utilised the eastern section (40 km²) between the lakeshore and the railway line, which bisects the reserve from the southern border to the northwest fence line.

Phinda private game reserve (PPGR) is situated in southern Maputaland and covers an area of 180 km² (27°92′–27°68′ S; 32°44′–32°20′ E). The reserve has a diverse range of habitats, including the endemic sand forest, sweet lowveld bushveld, Natal lowveld bushveld and the coastal bushveld of the savanna biome (Low and Rebelo 1996). The reserve has a ten-year average rainfall of approximately 750 mm and a maximum temperature of 35 °C during the summer months. The minimum temperature experienced in winter is approximately 10 °C. There is one river that runs through the southern section of the reserve and six dams which are fed with water from boreholes during the dry season. PPGR has a total population of 80 individuals, consisting of five family groups with 21 adult females and 19 adult males. Only four of these males were above 30 years of age and considered fully grown.

Data collection

Data were collected over a 2.5-year period (January 2003–July 2005). The two populations were selected because of reserve access, stable herd structure and habituation of the elephants to research vehicles. After the elephant(s) had been located using telemetry or traditional tracking methods, the position of the observer was recorded with a global positioning system (GPS) and corrected by calculating the distance and the bearing to the focal animal.

Once a sufficient time period had elapsed for the observer and vehicle to be ignored, behavioural observations were carried out. Adult elephants were selected at random, and as soon as they initiated a foraging bout on a tree (>0.5 m in height in order to distinguish woody species from forbs and grass) the exact time was recorded and the numbers of mouthfuls were counted. An individual mouthful was taken to be each occurrence of the trunk delivering food into the mouth. The parts of each tree targeted during feeding bouts were recorded, along with the species name. Once the elephant moved away from a particular tree, the time was noted. At the end of a foraging bout, the tree height and feeding

height were measured. The total biomass removed and biomass utilised were estimated. This was done by appraising the canopy as a whole prior to a feeding bout and estimating how much of the canopy remained. The canopy removed was further broken down into estimates of the amount ingested by the elephant compared to that left lying on the ground. The feeding bout was then classified on a five-point scale depending upon the intensity of feeding and the amount of biomass removed (Table 1). Where possible, the reason for the cessation of the feeding bout was also stated. This included five broad categories: (1) feeding close-by on a separate tree; (2) displaced by another elephant; (3) social interactions and demands of the group; (4) walking away from the feeding site; or (5) other.

The elephant would be sampled again if it moved to a second tree within close and observable range. If not, a second individual was selected until the group moved out of sight. Data were discarded if it was felt that an individual curtailed a foraging bout due to interference from the observer or another human source, or the bout was less than 15 s in duration, as this was considered to be too short to constitute an actual foraging event. Data were collected throughout the study by a pair of observers, and therefore foraging bouts of two elephants could be carried out simultaneously. In the rare event that more than two elephants fed from the same tree, the data collection was discontinued, due to the difficulty involved with recording the relative utilisation and impact of each individual.

Statistical analysis

The data were separated into male and female categories with only adult animals (>15 years old for males and females with calves) included in the majority of analyses. The analyses were carried out separately for the two reserves. The PGR data set was the most comprehensive of the two, with a total of 394 feeding bouts (female $n=218$ and male $n=176$), whilst the PPGR data

set consisted of 102 feeding bouts (female $n=34$ male $n=68$). The data were imported into the SPSS statistical package and analysed using ANOVA in order to establish whether there was significant variation in the length of feeding bouts, the heights of trees targeted and the mean feeding height, with sex being used as the independent variable. As the data involved repeat samples of a fixed number of elephants, an ANOVA was used to establish if a significant individual effect existed within the female and male datasets. A regression was employed to test the relationship between age and foraging behaviour. Both reserves and sexes were combined for the initial analysis. The data were then separated into respective sexes, a line of best fit plotted, and the r^2 value calculated.

Two-way ANOVAs were used to investigate the influence of season on tree height and feeding bout length. ANOVA was also used to explore the feeding rates of both sexes in the two reserves. Patterns of feeding behaviour for male and female elephants were analysed with a G-test to establish whether the intensity of feeding bouts varied between the sexes. The data for each reserve were compared, to investigate whether the sexes had similar approaches in different reserves. Plant parts fed upon, canopy utilisation and the reasons for the end of the feeding bouts were also compared for females and males using a G-test in order to establish whether the foraging approach differed significantly between the two sexes.

The destructive feeding bouts were examined in more detail, as they often lead to the removal of a tree and as such may have a significant impact on the ecosystem (Laws 1970; Midgley et al. 2005). A number of different methods were used by the elephants, including debarking, uprooting and stem breaking. The heights of the trees and the lengths of the destructive feeding bouts were explored for both sexes using ANOVA. All of the datasets were also analysed according to season (winter and summer), since this has a significant influence on the ranging behaviour of

Table 1 The five-point classification of foraging behaviour

Foraging behaviour	Description
1: Very selective	1–4 small mouthfuls, short time spent at the tree (<1 min), impact negligible
2: Selective	5–10 mouthfuls, small branches and leaves, 1–3 min, <10% of canopy removed
3: Moderate	>10 mouthfuls, removal of some medium branches, 3–5 min duration
4: Intensive	>10 large mouthfuls, breaking of large branches, >5 min duration
5: Destructive	Removal of more than 50% of canopy, tree pushed over or debarked

elephant (Stokke and du Toit 2002; Shannon et al. 2006), biomass availability (East 1984) and plant phenology (Prins and Loth 1988).

Results

Length of feeding bout

Individual elephants had no effect on the feeding bout lengths for either the male or female datasets in PGR (female = $F_{(1,203)}=0.95$, $P>0.5$ and male = $F_{(1,172)}=2.15$, $P=0.1$) and PPGR (female = $F_{(1,28)}=0.69$, $P>0.6$ and male = $F_{(1,58)}=0.36$, $P>0.9$). The duration of feeding bouts in PGR was significantly different between the sexes ($F_{(1,392)}=29.90$, $P<0.01$), with the males having a mean feeding time of 426 s compared to 174 s for the females (Fig. 1). There were no seasonal differences in feeding bout length for either the males or females ($F_{(1,390)}=1.20$, $P>0.25$). Data for females in PPGR were similar to those in PGR, with an average feeding bout length of 168 s. The feeding bouts of male elephants in PPGR were not significantly different from the females, with a mean of 228 s ($F_{(1,100)}=1.11$, $P>0.25$). This value was, however, different to that of the males in PGR ($F_{(1,242)}=6.818$, $P=0.01$). No seasonal effect on feeding time was noted for either sex in PPGR.

Data for the young adult male in PGR were also analysed separately. The average feeding bout length was 228 s, compared to 475 s for the three older males. The mean values for each of the adult males were 366, 468 and 558 s. Data for the young male in PGR were distinctly different from those for the adult males

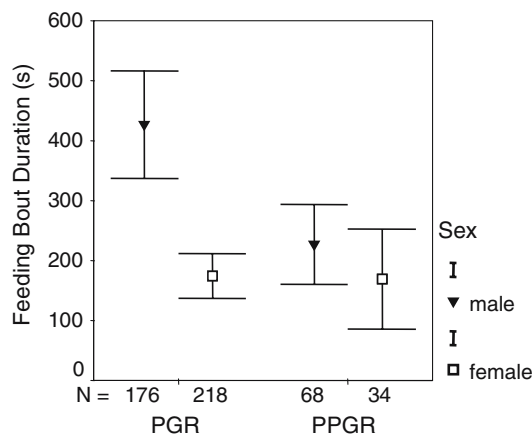


Fig. 1 The mean feeding bout duration of male and female elephants in PGR and PPGR. Males in PGR were feeding on average significantly longer than females, whilst no significant difference was evident for PPGR (data are mean $95\% \pm$ CI and N is the number of focal samples)

($F_{(1,169)}=5.26$, $P<0.02$) but nonsignificant when compared with the PPGR males ($F_{(1,104)}=0.00$, $P>0.95$). Feeding bout length increased linearly with age ($F_{(1,14)}=26.90$, $P<0.01$, $r^2=0.66$). Male elephants ($F_{(1,9)}=48.25$, $P<0.001$, $r^2=0.84$) exhibited longer feeding bouts than females ($F_{(1,9)}=18.50$, $P<0.01$, $r^2=0.66$) after the age of 18 years; this coincides with rapid growth in male body size whilst the female puts energy into reproduction and lactation (Fig. 2).

Tree height and feeding height

Tree height had no effect in either the male or female datasets when individuals were analysed as the independent variable (PGR female = $F_{(1,203)}=1.07$, $P>0.35$, male = $F_{(1,172)}=1.94$, $P>0.1$, PPGR female = $F_{(1,28)}=0.66$, $P>0.65$, male = $F_{(1,58)}=1.50$, $P>0.15$). However, there was a sex effect in PGR with male elephants selecting taller trees on average than females ($F_{(1,392)}=15.45$, $P<0.001$) (Fig. 3). In PPGR, there was no difference in the heights of trees targeted by males and females ($F_{(1,100)}=0.24$, $P>0.5$) (Fig. 3). There was a significant difference in the height of trees selected by females in PGR compared to females in PPGR ($F_{(1,250)}=6.44$, $P<0.025$). There was, however, no significant difference in the selection of tree heights by males in PGR compared to those in PPGR ($F_{(1,242)}=1.50$, $P>0.2$). The interaction term of reserve and sex was not significant, indicating similar patterns of behaviour in both reserves ($F_{(1,492)}=4.258$, $P>0.3$).

Male elephants in PGR fed at an average (mean and median) height of 2 m compared to 1.8 m for females. An ANOVA of the mean feeding heights of the two sexes was nonsignificant ($F_{(1,390)}=3.28$, $P=0.07$). The range of feed heights was slightly larger for males 0.5–5.5 m, whilst for females it was 0.5–5.2 m. In PPGR,

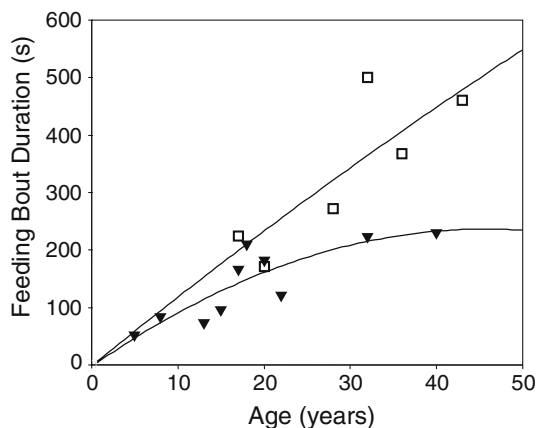


Fig. 2 The effect of age on feeding bout length for both male (open squares) and female (filled inverted triangles) elephant

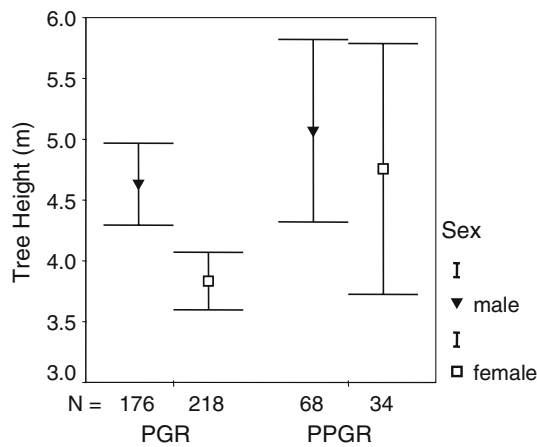


Fig. 3 Tree heights selected by male and female elephants in PGR and PPGR. Males were selecting taller trees on average in both reserves; however, the PPGR result was not significant (data are mean ± 95% CI and *N* is the number of focal samples)

both male and female elephants had a mean feeding height of 2.2 m ($F_{(1,100)}=0.00, P>0.9$). The median was 2.3 for males and 2.45 m for females. The range of feeding heights was similar, with values of 0.5–4.75 m for males and 0.5–4.5 m for females.

Feeding intensity

Male elephants exhibited more destructive feeding behaviour than females, with 31% of total feeding bouts (PGR and PPGR combined) being categorised as destructive compared to 11% for the females (Fig. 4a). There was a significant difference between the intensities of feeding across all five categories between the herd females and males of PGR ($\chi^2_4=65.54, P<0.001$). A significant result was also obtained when comparing the orphan females in PGR with males ($\chi^2_4=49.91, P<0.001$). However, when the two female groups were compared, the result was non-significant ($\chi^2_4=4.50, P>0.25$). On comparing the results for PPGR, the males and females exhibited no statistical differences from one another in terms of their feeding bout classifications ($\chi^2_4=4.92, P>0.25$). Both the PGR herd and the orphan group did not exhibit significant differences compared to the feeding behaviour of the females in PPGR. The males of PGR did, however, behave differently when compared to both the females and males in PPGR ($\chi^2_4=47.45, P<0.001, \chi^2_4=52.77, P<0.001$, respectively).

The trees targeted by males during destructive feeding bouts in PGR were significantly taller (4.8 m) than those targeted by females (3.6 m) ($F_{(1,89)}=6.79, P<0.05$). There was a significant relationship between the season and the height of trees selected during destructive

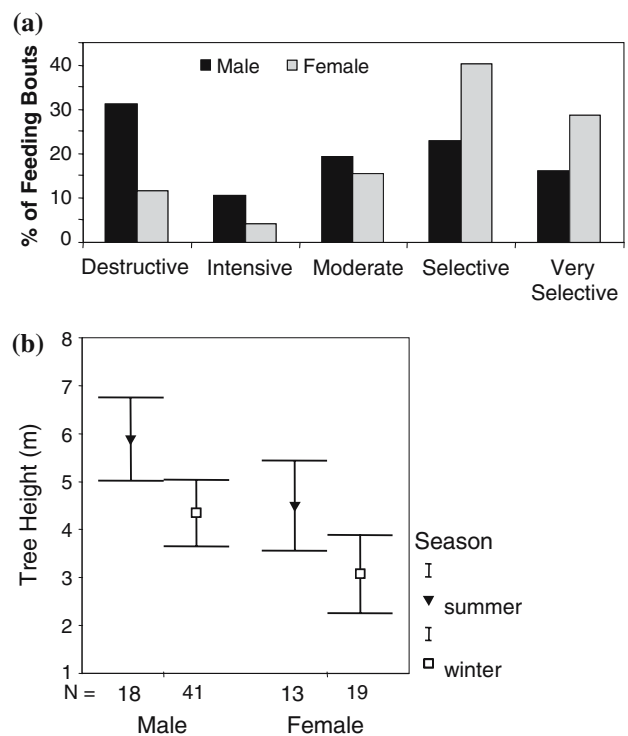


Fig. 4a–b Comparing the intensity of feeding behaviour exhibited by male and female elephant. **a** The relative proportions of feeding bouts classified into five different categories of foraging intensity (PGR and PPGR data combined). **b** The relationship between season, sex and the height of trees targeted during destructive feeding bouts in PGR (data are mean ± 95% CI)

feeding bouts for both sexes ($F_{(1,87)}=11.29, P=0.01$), with the trees targeted in summer being taller than those selected during the winter months (Fig. 4b). There were insufficient data from PPGR to carry out the same analyses.

Feeding rates were also analysed. In PGR, the males had a mean of 3.1 mouthfuls/min compared to 4.1 mouthfuls/min for the females ($F_{(1,392)}=15.37, P<0.01$). The results from PPGR were slightly higher for both sexes, with males having a mean of 3.3 mouthfuls/min and females 4.3 mouthfuls/min ($F_{(1,100)}=5.75, P<0.02$) (Fig. 5). There was no individual effect on feeding rate in either of the reserves (PGR female = $F_{(1,203)}=1.26, P>0.2$, male = $F_{(1,172)}=1.49, P>0.2$, PPGR female = $F_{(1,28)}=0.75, P>0.55$, male = $F_{(1,58)}=1.04, P>0.4$).

Tree parts targeted during feeding bouts

The majority of feeding bouts involved both sexes targeting leaves and small branches. Despite this, there appeared to be distinct differences in the proportions of other tree parts that were consumed, with males feeding on roots and medium-sized branches to a greater extent, whilst females selected leaves, flowers

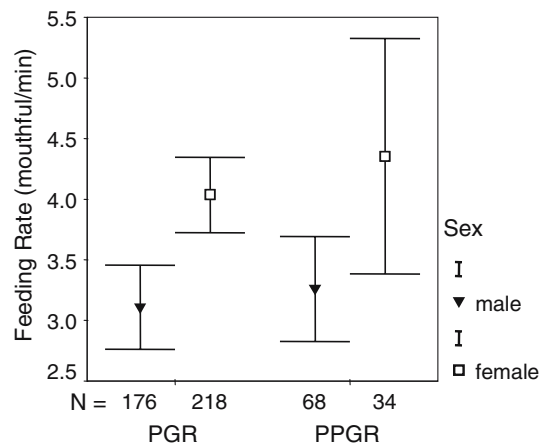


Fig. 5 The feeding rates (mouthfuls/min) of male and female elephants in PGR and PPGR (data are mean \pm 95% CI)

and fruit in higher proportions. A G-test confirmed that the tree parts eaten during the feeding bouts differed significantly between both the males and females in the herd ($\chi^2_8=54.29$, $P<0.001$) and males and females in the orphan group ($\chi^2_8=48.26$, $P<0.001$). There was no difference in the selection of plant parts between adult females from the herd and the orphan family group ($\chi^2_8=12.94$, $P>0.1$), indicating a similar foraging approach. The PPGR data exhibited less variation, with no difference in the selection of tree parts by males or females ($\chi^2_8=2.55$, $P>0.9$). There was no difference between the orphan family group in PGR and female data from PPGR ($\chi^2_8=12.55$, $P>0.1$). The PPGR males had significantly different preferences when compared with those of the males in PGR ($\chi^2_8=27.31$, $P<0.001$).

Species use

Females in both reserves exhibited a preference for a greater diversity of tree species than the males. In PGR, males selected an average of 14 species/100 feeding bouts, whilst females selected 17 species/100 feeding bouts, with a total of 77 species available. In PPGR, these values were much higher, with 28 species/100 feeding bouts for males and 40 species/100 feeding bouts for females, and a total of 220 species available. In PGR, *Acacia nigrescens* was the most commonly selected species, occurring in over 20% of foraging bouts for both sexes. Seventy percent of recorded male and female feeding bouts consisted of only six species in PGR, with males in PGR exhibiting a preference for *A. nigrescens*, *A. tortilis*, *A. nilotica*, *Dichrostachys cinerea*, *Sclerocarya birrea* and *Grewia flava*. Females showed a preference for the same four *Acacia* species

and *Dichrostachys cinerea*, but in addition they also selected *A. leuderitzii* and *Grewia villosa*.

Tree utilisation

The percentages of the canopy, roots and bark removed were recorded for all feeding bouts. In PGR, females utilised only 1–5% of the available biomass in 70% of their feeding bouts, compared to 45% for the males. Male elephants utilised greater amounts of biomass per tree, with a mean of 12% utilisation compared to 8% for the females ($G^2_6=28.96$, $P<0.001$). In PPGR, the mean utilisation for males was 8.5 and 5% for females; however, these results were not significantly different ($G^2_4=3.12$, $P>0.5$).

Feeding bout cessation

In PGR, moving to and feeding on a nearby tree was the primary reason for both males (57%) and females (45%) to end their feeding bouts. Females were also strongly affected by social dynamics, resulting in 40% of their feeding bouts ending, compared to 20% for males. Male elephants had a higher proportion of feeding bouts ending due to them moving away from the feeding site (10 and 2% for females). Overall, the differences were highly significant ($G^2_4=28.59$, $P<0.001$). There were insufficient data available from PPGR for this analysis.

Discussion

The lengths of feeding bouts were significantly shorter for females than males in PGR, and this concurs with the results from the study in Chobe National Park, where male foraging bouts averaged 540 s compared to 216 s for the females (Stokke and du Toit 2000). Shorter feeding bouts indicate a more selective foraging approach (Stokke and du Toit 2000). In PPGR, the feeding bout lengths of males and females were not significantly different. Despite the relatively small sample size, it is also important to note that only three of the 20 males sampled in PPGR are above the age of 30 (only 15% of feeding bouts), whilst three out of the four males in PGR were ≥ 32 years of age and therefore considered fully grown (75% of the feeding bouts).

Our results suggest that the feeding bouts of males and females are of a similar length until they reach approximately 15–20 years of age, which may explain the nonsignificant result in PPGR. Beyond 20 years of age, there is a divergence in behaviour, with males

continuing to increase their feeding bout length as they get older, whilst the feeding duration of the females levels off at approximately 230 s. The male response is directly correlated to increasing body size and greater digestive efficiency (Demment 1983; Demment and Van Soest 1985), whilst the females begin to invest heavily in reproduction (Moss and Poole 1983; Poole 1994; Lee and Moss 1995) and therefore have greater relative energy demands and social restrictions. This requires a more selective foraging approach, with higher quality food resources being targeted (Beier 1987; Stokke and du Toit 2000). The relationship between feeding bout duration and age match closely with the correlations of body mass and age for both sexes (Laws et al. 1975; Lee and Moss 1995).

The sub-adult male in PGR (approximately 17 years old) had a very similar mean feeding bout length when compared to the data for the males in PPGR (average age of 25 years). This is consistent with the body size hypothesis, as a 20-year-old male elephant is approximately half the weight of a fully grown adult (Laws et al. 1975). This disparity in body size is likely to have a significant influence on foraging behaviour when comparing fully grown adult males to sub-adult males, due to the scaling of allometric relationships such as metabolism and gut size (Bell 1971; Jarman 1974; Demment and Van Soest 1985; Stokke and du Toit 2000).

Male body size has also been observed to influence the feeding behaviour of bighorn sheep (*Ovis canadensis*), with adults spending less time feeding and more time ruminating compared to sub-adults (Pelletier and Festa-Bianchet 2004). The greater kudu (*Tragelaphus strepsiceros*) also exhibited distinct differences in foraging behaviour linked to body size, with sub-adult males feeding for approximately 10% more time than adults (Owen-Smith 1998). In sexually dimorphic ungulates, it is predicted that the mass-specific energy requirements of sub-adult males are higher than those of fully grown adults, due to their smaller body sizes and the substantial energetic costs of growth (Ruckstuhl et al. 2003). Ultimately, this could lead to segregation between age groups as well as sex (Ruckstuhl 1998; Bon et al. 2001; Michelena et al. 2006).

It is also noteworthy that the elephant population in PPGR was established using orphans from the Kruger National Park. The sociological impacts associated with removing these young elephants from stable herd structures has been highlighted in the past (Slotow et al. 2000; Slotow and van Dyk 2001; Garai et al. 2004). In PPGR, young male elephants (≥ 15 years) were often to be observed following the female groups at discrete distances (H. Druce, personal communication),

resulting in the majority of male feeding bouts being recorded in close proximity to females. It is also evident that the feeding bout duration of the PPGR males falls below the line of best fit (Fig. 2.). These negative residuals may well be a direct result of the association between the two sexes, which constrains the foraging behaviour of the males.

Trees targeted by males in PGR were significantly taller than the ones selected by females, and this may be explained by the larger body size and greater reach of males (Owen-Smith 1992). Despite this, the average feeding height was the same for both sexes in PGR and PPGR. It is therefore unlikely that the SCH plays an important role in the segregation of the sexes, otherwise resource partitioning would be marked, with males feeding higher in the canopy due to competition from females, especially during periods of resource scarcity (du Toit 1990). Stokke and du Toit (2000) also found that females fed at similar average heights to males (1.25 m compared with 1.5 m). The relative abundance of low-quality forage is also a significant factor in the lack of observed competition between elephant and other large herbivores in the savanna ecosystem (Ginnett and Demment 1999; Ruckstuhl and Neuhaus 2000; Stokke and du Toit 2000). In this study and those of Guy (1976) and Stokke and du Toit (2000), it was noted that the majority of foraging bouts occurred at < 2 m, which is well within the reach of many smaller browsers and well below an elephant's maximum reach (du Toit 1990), suggesting that neither intra nor intercompetition have significant roles to play in the development of elephant foraging strategies.

Females rarely displayed destructive behaviour, and when it did occur it was mainly debarking. This finding is consistent with that of Guy (1976) in Zimbabwe, where males accounted for 80% of the trees pushed over. Male elephants in PGR were also more likely to push trees over in the winter season, a result which also concurs with the findings of Guy (1976). This behaviour may be due to reduced foraging opportunities during the dry season, resulting in roots, branches and bark being targeted in greater amounts (Owen-Smith 1992; Ruggiero 1992). In PGR, both sexes targeted taller trees in destructive foraging bouts during the summer. This may be an artefact of habitat selection, with the larger trees occurring in the north of the reserve on shallow, well-drained soils. These habitats were avoided during the winter periods (Shannon et al. 2006).

The feeding approaches of the sexes differed in both study areas, but more significantly in PGR, with over 50% of the female feeding bouts being classified as selective or very selective compared to 25% for males.

This fits well with the body size hypothesis, which suggests that females should forage more selectively, whilst males which are larger and more independent in nature are less constrained. Our results concur, with 43% of the male feeding bouts in PGR being classified as destructive, compared to 13% for females.

Female elephants exhibited a wider diet selection than males in both reserves, yet in PGR only six species accounted for 70% of the feeding bouts of both sexes. This may be a result of the relatively simple vegetation structure of the savanna in PGR, with 77 recorded species compared to approximately 220 in the PPGR. The difference in species richness between the two reserves is also likely to explain the greater number of woody species targeted per hundred feeding bouts by the PPGR elephants. The disparity in female and male feeding approaches was also evident with regard to the tree parts targeted during foraging bouts and the quantities of biomass removed. Females were more likely to select the small branches, leaves fruits and flowers which are likely to contain the least fibre and provide the highest nutritional return (McNaughton and Georgiadis 1986). Males selected larger branches and roots more commonly than females, and often used their greater body size to push trees over (Guy 1976; Owen-Smith 1992).

Bite rates were significantly different between the two sexes, with females taking more bites per min than males, probably in response to their smaller selective mouthfuls (Stokke and du Toit 2000; Spaeth et al. 2004). In order to meet higher relative energy demands, females process mouthfuls quicker than males. This behaviour has also been exhibited by big-horn sheep (*Ovis canadensis*) (Ruckstuhl et al. 2003), moose (*Alces alces*) (Spaeth et al. 2004), and in a study by Murray and Brown (1993) which compared the bite rates of three different-sized herbivores in the African savanna. Ruckstuhl et al. (2003) also showed that lactating females had higher bite rates than both adult males and nonlactating females, indicating that bite rate is related to energy demand.

Male elephants exploited more of the available biomass per tree than females. Considering the longer feeding bouts and the larger sizes of the males, this is expected and validates the theory that males tolerate greater quantities of fibrous forage than females (Dement 1983). Females were more likely to end their feeding bout due to the social constraints of group living compared to males, who were more likely to move on and feed upon another tree or walk away from the feeding site. This exhibits the more independent nature of the male elephants compared to females, who are operating under the constraints of group living

(Fritz and De Garine-Wichatitsky 1996). The social nature of elephants is highly developed, and the matriarch has a strong influence on the behaviour of the group as a whole (McComb et al. 2001), although it has been demonstrated that democratic decisions are more effective for the group than individual decisions, even those taken by the most experienced member (Conradt and Roper 2003). Despite this, there are distinct costs associated with group living, including competition (Fritz and De Garine-Wichatitsky 1996; Spaeth et al. 2004) and synchronisation of behaviour (Conradt 1998; Ruckstuhl 1998). Male elephants do not undergo such pressure, and this is reflected in their independent ranging, longer feeding bouts, and more destructive foraging behaviour. The data presented here highlight the significant differences in the foraging behaviour of male and female elephants, which are pronounced enough to drive sexual segregation at the plant scale. Our findings are consistent with those of Stokke and du Toit (2000), and support the FSH as an explanation for the spatial segregation observed in elephants.

Conclusion

Body size dimorphism, coupled with contrasting reproductive strategies, has a significant influence on the foraging behaviour and ultimately the spatial segregation of male and female elephants. Females are smaller, have a higher reproductive input and live in permanent groups with close social bonding. This results in a feeding approach that maximizes nutritional intake, through selective foraging bouts of relatively short duration. Males, on the other hand, are able to feed in situ for longer and utilise the more abundant but lower quality forage, as they do not experience the same social and energetic constraints as females. The male approach might in fact be a time-minimizing strategy which allows them to concentrate on other activities including reproduction and ranging. Male-driven impacts such as tree-pushing are likely to be more severe than for females, with trees commonly targeted both as a feeding strategy and for social reasons (e.g. displacement behaviour). Results here show little evidence to support the SCH, but it is highly probable that the FSH explains the pronounced spatial segregation in elephant. This study demonstrates how male and female elephants are markedly different with regard to their foraging behaviour and effectively act as distinct “ecological species”. Other sexually dimorphic herbivores could have similar differences and, where applicable, such differences should be considered carefully in order to prevent oversimplification of ecological

systems in both management and conservation efforts (Bowyer 2004).

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References

- Acocks JPH (1988) Veld types of South Africa, 3rd edn. Botanical Research Institute, Pretoria
- Anderson M (1994) Sexual selection. Princeton University Press, Princeton, NJ
- Barnes RFW (1979) Elephant ecology in Ruaha National Park, Tanzania. PhD Thesis, Cambridge University, Cambridge, UK
- Beier P (1987) Sex differences in quality of white-tailed deer diets. *J Mammal* 68:323–329
- Bell RH (1971) A grazing ecosystem in the Serengeti. *Sci Am* 225:86–93
- Blanchard P (2005) On lactation and rumination in bighorn ewes (*Ovis Canadensis*). *J Zool Lond* 265:107–112
- Bon R, Rideau C, Villaret J, Joachim J (2001) Segregation is not only a matter of sex in Alpine ibex *Capra ibex ibex*. *Anim Behav* 62:495–504
- Bowyer RT (2004) Sexual segregation in ruminants: definitions, hypotheses and implications for conservation and management. *J Mammal* 85:1039–1052
- Brown JS (2000) Foraging ecology of animals in response to heterogeneous environments. In: Hutchings J, John EA, Stewart A (eds) The ecological consequences of environmental heterogeneity. Blackwell, Oxford, UK, Chap 10, pp 181–214
- Charif RA, Ramey RR, Langbauer WR, Payne KB, Martin RB, Brown LM (2005) Spatial relationships and matrilineal kinship in African savanna elephant (*Loxodonta africana*) clans. *Behav Ecol Sociobiol* 57:327–338
- Clauss M, Frey R, Kiefer B, Lechner-Doll M, Loehlein W, Polster C, Rossner GE, Streich WJ (2003) The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut and adaptations of hindgut fermenters. *Oecologia* 136:14–27
- Clutton-Brock TH, Guinness FE (1987) Sexual segregation and density related changes in habitat use in male and female deer (*Cervus elephus*). *J Zool Lond* 211:275–289
- Clutton-Brock TH, Harvey PH (1978) Mammals, resources and reproductive strategies. *Nature* 273:191–195
- Clutton-Brock TH, Albon SD, Guinness FE (1989) Fitness costs of gestation and lactation in wild mammals. *Nature* 337:260–262
- Conradt L (1998) Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? *Proc Biol Sci* 265:1359–1363
- Conradt L (1999) Social segregation is not a consequence of habitat segregation in red deer and feral soay sheep. *Anim Behav* 57:1151–1157
- Conradt L, Roper TJ (2003) Group decision-making in animals. *Nature* 421:155–158
- Darwin C (1871) The descent of man, and selection in relation to sex. John Murray, London
- Demment MW (1983) Feeding ecology and the evolution of body size of baboons. *Afr J Ecol* 21:219–233
- Demment MW, Van Soest PJ (1985) A nutritional explanation for body size patterns of ruminant and non-ruminant herbivores. *Am Nat* 125:641–672
- East R (1984) Rainfall, soil nutrient status and biomass of large African savanna mammals. *Afr J Ecol* 22:245–270
- Fritz H, De Garine Whichatitsky M (1996) Foraging in a social antelope: effects of group size on foraging choices and resource perception in impala. *J Anim Ecol* 65:736–742
- Garaï ME, Slotow R, Carr RD, Reilly B (2004) Elephant reintroductions to small fenced reserves in South Africa. *Pachyderm* 37:28–36
- Ginnet TF, Demment MW (1999) Sexual segregation by Masai giraffes at two spatial scales. *Afr J Ecol* 37:93–106
- Guy PR (1976) The feeding behaviour of elephants (*Loxodonta africana*) in the Sengwa area of Rhodesia. *S Afr J Wildl Res* 6:55–63
- Illius AW, Gordon IJ (1987) The allometry of food intake in grazing ruminants. *J Anim Ecol* 56:989–999
- Jarman PJ (1974) The social organisation of antelope in relation to their ecology. *Behaviour* 48:215–266
- Jetz W, Carbone C, Fulford J, Brown JH (2004) The scaling of animal space use. *Science* 306:266–268
- Kleiber M (1961) The fire of life: an introduction to animal energetics. Wiley, New York
- Krebs JR, Davies NB (1993) An introduction to behavioural ecology, 3rd edn. Blackwell, Oxford, UK
- Laws RM (1970) Elephants as agents of habitats and landscape change in East Africa. *Oikos* 21:1–15
- Laws RM, Parker ISC, Johnstone RCB (1975) Elephants and their habitats. The ecology of elephants in Northern Bunyoro, Uganda. Clarendon Press, Oxford, UK
- Le Blanc M, Festa-Bianchet M, Jorgenson JT (2001) Sexual size dimorphism in bighorn sheep (*Ovis canadensis*): effects of population density. *Can J Zool* 79:1661–1670
- Lee PC, Moss CJ (1995) Satural growth in known-age African elephants (*Loxodonta africana*). *J Zool Lond* 236:29–41
- Loison A, Gaillard J, Pelabon C, Yoccoz NG (1999) What factors shape sexual size dimorphism in ungulates? *Evol Ecol Res* 1:611–633
- Loudon ASI (1985) Lactation and neonatal survival of mammals. *Symp Zool Soc Lond* 54:183–207
- Low AB, Rebelo AG (eds) (1996) Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria
- Main MB, Weckerley FW, Bleich VC (1996) Sexual segregation in ungulates: new directions for research. *J Mammal* 77:449–461
- McComb K, Moss C, Durant SM, Baker L, Sayialel S (2001) Social knowledge in African elephants. *Science* 292:491–494
- McElligott AG, Gammell MP, Harty HC, Paini DR, Murphy DT, Walsh JT, Hayden TJ (2001) Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? *Behav Ecol Sociobiol* 49:266–272
- McNaughton SJ, Georgiadis NJ (1986) Ecology of African grazing and browsing mammals. *Annu Rev Ecol Syst* 17:39–65
- Michelena P, Noël S, Gautrais J, Gerard J, Deneubourg J, Bon R (2006) Sexual dimorphism, activity budget and synchrony in groups of sheep. *Oecologia* 148:170–180
- Midgley JJ, Balfour D, Kerley G (2005) Why do elephants damage savanna trees? *S Afr J Sci* 101:213–215
- Moss CJ, Poole JH (1983) Relationships and social structure of African elephants. In: Hinde RA (ed) Primate social relations. Blackwell, Oxford, UK, pp 315–325

- Murray M, Brown D (1993) Niche separation of grazing ungulates in the Serengeti: an experimental test. *J Anim Ecol* 62:380–389
- Mysterud A (1998) The relative roles of body size and feeding type on activity time of temperate ruminants. *Oecologia* 113:442–446
- Owen-Smith N (1992) Megaherbivores: the influence of very large body size on ecology. Cambridge University Press, Cambridge, UK
- Owen-Smith N (1998) How high ambient temperature affects the daily activity and foraging time of a subtropical ungulate, the greater kudu (*Tragelaphus strepsiceros*). *J Zool Lond* 246:183–192
- Pelletier F, Festa-Bianchet M (2004) Effects of body mass, age, dominance and parasite load on foraging time of big horn rams, *Ovis canadensis*. *Behav Ecol Sociobiol* 56:546–551
- Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge, UK
- Poole JH (1994) Sex differences in the behaviour of African elephants. In: Short RV, Balaban E (eds) The difference between the sexes. Cambridge University Press, Cambridge, UK, pp 331–346
- Prins HHT, Loth PE (1988) Rainfall patterns as a background to plant phenology in northern Tanzania. *J Biogeogr* 15:451–46
- Rands SA, Colishaw G, Pettifor RA, Rowcliffe JM, Johnson RA (2003) Spontaneous emergence of leaders and followers in foraging pairs. *Nature* 423:432–434
- Ruckstuhl KE (1998) Foraging behaviour and sexual segregation in bighorn sheep. *Anim Behav* 55:99–106
- Ruckstuhl KE, Neuhaus P (2000) Sexual segregation in ungulates: a new approach. *Behaviour* 137:361–377
- Ruckstuhl KE, Festa-Bianchet M, Jorgenson JT (2003) Bite rates in rocky mountain bighorn sheep (*Ovis canadensis*): effects of season, age sex and reproductive status. *Behav Ecol Sociobiol* 54:167–173
- Ruggiero RG (1992) Seasonal forage utilisation by elephants in central Africa. *Afr J Ecol* 30:137–148
- Seagle SW, McNaughton SJ (1992) Spatial variation in forage nutrient concentrations and the distribution of Serengeti grazing ungulates. *Landscape Ecol* 7:229–241
- Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE, Swift DM (1987) Large herbivore foraging and ecological hierarchies. *Bioscience* 37:789–799
- Shannon G, Page B, Duffy K, Slotow R (2006) African elephant home range and habitat selection in Pongola Game Reserve, South Africa. *Afri Zool* 41:37–44
- Skarpe C, Bergström R, Bråten AL, Danell K (2000) Browsing in a heterogenous savanna. *Ecography* 23:632–640
- Slotow R, van Dyk G (2001) Role of delinquent young ‘orphan’ male elephants in high mortality of white rhinoceros in Pilansberg National Park, South Africa. *Koedoe* 44:85–94
- Slotow R, van Dyk G, Poole J, Page B, Klocke A (2000) Older bull elephants control young males. *Nature* 408:425–426
- Spaeth DF, Bowyer RT, Stephenson TR, Barboza PS (2004) Sexual segregation in moose *Alces alces*: an experimental manipulation of foraging behaviour. *Wildl Biol* 10:59–72
- Spinage CA (1994) Elephants. T & AD Poyser, London
- Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton, NJ
- Stokke S, du Toit J (2000) Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography* 23:70–80
- Stokke S, du Toit JT (2002) Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *Afr J Ecol* 40:360–371
- du Toit JT (1990) Feeding-height stratification among African browsing ruminants. *Afr J Ecol* 28:55–61
- Van Soest PJ (1996) Allometry and ecology of feeding behaviour and digestive capacity in herbivores: a review. *Zoo Biol* 15:455–479
- Wittermeyer G, Douglas-Hamilton I, Getz WM (2005) The socioecology of elephants: analysis of the processes creating multitiered social structures. *Anim Behav* 69:1357–1371