

The influence of sexual dimorphism on the foraging behaviour of the nyala *Tragelaphus angasii* *

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Abstract Sexual dimorphism is pronounced in nyala *Tragelaphus angasii* and is predicted to have a significant influence on their foraging behaviour and habitat selection due to the allometric relationships associated with increasing body size. A continuous behavioural sampling method was used to detect male and female differences in habitat and plant utilisation. Food species were recorded and feeding heights compared between the sexes. Vegetation surveys were conducted once a feeding bout had ended using the point centred quarter (PCQ) technique. A Discriminant Function Analysis was then used to identify whether species and height class preferences were significantly different between the sexes. Female nyala spent a similar proportion of time foraging in all three habitats, whilst males exhibited a preference for sand forest. The differences within habitats were even more marked, with males selecting a greater proportion of woody species and feeding at a greater average height, whilst females preferred to forage lower down in the herbaceous layer. Male and female nyala appear to exhibit dietary and spatial segregation within habitats at the plant and patch scale. We suggest that this is a result of different nutritional and energetic demands which are driven by body size dimorphism and divergent reproductive strategies. Ultimately browsers may exhibit spatial segregation within woody habitats due to the increased spatial heterogeneity that is generated by their complex structure [*Acta Zoologica Sinica* 54 (4): 561-568, 2008].

Key words Sexual segregation, Foraging, Browser, Herbivore

安氏薮羚的性二型对采食行为的影响 *

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摘要 安氏薮羚 (*Tragelaphus angasii*) 是具有性别体二型的动物, 其体型大小的差异可能对采食行为和生境选择有显著影响。利用连续行为取样法检测了雌雄个体在生境和植物利用上的差异, 记录采食植物种类和采食高度并进行了性别间比较。在每个采食周期末, 采用点中心方形样方法 (PCQ) 对植被进行一次调查, 利用判别函数分析鉴别雌雄个体之间在种类和高度上是否存在差异。雌羚在三类生境中花费的采食时间相似, 但雄羚表现出对砂地林的偏好。另外, 在同一生境内雄羚利用更多的木本种类且采食较高的部位, 而雌羚喜欢采食低层草本植物。安氏薮羚雌雄个体在生境内具有食性 (采食种类) 和空间 (生境斑块) 上的分离。我们认为这是由性二型引起的性别间营养与能量需求差异和不同繁殖策略造成的, 最终使得精食者动物在具有复杂结构空间异质性的生境内表现为空间性别分离 [*动物学报* 54 (4): 561-568, 2008]。

关键词 性别分离 采食 精食者 行为

Sexual dimorphism is a common physiological trait amongst large herbivores, whereupon males are significantly larger than females (Abouheif and Fairbairn,

1997; Ruckstuhl and Neuhaus, 2000; Le Blanc et al., 2001). This disparity in body size is believed to have evolved due to divergent reproductive strategies (Loison et

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al., 1999; Weckerly, 1998). Males exhibit a comparatively low investment in reproduction and are limited only by the availability of receptive mates, whereas females are constrained by the high energetic costs associated with gestation and weaning (Clutton-Brock et al., 1989). As a result, females actively select mates on the basis of strength and dominance, a key factor in determining mating systems (Alonzo and Warner, 2000), and one which confers and immediate advantage to larger and more powerful males (Clutton-Brock and Harvey, 1978; Poole, 1989; McElligott et al., 2001).

Sexual dimorphism is predicted to have a significant influence on both habitat utilisation and foraging behaviour due to the allometric relationships associated with increasing body size (Ruckstuhl, 1998; Barboza and Bowyer, 2000; Stokke and du Toit, 2000, 2002). These include a reduction in mass specific energy requirements (energy/kg) as metabolic rates scale with a factor of $0.75 M$ (M = body mass) (Kleiber, 1961), owing to increased muscular efficiency and reduced heat loss. Furthermore there is a proportional increase in gut size and retention time, enabling larger individuals to target and process lower quality forage to meet their nutritional demands – the Jarman-Bell principle (Bell, 1971; Jarman, 1974). Recently the direct correlation between body size and digestive efficiency has been challenged, as a result of weak relationships in both inter and intra-specific allometric scaling (Clauss et al., 2007; Ramzinski and Weckerly, 2007). It also appears that larger bodied herbivores must contend with lower gut surface : gut volume ratio, increased loss in faecal bacterial material through fermentation and the digestion of larger particles of ingesta (Clauss and Hummel, 2005).

Despite this, the forage selection hypothesis remains one of the key theories in explaining the sexual segregation of large herbivores (Main et al., 1996). The sexes are predicted to exhibit different foraging approaches due to their divergent body sizes (Jarman-Bell principle) and distinct reproductive strategies (e.g. weaning and pregnancy are energetically expensive for females, Barboza and Bowyer, 2000, 2001). Ultimately this may result in the sexes perceiving their environment and feeding opportunities at different scales of resolution (Houston and Shine, 1993; Ruckstuhl, 1998; Kie and Bowyer, 1999). For example, giraffe *Giraffa camelopardalis* (Ginnet and Demment, 1997, 1999) and elephant *Loxodonta africana* (Stokke, 1999; Stokke and du Toit, 2000; Shannon et al., 2006a) exhibit segregation in terms of feeding patch choice, species selection and the time spent feeding.

Understanding the ecological effects of sexual dimorphism has important implications for the conservation and management of large herbivore species, due to its apparent influence on spatial use, foraging behaviour,

population dynamics and sociality (Conradt, 1998a; Bowyer, 2004).

Nyala Tragelaphus angasii—a southern African antelope species—are classified as mixed or intermediate feeders, although their diet comprises primarily browse (Vincent et al., 1968; Anderson and Pooley, 1977; van Rooyen, 1992). They are sexually dimorphic with males reaching a mean shoulder height of 1.1 metres and a mean mass of 110 kilograms, whilst females have a mean shoulder height of 0.9 metres and a mean mass of 65 kilograms (Vincent et al., 1968). They breed year-round and are not territorial, occurring in either mixed or single-sex groups, with older bulls tending to be solitary (van Rooyen, 1993).

In northern Zululand, South Africa, nyala are locally abundant medium sized browsers and as such they are believed to have a substantial impact on the woody vegetation recruitment and community dynamics of the savanna ecosystem (Prins and van der Jeugd, 1993). Understanding the drivers affecting nyala distribution and impact is important for effective management. The aim of this study was to establish whether male and female nyala are exhibiting distinct patterns in foraging behaviour as a result of their pronounced sexual dimorphism.

1 Materials and methods

1.1 Study site

Phinda Private Game Reserve (PPGR) is approximately 180 km² in extent and is located in northern KwaZulu-Natal, South Africa (27°92' – 27°68'S, 32°44' – 32°20' E). The climate is warm to hot, humid subtropical, and the area experiences two distinct seasons; a warm dry winter from April until mid-September and a hot humid summer from mid-September to March (Hunter, 1998). Phinda lies in the Natal lowveld bushveld/coastal bushveld-grassland vegetation zones (Low and Rebelo, 1996) and contains seven distinct vegetation types, namely mixed bushveld (which is further categorised as open or closed), red sand bushveld (open and closed), palm veld, grasslands, dry mountain bushveld, riparian woodland and sand forest (Hunter, 1998).

This study was conducted exclusively in the northern section of the reserve as nyala are rarely encountered in the south. As a result the vegetation types sampled were mixed bushveld, red sand bushveld, palm veld, grassland and sand forest. The majority of nyala sightings were made in open and closed red sand bushveld and sand forest and despite the fact that they were occasionally seen in the other habitat types, they did not appear to be foraging within them. Behavioural data were therefore only collected in open and closed red sand bushveld and sand forest.

Open and closed red sand bushveld are differentiated using the distance between neighbouring large trees (> 6 metres in height). In open red sand bushveld, large trees

are more than 10 metres apart, whilst in closed red sand bushveld they are less than 10 metres apart. Common tree species include *Acacia burkeii*, *Combretum molle*, *Ziziphus mucronata*, *Sclerocarya caffra*, *Albizia versicolor* and *Terminalia sericea*, and common grass species include *Aristida* spp., *Panicum maximum*, *Eragrostis rigidior*, *Eragrostis pallens*, and *Pogonarthria squarrosa* (Hunter, 1998). Sand forest is a rare and sensitive habitat type characterised by dense woody vegetation with a high canopy of up to 25 m, and a virtually absent understorey. It grows on dry sandy soils and is endemic to the Maputaland region (Matthews, 2001). Examples of sand forest tree species include *Newtonia hildebrandtii*, *Cleistanthus schlechteri*, *Hymenocardia ulmoides*, *Pteleopsis myrtifolia*, *Dialium schlechteri*, *Croton gratissimus* and *Strychnos henningsii* (Hunter, 1998).

1.2 Data collection

Data were collected during two sampling periods in 2004: April 9 – 19 and June 14 – 23. The reserve's roads were driven between 7 am – 6 pm, with caution being taken to sample each route equally, in terms of the frequency of sampling and the time of day. Upon encountering a herd of nyala, one individual was selected for observation after a suitable period of time had elapsed in order to allow the animals to relax. Selection was based on the visibility of the animal from the vehicle, whilst also ensuring that equal numbers of males and females were sampled. During the study a sample size of 162 females and 189 males was achieved—the success rate varied from day to day but the sampling approach was maintained throughout the study period. The time of day was recorded along with the individual's sex, herd size, the GPS coordinates of the sampling site, the weather conditions and the habitat type.

Continuous sampling of behaviour was carried out for a period of ten minutes or until the animal moved out of sight, every activity and its duration were recorded. The location of feeding was carefully noted so that plant species which were fed upon could be identified. At the end of the observation period, the vegetation was sampled using the point-centred quarter (PCQ) method for woody vegetation (Glover and Mitchell, 2001) and 1 m² quadrats for herbaceous vegetation and grasses (Page and Walker, 1978). The centre of the PCQ was located either at the last feeding site or the last recorded position, if foraging behaviour was not observed. The last plant fed upon was identified, and if a woody species its height, the height below canopy, plant parts eaten and the feeding height were all recorded. The surrounding woody vegetation was assessed by identifying the nearest plant in each quarter and its distance from the central point, height and height below canopy. This was repeated for three different height classes: total height < 0.5 m (height class 1) which included all seedlings; total height = 0.5 m – 1.2 m (height class 2) which included plants

available for browsing to both males and females; and finally trees where the bottom of the canopy was ≥ 1.2 m (height class 3), to include biomass which is available exclusively to males. The cut-off of 1.2 m was decided upon as the upper limit of browse availability for females by estimating the average shoulder height of females and the average horn tip height of males and then calculating the midpoint.

The percentage cover of herbaceous vegetation and grass was assessed by placing three 1 m² quadrats in the area immediately surrounding the central point of the PCQ. All grass species within a quadrat were identified and the estimated percentage cover of each species was calculated. Herbaceous plants were grouped together and recorded as such, along with an estimated percentage cover. If the last plant fed upon during a feeding observation was a non-woody species then a fourth quadrat was positioned to include the feeding site, due to the difficulty of locating the precise bite location. This ensured that the forage species was included in the sample.

1.3 Data analysis

The woody vegetation data were separated according to height class and the absolute density of each species was calculated as per Glover and Mitchell (2001). A matrix was constructed for the three height classes showing the density of each species, sex of the focal animal and the site location. Plant species that occurred fewer than three times across all sites were removed from the dataset in order to minimize the number of variables. A Discriminant Function Analysis (Ferrar and Walker, 1974) was used to determine whether males and females were selecting species and height classes differently. Similarly, for the non-woody vegetation a mean percentage cover was calculated for each species at all of the sites. Species that occurred in less than three sites were removed from the dataset. A Discriminant Function Analysis was also performed on the herbaceous vegetation and grass data.

The data analysis programme Statistica[®] detected only one discriminant function, thus a scatter plot could not be produced. Instead, four separate plots (one for each height class) of the un-standardised canonical scores were carried out for both males and females to indicate the level of discrimination between the sexes. Plots of the standardised coefficients versus plant species were used to highlight the species that have the most power in discriminating between the sexes. The discriminant functions for both sexes in each height class were analysed using a Kruskal-Wallis test, to determine whether there was significant segregation of the sexes. A table was formulated showing the most discriminatory plant species for males and females for all height classes. Browsing heights were compared between the sexes using an ANOVA.

2 Results

There was a significant discrimination ($\chi^2_1 = 15.463$, $P < 0.05$) between the sexes for all height classes, with the points representing males tending to fall at the opposite end of the X-axis to those representing

females (Fig.1 and 2). The plant species that contributed most strongly to differential patch and habitat selection were those whose discriminant functions were strongly positive or negative (Fig.1 and Table 1). Males and females differed in terms of the plant species that characterised the patches and habitats in which they were

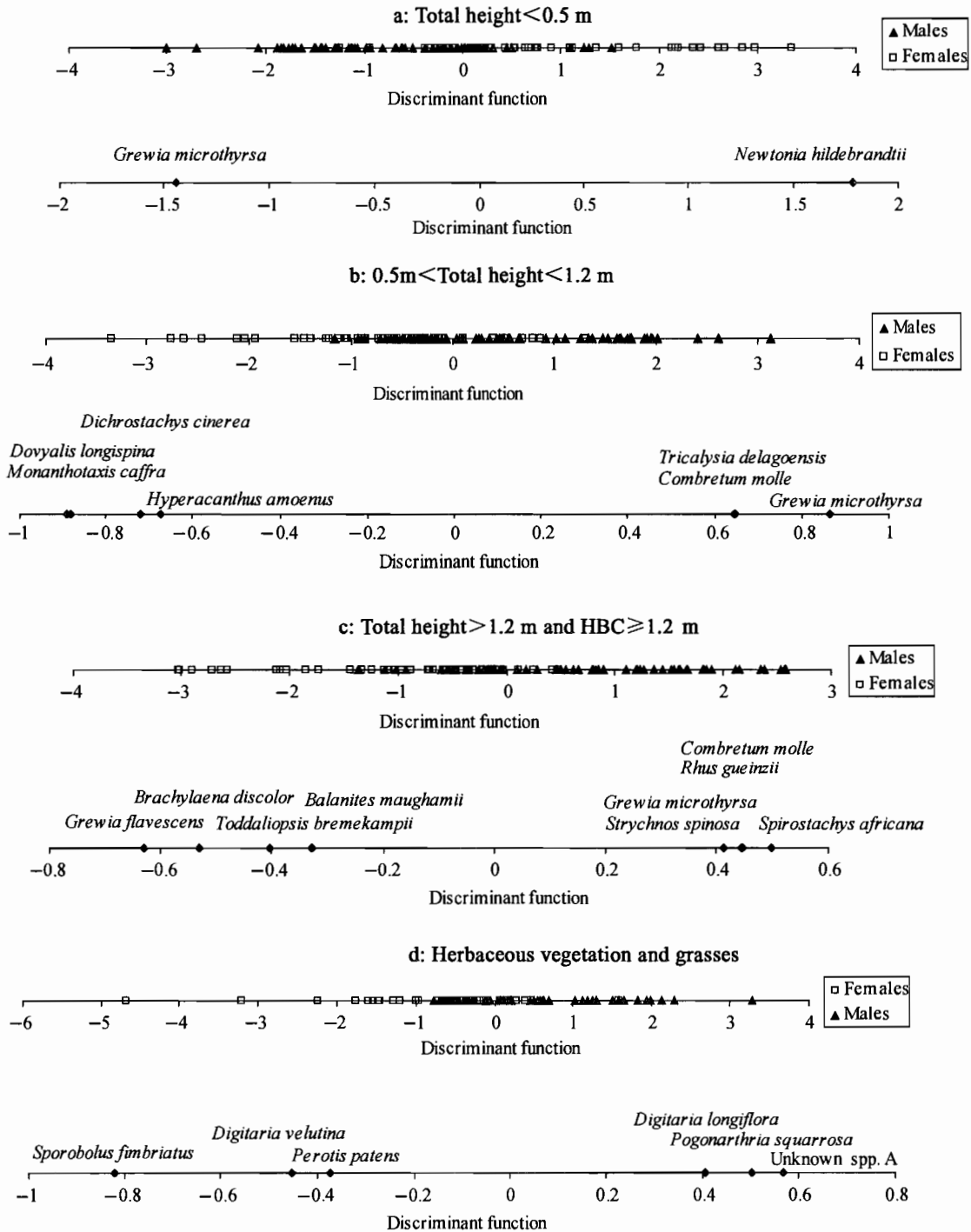


Fig.1 Spatial segregation of male and female nyala for (a) height class 1 (total height < 0.5 m), (b) height class 2 (0.5 m < total height < 1.2 m), (c) height class 3 (Height below canopy (HBC) ≥ 1.2 m and total height > 1.2 m), and (d) herbaceous vegetation and grasses

Data illustrate the range of discriminant function values for males and females on the upper axis, and the discriminant function values for the most powerfully discriminating plant species in the height class on the lower axis.

found. For example, *Newtonia hildebrandtii*, the discriminant species for females in height class 1 (Table 1), is a characteristic sand forest species (Poole, 1993), while *Grewia microthyrsa*, one of the discriminant species for males in all three height classes is found in both sand forest and in open areas like red-sand-bushveld (Pooley, 1993). Similarly for height class 2 (Table 1), the species selected by females occurred on the fringes of the

sand forest habitat, while those preferred by males occurred more in the red sand bushveld habitats (pers. obs.). For height class 3 (Table 1), the preferred species of males can be related to decidedly more open habitats than those for females, which again are sand forest-specific species, particularly *Balanites maughamii* and *Toddaliopsis bremekampii* (Pooley, 1993).

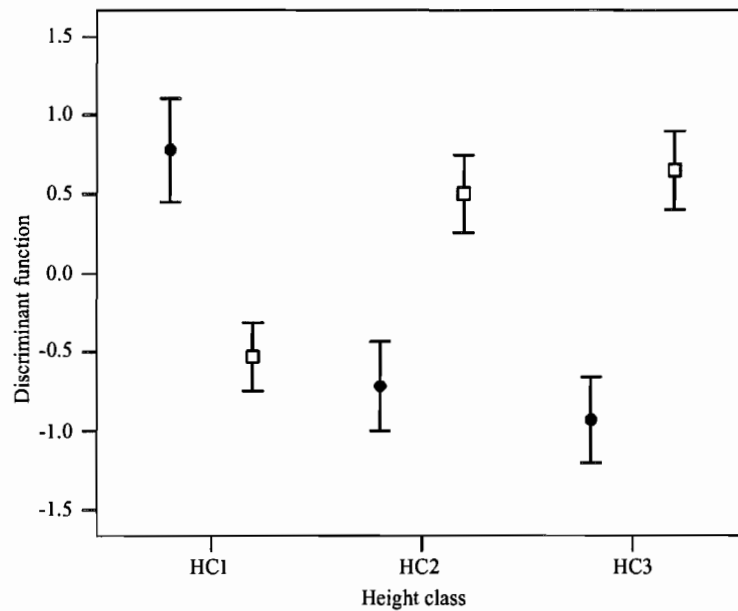


Fig. 2 Spatial segregation in male \square and female \bullet nyalas for height classes 1, 2 and 3, with the mean discriminant function for males and females shown against the vegetation height class

Data are shown as mean \pm 95% confidence intervals. $n = 47$ females and 70 males for height class 1, and 48 females and 69 males for height classes 2 and 3. HC1 = height class 1 (height < 0.5 m), HC2 = height class 2 (height > 0.5 m and < 1.2 m), HC3 = height class 3 (height of canopy bottom \geq 1.2 m).

Table 1 Most strongly discriminating plant species for inter-sexual differences in habitat selection for woody and non-woody vegetation

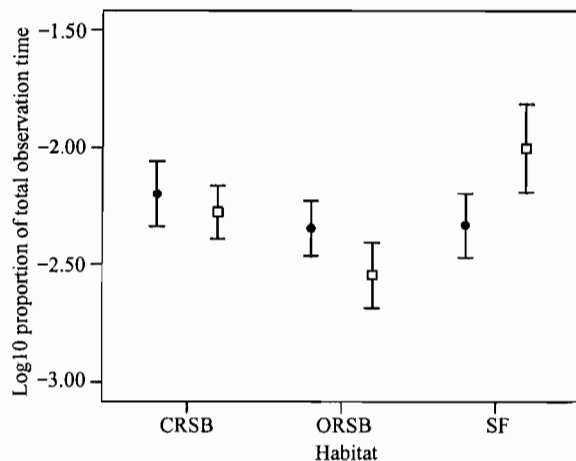
	Height class	Males	Females
Woody	Height < 0.5 m	<i>Grewia microthyrsa</i>	<i>Newtonia hildebrandtii</i>
		<i>Grewia microthyrsa</i>	<i>Monanthonax affra</i>
		<i>Combretum molle</i>	<i>Dichrostachys cinerea</i>
	0.5 m < Height < 1.2 m	<i>Tricalysia delagoensis</i>	<i>Dovyalis longispina</i>
			<i>Hyperacanthus amoenus</i>
		<i>Grewia microthyrsa</i>	<i>Grewia flavescens</i>
	Height of canopy bottom \geq 1.2 m	<i>Combretum molle</i>	<i>Brachylaena discolor</i>
		<i>Strychnos spinosa</i>	<i>Toddaliopsis bremekampii</i>
		<i>Rhus gueinzii</i>	<i>Balanites maughamii</i>
Non-woody		<i>Spirostachys africana</i>	
		Unknown spp. A	<i>Perotis patens</i>
		<i>Digitaria longiflora</i>	<i>Sporobolus fimbriatus</i>
		<i>Pogonarthria squarrosa</i>	<i>Digitaria velutina</i>

There were sex differences in species selection, with a number of plant species consumed predominantly or exclusively by one sex (Table 2). Females fed much more frequently in the herbaceous layer compared to males, which targeted height classes 2 and 3 with greater frequency (Fig. 2). Overall, this resulted in a significant difference in the mean feeding heights of the sexes ($F_{1,35}$

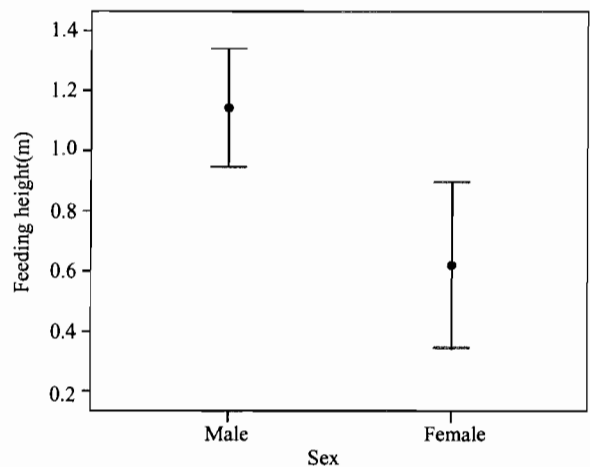
$= 10.206$, $P < 0.05$; Fig. 4). Moreover males and females responded differently with regard to the proportion of time spent feeding in each habitat ($F_{2,345} = 6.77$, $P = 0.01$). Females did not exhibit a statistical difference ($F_{2,159} = 1.56$, $P > 0.2$), whilst males demonstrated a preference for foraging in the sand forest habitat ($F_{2,186} = 12.37$, $P < 0.001$) (Fig. 3).

Table 2 Frequencies with which males and females were observed to consume various plant species

		Frequency (%)	
		Males	Females
Woody	<i>Strychnos madagascariensis</i>	8.70	0.00
	<i>Boscia albitrunca</i>	8.70	0.00
	<i>Strychnos spinosa</i>	4.35	0.00
	<i>Tricalysia capensis</i>	4.35	0.00
	<i>Acacia robusta</i>	2.17	0.00
	<i>Azima tetracantha</i>	2.17	0.00
	<i>Hyperacanthus amoenus</i>	2.17	0.00
	<i>Landolphia kirkii</i>	2.17	0.00
	<i>Pappia capensis</i>	2.17	0.00
	<i>Vitex amboniensis</i>	2.17	0.00
	<i>Zanthoxylum capense</i>	2.17	0.00
	<i>Ziziphus mucronata</i>	2.17	0.00
	<i>Pteleopsis myrtifolia</i>	8.70	6.45
	<i>Cassine aethiopica</i>	4.35	3.23
	<i>Grewia flavescens</i>	4.35	3.23
	<i>Coddia rudis</i>	2.17	3.23
	<i>Acacia burkei</i>	0.00	3.23
	<i>Ancylanthos monteiroi</i>	0.00	3.23
	<i>Brachylaena discolor</i>	0.00	3.23
	<i>Dichrostachys cinerea</i>	0.00	3.23
<i>Hymenocardia ulmoides</i>	0.00	3.23	
<i>Sapium integrinum</i>	0.00	3.23	
<i>Tricalysia delagoensis</i>	0.00	3.23	
<i>Terminalia sericea</i>	0.00	3.23	
Non-woody	Herbaceous	30.43	51.61
	<i>Panicum maximum</i>	6.52	3.23
	<i>Dactyloctenium australe</i>	0.00	3.23

**Fig. 3** The proportion of time spent feeding by male □ and female ● nyala in the different habitat types sampled

Data are shown as mean \pm 95% confidence intervals. $n = 351$. CRSB = closed red sand bushveld, ORSB = open red sand bushveld, SF = sand forest.

**Fig. 4** Comparison of heights at which males and females were observed to feed

Data are shown as mean \pm 95% confidence intervals. $n = 25$ males and 12 females.

3 Discussion

Female nyala fed at lower average heights than males, consumed herbaceous vegetation more frequently and targeted a range of different woody plant species during their foraging events. Lower feeding heights are likely to include saplings and forbs of higher nutritional quality than taller, more mature trees which have greater fibrous biomass (du Toit, 2003). Our results suggest that females may be targeting higher quality forage opportunities as predicted by the forage selection hypothesis (Main et al., 1996). Males in contrast, appear to feed at significantly greater heights, focussing on plants and height classes which are likely to provide greater available biomass (Woolnough and du Toit, 2001).

Previously the stratification of feeding heights in browsers has been predicted to result from inter-specific competition, with larger bodied herbivores using their reach to avoid competing with smaller more selective species (du Toit, 1990; Woolnough and du Toit, 2001). However, further investigation into the feeding heights of small to medium sized African browsers exhibited significant overlap, suggesting that competition is not a significant factor in the resource partitioning of different species, a result which is further highlighted by the fact that elephants also concentrate their feeding between 1 – 2 m, well below their reach and in direct competition with other browsers (Guy, 1976; Stokke and du Toit, 2000; Shannon et al., 2006a).

Nonetheless intra-specific differences in feeding height stratification have been shown, with male giraffe feeding higher in the canopy than females (Ginnet and Demment, 1999). Once again there was limited evidence of competition between the sexes and instead it was proposed that males are rate maximizers, taking larger bites and staying in taller patches for longer periods to

satisfy their energy requirements in the shortest time possible (Ginnet and Demment, 1997, 1999). Nyala may also be following a similar strategy, with the larger-bodied males targeting greater plant biomass to maximize their intake (Bell, 1971; Jarman, 1974). A degree of caution is required when inferring such a conclusion, particularly in light of the fact that larger body size does not necessarily imply greater digestive efficiency (Clauss and Hummel, 2005; Clauss et al., 2007).

However, despite substantial overlap in their diets, a number of plant species exist that are strongly selected for by either male or female nyala. This foraging approach appears to be a result of body size and the pattern is consistent with the predictions of the forage selection hypothesis, with females seeking out higher quality foraging opportunities than males (Shannon et al., 2006a). Further evidence of this relationship was exhibited by females showing a much stronger preference for herbaceous plant material, which is likely to be less fibrous in structure (du Toit, 2003). The sexes are also exhibiting differential patterns of habitat use with regard to foraging, with males preferring sand forest over the open red sand bushveld. Females, on the other hand, exhibit similar foraging patterns across all three habitat types.

The results of this study suggest that differences in foraging behaviour of nyala are significant and may lead to spatial segregation of the sexes at the plant scale and to a lesser extent at the habitat scale. Similar results have been found for other browsing species (Ginnet and Demment, 1997, 1999; Stokke, 1999; Stokke and du Toit, 2000; Shannon et al., 2006a, b). To date, the majority of research on sexual segregation has focussed on temperate grazers and whilst marked habitat segregation has been recorded (Ruckstuhl, 1998; Conrath, 1999; Bonenfant et al., 2004), there has been little indication that body size influences digestive efficiency or foraging behaviour at the plant scale (Pérez-Barbería et al., 2007). This may well be a function of the homogenous distribution and structure of grass species.

For grazers to select higher quality foraging opportunities, they may well have to make decisions at the habitat scale whereupon climatic conditions and abiotic variables differ sufficiently to alter the species composition. In contrast, woody species are more heterogeneous in their structure and distribution, with different plant parts varying significantly in nutritional quality (Skarpe, 2000; du Toit, 2003). Furthermore trees are stratified according to height, with many individuals being above the browsing height of medium-sized browsers such as nyala. The distinct resource heterogeneity within habitats may well be sufficient to drive spatial segregation, without strong evidence of habitat segregation (Stokke and du Toit, 1999, 2000; Shannon, et al., 2006a, b). This highlights a very interesting difference in the perception of scale by

browsing and grazing species of large herbivore, as well as the distinct behavioural approaches of the sexes. Whilst the precise role of allometric relationships remains unclear, it is worth considering that other factors may also contribute to driving sex-specific foraging behaviour, including rumination time, gut fill tolerance, nutrient preferences and the energetic demands of reproduction (Barboza and Bowyer, 2000; Ramzinski and Weckerly, 2007).

From a management perspective these results have implications for the conservation of the sand forest vegetation type, which is slow to regenerate and therefore sensitive to fire and heavy browsing pressure (Kirkwood and Midgley, 1996; Matthews et al., 2001). The primary concern in terms of impact on the sand forest is the removal of young plants and seedlings as this prevents the recruitment of new individuals. Our study provides further evidence of the substantial differences in the foraging ecology of sexually dimorphic species, suggesting that for effective management and conservation they may need to be considered as ecologically distinct species (Bowyer, 2004; Shannon et al., 2006a).

In summary, sexual dimorphism appears to drive significant differences in the foraging behaviour of male and female nyala. Although differences in habitat utilisation were noted, they were not as strong as those at the plant scale and we believe that this provides further evidence that browsing species can segregate within habitats due to the spatially heterogeneous nature of woody plants. Our study also highlights the importance of elucidating the correct scale of investigation with regard to sexual segregation and the conservation of large herbivores.

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References

- Abouheif E, Fairbairn DJ, 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *Am. Nat.* 149: 540 – 562.
- Alonzo SH, Warner RR, 2000. Female choice, conflict between the sexes and the evolution of male alternative reproductive behaviours. *Evol. Ecol. Res.* 2: 149 – 170.
- Anderson JL, Pooley, ES, 1977. Some plant species recorded from nyala rumena in Ndumu Game Reserve. *Lammergeyer* 23: 40 – 45.
- Barboza PS, Bowyer RT, 2000. Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. *J. Mammal.* 81: 473 – 489.
- Barboza PS, Bowyer RT, 2001. Seasonality of sexual segregation in dimorphic deer: extending the gastrocentric model. *Alces* 37: 275 – 292.
- Bell RHV, 1971. A grazing ecosystem in the Serengeti. *Sci. Am.* 225:

- 86 - 93.
- Bon R, Campan R, 1996. Unexplained sexual segregation in polygamous ungulates: a defense of an ontogenetic approach. *Behav. Proc.* 38: 131 - 154.
- Bonenfant C, Loe EL, Myserud A, Langvatn R, Stenseth N, Gaillard J, Klein F, 2004. Multiple causes of sexual segregation in European red deer: enlightenments from varying breeding phenology at high and low altitude. *Proc. R. Soc. Lond.* 271: 883 - 892.
- Bowyer RT, 2004. Sexual segregation in ruminants: definitions, hypotheses and implications for conservation and management. *J. Mammal.* 85: 1039 - 1052.
- Bowyer RT, Kie JG, 2004. Effects of foraging activity on sexual segregation in mule deer. *J. Mammal.* 85: 498 - 504.
- Clauss M, Hummel J, 2005. The digestive performance of mammalian herbivores: why big may not be much better. *Mammal. Rev.* 35: 174 - 187.
- Clauss M, Schwarm A, Ortmann S, Streich WJ, Hummel J, 2007. A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores. *Comp. Biochem. Physiol. A.* 148: 249 - 265.
- Clutton-Brock TH, Harvey PH, 1978. Mammals, resources and reproductive strategies. *Nature* 273: 191 - 195.
- Clutton-Brock TH, 1989. Mammalian mating systems. *Proc. R. Soc. Lond. B. Biol. Sci.* 236: 339 - 372.
- Conradt L, 1998a. Measuring the degree of sexual segregation in group-living animals. *J. Anim. Ecol.* 67: 217 - 226.
- Conradt L, 1999. Social segregation is not a consequence of habitat segregation in red deer and feral soay sheep. *Anim. Behav.* 57: 1151 - 1157.
- du Toit JT, 1990. Feeding height stratification among African browsing ruminants. *Afri. J. Ecol.* 28: 55 - 61.
- du Toit JT, 2003. Large herbivores and savanna heterogeneity. In: du Toit JT, Rogers KH, Biggs HC ed. *The Kruger Experience*. Washington, D. C.: Island Press, 292 - 309.
- Ferrar AA, Walker BH, 1974. An analysis of herbivore/habitat relationships in Kyle National Park. *Journal of the Southern African Wildlife Management Association* 4: 137 - 147.
- Ginnett TF, Demment MW 1997. Sex differences in giraffe foraging behaviour at two spatial scales. *Oecologia* 110: 291 - 300.
- Ginnett TF, Demment MW, 1999. Sexual segregation by Masai giraffes at two spatial scales. *Afri. J. Ecol.* 37: 93 - 106.
- Glover T, Mitchell K, 2001. *An Introduction to Biostatistics*. New York: McGraw-Hill.
- Guy PR, 1976. The feeding behaviour of elephants *Loxodonta Africana* in the Sengwa area, Rhodesia. *S. Afri. J. of Wildl. Res.* 6: 55 - 63.
- Houston D, Shine R, 1993 Sexual dimorphism and niche divergence: feeding habits of the *Arafura filesnake*. *J. Anim. Ecol.* 62: 737 - 748.
- Hunter LTB, 1998. The behavioural ecology of reintroduced lions and cheetahs in the Phinda Resource Reserve, KwaZulu-Natal, South Africa. Ph. D. thesis, University of Pretoria.
- Jarman PJ, 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48: 215 - 267.
- Kirkwood D, Midgley J, 1996. Sand forests of Maputaland. *Veld & Flora* 82: 108 - 109.
- Kie JG, Bower RT, 1999. Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection and dietary niche. *J. Mammal.* 80: 1004 - 1020.
- Kleiber M, 1961. *The Fire of Life: An Introduction to Animal Energetics*. New York: John Wiley & Sons.
- 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.
- Loison A, Gaillard J, Pelabon C, Yoccoz NG, 1999. What factors shape sexual size dimorphism in ungulates? *Evol. Ecol. Res.* 1: 611 - 633.
- Low AB, Rebelo AG, 1996. Vegetation of South Africa, Lesotho and Swaziland. Pretoria: Department of Environmental Affairs and Tourism.
- Main MB, Weckerly FW, Bleich VC, 1996. Sexual segregation in ungulates: new directions for research. *J. Mammal.* 77: 449 - 461.
- Matthews WS, van Wyk AE, van Rooyen N, Botha GA, 2001. Vegetation of the Tembe Elephant Park, Maputaland, South Africa. *S. Afri. J. Bot.* 67: 573 - 594.
- McElligott AG, Gammell MP, Harty HC, Pains 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. Soc.* 49: 266 - 272.
- Page BR, Walker BH, 1978. Feeding niches of four large herbivores in the Hluhluwe Game Reserve. *Natal. Proc. Grass. Soc. S. Afr.* 13: 117 - 122.
- Pérez-Barbería FJ, Gordon IJ, 1999. Body size dimorphism and sexual segregation in polygynous ungulates: an experimental test with Soay sheep. *Oecologia* 120: 258 - 267.
- Pérez-Barbería FJ, Robertson E, Gordon IJ, 2005. Are social factors sufficient to explain sexual segregation in ungulates? *Anim. Behav.* 69: 827 - 834.
- Pérez-Barbería FJ, Robertson E, Soriguer R, Aldezabal A, Mendizabal M, Pérez-Fernández E, 2007. Why do polygynous ungulates segregate in space? Testing the activity-budget hypothesis in Soay sheep. *Ecol. Mono.* 77: 631 - 647.
- Prins HHT, van der Jeugd HP, 1993. Herbivore population crashes and woodland structure in East Africa. *J. Ecology* 81: 305 - 314.
- Poole JH, 1989. Announcing intent: the aggressive state of musth in African elephants. *Anim. Behav.* 37: 140 - 152.
- Pooley E, 1993. *The complete field guide to trees of Natal, Zululand and Transkei*. Durban: Natal Flora Publications Trust.
- Ramzinski DM, Weckerly FW, 2007. Scaling relationship between body weight and fermentation gut capacity in axis deer. *J. Mammal.* 88: 415 - 420.
- 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.
- Shannon G, Page BR, Duffy KJ, Slotow R, 2006a. The role of foraging behaviour in the sexual segregation of the African elephant. *Oecologia* 150: 344 - 354.
- Shannon G, Page BR, Duffy KJ, Slotow R, 2006b. The consequences of body size dimorphism: are African elephants sexually segregated at the habitat scale? *Behaviour* 143: 1145 - 1168.
- Skarpe C, Bergström R, Bråten A-L, Danell K, 2000. Browsing in a heterogenous savanna. *Ecography* 23: 632 - 640.
- Stokke S, 1999. Sex differences in feeding-patch choice in a megaherbivore: elephants in Chobe National Park, Botswana. *Can. J. Zool.* 77: 1723 - 1732.
- 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.
- Vincent J, Hitchins PM, Bigalke RC, Bass AJ, 1968. Studies on a population of nyala. *Lammergeyer* 9: 5 - 17.
- van Rooyen AF, 1992. Diets of impala and nyala in two game reserves in Natal, South Africa. *S. Afri. J. Wildl. Res.* 22: 98 - 101.
- van Rooyen AF, 1993. Variation in body condition of impala and nyala in relation to social status and reproduction. *S. Afri. J. Wildl. Res.* 23: 36 - 38.
- Weckerly FW, 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *J. Mammal.* 79: 33 - 52.
- Woolnough AP, du Toit JT, 2001. Vertical zonation of browse quality in tree canopies exposed to a size-structured guild of African browsing ungulates. *Oecologia* 129: 585 - 590.