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Vertical zonation of browse quality in tree canopies exposed to a size-structured guild of African browsing ungulates

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Abstract We investigated whether the food quality of tree foliage for African savanna browsers varies across the feeding height range of the guild. This was to address the question of why giraffes (*Giraffa camelopardalis*) generally feed at a higher level in the canopy than is accessible to all other browsers. We defined a giraffe browse unit (GBU) as the length of twig corresponding to the average “bite” taken by giraffes from two staple browse plants: *Acacia nigrescens* and *Boscia albitrunca*. We sampled at three study sites in South Africa in the late dry season, at each site clipping GBUs at three heights above ground: 0.5 m, 1.5 m and 2.5 m; these representing the levels typically browsed by small, medium and large-bodied browsing ungulates respectively. For each GBU we measured leaf dry mass, total N, neutral detergent fibre and condensed tannin, using near-infrared spectroscopy calibrated by conventional laboratory analyses. We found no differences between height levels with regard to leaf chemistry concentrations, but leaf biomass per GBU was significantly higher at the 1.5-m and 2.5-m levels than at the 0.5-m level. The larger browsers thus gain a bite-size advantage by browsing above the reach of the smaller species. A likely reason for the reduced leaf biomass per GBU at the low browsing level is the tendency for small browsers to pluck individual leaves from shoots, while large browsers prune off whole shoots. We contend that our findings are analogous to those from parallel studies on the grazing guild, and are consistent with the hypothesis that the smaller members of ungulate guilds competitively displace the larger ones from shared feeding sites when resources become restricted. A prediction of this hypothesis is that the smaller members of each guild drive the grazing succession from behind and maintain browsing height stratification from below.

Keywords Browsing height · African ungulate guilds · African savanna · Interspecific competition

Introduction

A key question for large mammal assemblages in general, and for African savanna ungulates in particular, is how shared resources are partitioned among coexisting species (Sinclair 1979; Sinclair and Norton-Griffiths 1982; Sinclair 1985; McNaughton and Georgiadis 1986). The African savanna biome includes at least 46 extant ungulate species, which is more than on any other continent (Owen-Smith and Cumming 1993). One important ecological separation is between the browsing and grazing guilds (du Toit 1995a), and within each guild coexisting species tend to differ in body size (Owen-Smith 1985). To date, however, research into the factors governing interspecific interactions within these size-structured guilds has advanced with a distinct focus on grazers (e.g. Gwynne and Bell 1968; Bell 1970, 1971; McNaughton and Georgiadis 1986; Illius and Gordon 1987; Gordon and Illius 1989; Murray and Illius 2000). Throughout these studies the Jarman-Bell Principle persists as a key factor, with the principle essentially being that an increase in ungulate body size is associated with an increase in dietary tolerance (Bell 1971, 1986; Geist 1974; Jarman 1974; Demment and van Soest 1985). Increased dietary tolerance (measured in terms of the range in fibre content, or digestibility, of herbage the animal can tolerate as food) results from the nutritional advantages that accrue to large herbivores through: (1) decreased mass-specific metabolic demands, and (2) increased gut capacities. Expressed ecologically, the smallest size classes in an ungulate guild have to feed selectively on the highest quality food available. Although larger species also prefer high-quality food, their daily intake requirements force them to accept more abundant food of lower quality, which they can tolerate.

The Jarman-Bell Principle is illustrated by buffalo (*Syncerus caffer*), zebra (*Equus burchelli*) and wilde-

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beest (*Connochaetes taurinus*) ingesting more grass stem and less leaf than the smaller-bodied gazelles (*Gazella granti* and *G. thomsoni*) that follow behind the grazing succession on the Serengeti Plains of East Africa (Gwynne and Bell 1968; Bell 1970, 1971). The gazelles benefit from the coarse feeding and trampling actions of the larger grazers, which reduce the sward height, expose high-quality plant parts, and induce palatable regrowth (McNaughton 1976). From this Bell (1970, 1971) hypothesized that the grazing succession occurs by virtue of the larger grazers "facilitating" feeding opportunities for the smaller species. Subsequently, however, Sinclair and Norton-Griffiths (1982) dismissed the facilitation hypothesis because its predictions could not be upheld by 20 years of Serengeti census data. Furthermore the results of a modelling exercise (Illius and Gordon 1987) predict that the narrow-muzzled smaller grazers are more efficient feeders on short swards, while empirical evidence from the Serengeti shows that narrow-mouthed grazers feed with greater selectively in differentiated swards (Murray and Illius 2000). By removing only the high-quality plant parts they reduce the overall quality of shared swards and thus force the less selective (larger) grazers to move on. Consequently, there are theoretical and empirical grounds on which to argue that the positioning of the larger grazers at the front of the grazing succession is maintained by indirect competition from the smaller grazers following behind. Here we propose that fresh insights into the processes that structure ungulate communities can be gained by shifting the focus of the facilitation/competition debate away from the grazing guild and onto the browsing guild.

In the savanna habitats of southern Africa, food availability for ungulates is most restricted in the late dry season (du Toit 1995a). At this time browsing ungulates congregate along riverlines and watercourses where trees retain green foliage (Pellew 1984a; du Toit 1995b), and it is in these feeding patches that interspecific competitive interactions are most likely to become evident. The most common members of the browsing guild in southern African savannas are steenbok (*Raphicerus campestris*), impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*) and giraffe (*Giraffa camelopardalis*); four species well distributed across the entire body size range for ruminants. Giraffes, being the tallest land mammals and largest of all ruminants, feed mostly above the height levels accessible to the smaller species (du Toit 1990) despite being able to feed near to ground level as well (see also Pellew 1983,1984a; Ginnet and Demment 1997). This would in fact be predicted by the competition hypothesis on ungulate community structure, assuming that giraffes become displaced vertically (upwards) through the effects of selective feeding by the smaller species in the browsing guild. By analogy the process is equivalent to the largest grazers being displaced horizontally (forwards) by the smaller species in the rear of the grazing succession. A test of the underlying assumption requires evidence, however, that giraffes derive some nutritional advantage by feeding above the levels used by smaller browsers. In this paper we report on field and laboratory studies that specifically examined the vertical distribution of browsing in relation to browse availability and quality on trees from two staple species. Fieldwork was conducted in the late dry season at three savanna sites in South Africa, where in each case the indigenous browsing ungulate guild was intact and browsing intensity was high.

Materials and methods

Study species and sites

We collected browse samples from *Acacia nigrescens* and *Boscia albitrunca*, two phylogenetically independent tree species (families Leguminosae and Capparaceae, respectively) that are both staple browse plants in the late dry season (Coates Palgrave 1981; du Toit et al. 1990). Sampling sites were the Tshokwane region of Kruger National Park (*A. nigrescens*; 240°47′S, 310°52′E), Pilanesberg National Park (*B. albitrunca*; 250°13′S, 270°13′E) and Borakalalo National Park (*B. albitrunca*; 250°12′S, 270°48′E). Each site has a similar seasonal rainfall pattern with distinct wet and dry seasons, and giraffes, kudus, impalas and steenbok are all common at each site. Sampling of plants occurred just prior to the wet season of 1999/2000.

Definition of the sampling unit

Studies by Cooper and Owen-Smith (1985), Owen-Smith and Cooper (1987) and du Toit et al. (1990) identified crude protein (CP), fibre and condensed tannins (CTs) to be important factors in determining the quality of browse to southern African ruminants. To test for vertical zonation in these variables within foliage used by browsers, we had to sample at a scale that corresponds with the feeding actions of large browsers. We thus defined a giraffe browse unit (GBU) as our sampling unit. The GBU is equivalent to the length of twig pruned or leaf-stripped by a giraffe in a single "bite", measured from the terminal tip of the twig to the point proximal to the tree at which either pruning or leaf stripping began. The GBU encompasses the smaller bites of steenbok, impala and kudu. From a pilot study of twigs recently browsed by giraffes, the mean GBU length was 144 mm (SE=6.2 mm; *n*=78) for *A. nigrescens* and 89.5 mm (SE=5.3 mm; *n*=24) for *B. albitrunca*, reflecting the different leaf and twig morphologies of the two species.

Sampling protocol

Three stands were sampled for each tree species: stands 1–3 for *A. nigrescens* at Tshokwane; stands 4–5 for *B. albitrunca* at Pilanesberg; stand 6 for *B. albitrunca* at Borakalalo. A transect line was positioned through the middle of each stand along a randomly chosen compass bearing. While walking along the transect line, all trees of the study species were inspected when encountered to check for a full canopy of green foliage extending from near ground level to giraffe head height. The first ten trees satisfying this criterion at each stand were permanently marked. Three feeding-height levels were chosen to represent the average browsing heights of the common guild members: 0.5 m for steenbok and impala; 1.5 m for kudu; 2.5 m for giraffe (after du Toit 1990). Evidence of recent browsing of shoot ends was recorded on a presence/absence basis (see du Toit et al. 1990) for ten randomly selected shoots at each height level, providing a proportional index for comparing browsing intensity up and down the canopy.

At each tree, five GBUs were clipped with even spacing around the canopy at each of the three height levels. These GBUs (15 per tree) represented the twig and leaf material available to

Table 1 Performance of near infrared spectroscopy (NIRS) in measuring leaf constituents [coefficient of determination represented by r^2, with significance (Sig.) levels for regression being $P<0.001$]. For laboratory accuracy assessment, *n* represents the number of samples in the calibration set. SE of the laboratory (SEL) is: $SEL=\sqrt{(\Sigma(y_1-y_2)^2/n)}$ where y_1 and y_2 are duplicates of analyses (Smith and Flinn 1991; Aragones 1996). Ten samples for each leaf constituent [$n=6$ for condensed tannin (*CT*)], excluded from equation development defined as the "check set", were used to check for differences between laboratory measured values and equation predicted values. Values presented are means (±SD). No differences were observed between measured and predicted values using paired *t*-tests. Performance of the statistical model using least-squares linear regression analysis for predicted values for forage-quality variables, using NIR spectra, versus actual measurements made by laboratory analyses. Error between laboratory values and the values predicted by NIRS is measured by the SE of the cross-validation (SECV) and 1–variance ratio (*1–VR*). The SECV provides an estimate of accuracy (%) and 1–VR (where the VR is the explained variance divided by the total variance) explains variation (%) in the reference method values explained by NIRS (Shenk and Westerhaus 1992). *NDF* Neutral detergent fibre, *CT* condensed tannin, *MPLS* modified partial least squares

Nutrient	Laboratory accuracy assessment				Statistical model performance assessment							
					Regression equation							
	n	SEL	Check set measured	Check set predicted	Equation type	Math treatment	Slope	Intercept	r^2	SECV	1–VR	Sig.
Total N[a]	64	0.04	2.78±0.37	2.77±0.35	MPLS	1,4,4,1	0.99	0.05	0.98	0.59	0.97	***
NDF[a]	64	0.89	42.52±7.96	42.62±7.96	MPLS	2,4,4,1	0.96	2.10	0.96	2.67	0.93	***
CT[a]	22	–	11.38±1.19	11.51±1.50	MPLS	1,4,4,1	0.92	90.84	0.92	53.40	0.77	***

***$P<0.001$

[a] Percentage of dry matter

browsers at the time of sampling. Collected samples were immediately stripped of leaves and the leaf and twig material was placed together in a labelled paper bag for drying or freezing in the field. All samples were oven dried at 60°C to constant mass. For each GBU sampled, leaf dry mass, twig dry mass, twig length and proximal diameters were recorded. For analyses of browse quality, leaf material from the five GBUs clipped at each height level on each tree was pooled to form a single sample for each height level: three height levels per tree; ten trees per stand.

Browse quality

Total N, neutral detergent fibre (NDF) and CT concentrations for leaf material were measured using near infrared spectroscopy (NIRS) calibrated by conventional laboratory analyses. The analysis followed the protocols described by Foley et al. (1998) and Woolnough and Foley (in press). Briefly, near infrared spectra (1,100–2,500 nm) were collected with a NIRS spectrophotometer (5000; Infrasoft, USA) for 173 samples. Using ISI software (ISI version 3.01; Infrasoft) on centred samples, a calibration set of 64 samples and a check set of ten samples were selected. Conventional chemical analyses were carried out on the calibration and check sets using the Kjeldahl method (AOAC 1980) to determine N, the Goering and Van Soest (1970) method to determine NDF, and the acid butanol assay for proanthocyanidins (Porter et al. 1986) to determine CT concentrations. Predictive equations, using the modified partial least-squares technique (ASTM 1995), were generated with the ISI software. These equations were used to predict values of the above variables for the remaining 109 samples, including those in the check set. Because *B. albitrunca* was unexpectedly found to contain no CT in its leaves (see Results), the equation was restricted to just *A. nigrescens* ($n=22$). We estimated leaf CP concentrations by multiplying N concentrations by 6.25 (McDonald et al. 1973).

Statistical analyses

One set of analyses was performed to investigate variation in browsing intensity (% shoot ends browsed), leaf dry mass/GBU (g), and leaf chemistry (CT, NDF and CP expressed as % dry mass) across browsing heights within species at each sampling site. This involved arcsine-transforming all variables expressed in proportions and performing one-way ANOVAs with height being the factor in each case. Means were then compared using a posteriori multiple comparisons. A separate set of analyses was performed on the entire data set (including all six stands and both tree species) to test for variation in browsing intensity and leaf constituents per giraffe "bite" (CP, NDF and CP expressed as g/GBU), using two-way ANOVAs with height and stand as factors. The association between browsing intensity and leaf dry mass/GBU was investigated across feeding heights on *A. nigrescens*, with a one-way ANCOVA performed using browsing intensity as the variable, leaf dry mass/GBU as the covariable and height as the factor.

Results

NIRS equation development

Discrete equations were developed for each of the three leaf chemistry variables (Table 1). Each of the three equations provided highly significant agreement between the predicted values and the measured values in the check-set, as assessed by paired *t*-tests. The precision of the equations reflected the accuracy of the laboratory values as well as the structural properties of the selected plant compounds in relation to the reflectance of near infrared light. As with most NIRS studies, N exhibited the lowest SE of the laboratory (SEL) and had the highest equation precision as indicated by the high coefficient of determination (r^2) and the lowest SE of the cross-validation. The lower precision of the equation for NDF was due, in part, to the larger SEL resulting from very small sample sizes, as well as its structural properties. The unexpected result of no CT in *B. albitrunca* adversely affected the precision of this equation. Nonetheless, it was still able to reliably explain 92% of the variability and could be used to predict CT values for *A. nigrescens*. Measured and predicted values were comparable to those reported by Cooper and Owen-Smith (1985), Owen-Smith and Cooper (1987) and du Toit et al. (1990).

Table 2 Variation in browsing pressure and browse quality across three canopy height levels for *Acacia nigrescens* at one site (Tshokwane, three stands) and *Boscia albitrunca* at two sites (Pilanesberg, two stands; Borakalalo, one stand). An a posteriori analysis (Student-Newman-Keuls' multiple range test) determined which height levels were significantly different (*Diff.*). Values (mean±SD) for leaf constituents are expressed as % leaf dry mass. Leaf dry mass/giraffe browse unit (*GBU*) refers to the "bite size" that a giraffe would derive from stripping the leaves from one standardized GBU. Note that *B. albitrunca* was found to have no CT at all in its leaves. *CP* denotes crude protein; for other abbreviations, see Table 1

Site	Species	Variable	ANOVA result	Height 0.5 m	Diff. 0.5 vs. 1.5 m	Height 1.5 m	Diff. 1.5 vs. 2.5 m	Height 2.5 m	Diff. 0.5 vs. 2.5 m
Tshokwane	*A. nigrescens*	Browsed shoot ends (%)	****	13.7±14.7	*	30.7±26.6	**	51.0±26.4	***
		Leaf dry mass/GBU (g)	****	0.35±0.21	***	0.56±0.14	n.s.	0.59±0.20	***
		CP (%)	n.s.	16.9±1.73	n.s.	17.8±1.59	n.s.	17.7±1.50	n.s.
		NDF (%)	n.s.	38.1±3.47	n.s.	38.6±3.57	n.s.	39.6±3.46	n.s.
		CT (%)	n.s.	11.9±1.08	n.s.	11.7±1.06	n.s.	11.5±1.12	n.s.
Pilanesberg	*B. albitrunca*	Browsed shoot ends (%)	*	13.1±18.1	*	32.5±19.2	n.s.	24.5±18.2	n.s.
		Leaf dry mass/GBU (g)	*	0.25±0.09	*	0.40±0.19	n.s.	0.48±0.20	*
		CP (%)	n.s.	20.0±1.82	n.s.	19.7±1.71	n.s.	19.1±1.67	n.s.
		NDF (%)	n.s.	58.0±3.42	n.s.	59.0±3.35	n.s.	59.2±3.52	n.s.
Borakalalo	*B. albitrunca*	Browsed shoot ends (%)	n.s.	27.5±22.2	n.s.	53.0±21.1	n.s.	41.0±19.1	n.s.
		Leaf dry mass/GBU (g)	*	0.05±0.03	n.s.	0.19±0.10	*	0.26±0.11	*
		CP (%)	n.s.	17.3±3.54	n.s.	17.4±2.04	n.s.	16.7±1.83	n.s.
		NDF (%)	n.s.	43.1±2.26	n.s.	43.0±2.78	n.s.	40.9±2.86	n.s.

*$P<0.05$, **$P<0.01$, ***$P<0.001$, ****$P<0.0001$; *n.s.* no significant difference

Variation in browsing intensity and browse quality across canopy heights and tree stands

Browsing of *A. nigrescens* shoot ends increased with height up the canopy, with the highest browsing intensity being at the giraffe (2.5 m) level (Table 2). For *B. albitrunca* there were more shoots browsed at the kudu (1.5 m) and giraffe (2.5 m) levels than at the steenbok/impala (0.5 m) level, despite no significant variation between kudu and giraffe levels. Within each tree species there were, however, no significant variations in the measured leaf chemistry variables across canopy height classes (Table 2). This indicates that leaf quality to browsers, when measured in terms of concentrations of chemical constituents per unit dry mass, was essentially uniform in the sampled trees irrespective of feeding height.

In contrast, when the composition of the plant material was expressed in terms of GBUs, reflecting food gained per giraffe "bite", significant differences with height became apparent. This was because leaf dry mass/GBU increased with height up the canopy for both tree species (Table 2) and so across all stands CP and NDF levels per GBU increased significantly ($P<0.0005$) between the steenbok/impala (0.5 m) and giraffe (2.5 m) feeding heights. There was no interaction between stands and heights for CP and NDF. CT covaried with CP and NDF as expected in *A. nigrescens* (stands 1–3) but, surprisingly, was found to be completely absent from *B. albitrunca* (stands 4–6).

For *A. nigrescens* we found that browsing intensity (% shoot ends freshly browsed) increased significantly across browsing heights as a function of leaf dry mass/GBU ($P<0.005$), although there was no significant relationship between browsing intensity and leaf biomass within any one browsing height (Fig. 1). No similar trends were found for *B. albitrunca*, however, probably because giraffes tend to leaf-strip the non-spinescent *B. albitrunca* shoots more frequently than they prune them.

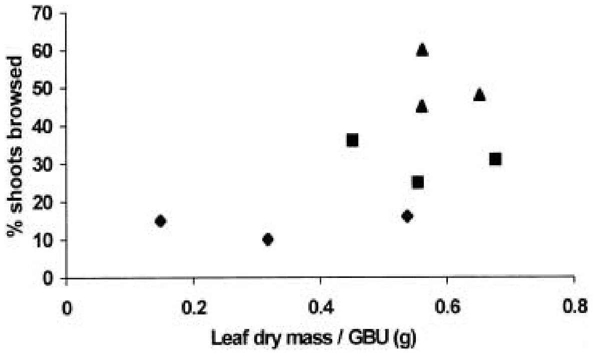

Fig. 1 Browsing pressure (% shoots freshly browsed) on *Acacia nigrescens* trees at three browsing heights (0.5 m, ◆; 1.5 m, n; 2.5 m, s) in three sample stands, plotted against mean leaf dry mass/giraffe browse unit (*GBU*) at the corresponding height levels and stands at the Tshokwane study site in the Kruger National Park. Although ANCOVA found no significant trends within height classes, there was a significant overall increase in browsing pressure with increasing leaf dry mass/GBU across all three heights and stands ($P=0.001$)

Discussion

In this study, all stands of trees sampled from both species (*A. nigrescens* and *B. albitrunca*) at each study site (Tshokwane, Borakalalo and Pilanesberg) were chosen for their occurrence in areas of high browsing intensity (>30% shoot ends browsed at the 1.5-m level). In these trees we found that although there was significant variation in browsing intensity across canopy heights, this was not associated with any significant variation in the concentrations of leaf chemical constituents measured in either species. There was, however, a significant pattern of vertical zonation with regard to the amount of food (leaf dry mass) available to giraffes in each GBU, indicating that giraffe feeding efficiency increases with height up the canopy. We interpret this finding as evidence that giraffes derive a nutritional advantage by feeding above the levels accessible to the smaller members of the browsing ungulate guild. Also, browsing intensity on *A. nigrescens* shoot ends increased consistently and significantly towards the upper browsing level (2.5 m) as a function of the amount of leaf available per shoot. This confirms that the larger browsers were indeed feeding mostly: (1) above the levels accessible to the smaller browsers, and (2) at canopy heights where they could obtain the most leaf mass per browsed shoot. The generality of this pattern could vary depending on the composition of the browsing guild and the browse resources available. For example, Ginnett and Demment (1997, 1999) found no significant variation in intake rate (g/min) across the 0- to 3-m feeding-height range for giraffes in Tanzania, but these were feeding mainly on trees that did not include *Acacia* species. On the other hand giraffes feeding on *Acacia* trees in Kenya (Young and Isbell 1991) achieved maximum feeding rates (bites/s) at heights of 2.5 m (females) and 3 m (males), which is completely consistent with our findings.

Impalas are selective feeders that usually pluck individual leaves from woody plants, seldom bite off shoot ends, and generally take <0.1 g (dry mass) of plant material per bite (Cooper and Owen-Smith 1986). Steenbok, being smaller than impalas, are even more selective feeders, only biting off *A. nigrescens* shoot ends when these are young and soft in the early growing season (du Toit 1993). Kudus, however, often shear off shoots with their cheek teeth and take the leaf and stem material together in bites that may exceed 0.3 g each (Cooper and Owen-Smith 1986). The usual feeding method that giraffes use to satisfy their large intake requirements is to bite on a shoot transversely, with the terminal portion protruding from one side of the mouth and the stem passing over the incisors. Pulling backwards, the giraffe strips off the leaves with its comb-like incisors and shears off the shoot end, yielding bites of about 2 g each (Pellew 1984b). From our measurements the leaf component of each giraffe bite (i.e. stem excluded) may exceed 0.5 g. These bite-size comparisons serve to demonstrate that at the lower levels of the tree canopy, the smaller browsers like steenbok and impala are expected to reduce the overall food quality of each GBU by taking small selective bites and removing individual leaves. It is thus more profitable for giraffes to feed on intact GBUs at higher levels in the canopy than are accessible to steenbok, impala, and possibly kudu, as predicted by the competition hypothesis. A contributing factor could be a tendency for trees to allocate less leaf biomass to shoots at low levels in the canopy as a feature of their growth patterns. Measuring the extent of the additional effect of selective browsing would require the use of exclosures, but we were unable to maintain exclosures in our study sites due to their destruction by elephants (*Loxodonta africana*).

We conclude that, at the very least, our results rule out the possibility that large browsers facilitate the feeding of smaller members of the guild. This is because the feeding actions of the large browsers, as indicated by pruning of shoot ends, were found to be concentrated at height levels above the reach of the smaller species (see also du Toit 1990). Rather, we argue that our results are consistent with parallel studies on the grazing guild (e.g. Illius and Gordon 1987; Murray and Illius 2000). These provide theoretical and empirical evidence that when ungulates occur at high densities on mixed swards, selective feeding by the smaller-bodied guild members causes attrition in the overall quality of forage available to the larger members. A logical prediction for both ungulate guilds is that selective feeding by the smaller-bodied members drives the grazing succession from behind and promotes browsing stratification from below.

The above prediction should also apply to intraspecific interactions within ungulate species that exhibit sexual size dimorphism, and for grazers indirect competition has indeed been proposed as an explanation for sexual segregation. In red deer (*Cervus elaphus*) it had been suggested that the smaller-bodied hinds and their offspring displace the larger-bodied stags from preferred grazing patches (Clutton-Brock et al. 1987). A more recent study has, however, concluded that the body-size differences between red deer hinds and stags is probably not large enough for the Jarman-Bell Principle to apply within this species (Conradt et al. 1999). Since sexual size dimorphism in ungulates is most pronounced among the largest species (Loison et al. 1999), further research on size-related intraspecific feeding interactions should therefore be directed at those species near the upper end of the body-size range. African elephants (*L. africana*) are obvious candidates (see Stokke and du Toit 2000) and so are giraffes (see Ginnett and Demment 1997), for which it has been shown that the larger bulls consistently feed at a higher level in the canopy than the cows and their offspring (du Toit 1990). There has been debate on the reasons for this (Young and Isbell 1991; Ginnett and Demment 1999) and further studies are required. Nevertheless for giraffes in southern African savannas our results suggest that bulls should derive a nutritional advantage by feeding higher in the canopy than cows, which in turn benefit by feeding above the levels accessible to smaller browsing species.

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