Afr. J. Ecol. 1990, Volume 28, pages 55–61

Feeding-height stratification among African browsing ruminants

J. T. DU TOIT*

Resource Ecology Group, Departments of Botany and Zoology, University of the Witwatersrand, P.O. Wits 2050, South Africa

Summary

This study investigated the hypothesis that the use of different feeding levels in the vegetation promotes resource partitioning among browsing ungulate species in African savannas. Focal animal feeding observations, recorded on a real-time basis using a computerized data-capture system, were conducted on giraffe (*Giraffa camelopardalis* Linnaeus), kudu (*Tragelaphus strepsiceros* Pallas), impala (*Aepyceros melampus* Lichtenstein) and steenbok (*Raphicerus campestris* Thunberg) in the central region of the Kruger National Park, South Africa. Although there was clear stratification in mean feeding heights among the four species throughout the seasonal cycle, there was considerable overlap in the feeding-height ranges of kudu, impala and steenbok. Hence, feeding-height stratification probably only separates giraffe from the other species. Giraffe bulls fed at a higher level in the vegetation than cows, often with head and neck extended vertically. It is suggested that bulls benefit in this by gaining access to nutritious new shoots in the upper canopy, but may suffer an increased predation cost due to reduced vigilance when in this posture.

Résumé

Cette étude a voulu vérifier l'hypothèse selon laquelle l'usage, à des fins alimentaires, de différents étages de la végétation favorise le partage des ressources entre les espèces d'ongulés brouteurs des savanes africaines. On a fait des observations d'animaux doisis en train de se nourrir, enregistrées en temps réel à l'aide d'un système informatisé de recueil de données, sur la girafe (*Giraffa camelopardalis* Linnaeus), le koudou (*Tragelaphus strepsiceros* Pallas), l'impala (*Aepyceros melampus* Lichtenstein) et le steenbok (*Raphicerus campestris* Thunberg), dans la région centrale du Parc National Kruger, en Afrique du Sud. S'il existait une nette stratification des hauteurs moyennes auxquelles les quatre espèces s'alimentaient tout au long du cycle saisonnier, il y avait un recouvrement considérable des niveaux alimentaires des koudou, impala et steenbok. On peut donc dire que les stratifications des étages alimentaires ne séparent probablement que les girafes des autres espèces. Les girafes mâles mangent une végétation plus haute que les femelles souvent avec le cou et la tête tendus verticalement. On suggère que l'avantage qu'ils en tirent ainsi est d'accéder aux jeunes pousses nourrissantes de la canopée mais ils sont d'autre part plus touchés par la prédation du fait que, dans cette position, leur vigilance est amoindrie.

*Present address: SFS Centre for Sustainable Development, 4 Fernleigh Road, Pomona, Harare, Zimbabwe.

Introduction

The African savanna biome includes a rich assortment of large mammalian herbivores (> 5 kg), numbering at least 31 species from 24 genera (Owen-Smith, 1982). As a consequence, early studies by big game biologists in Africa concentrated heavily on identifying mechanisms of resource partitioning among savanna ungulates. These studies found important factors to be (1) that syntopic species tend to differ in the proportions of grass and browse in their diets, and (2) that they tend to differ in body size (reviewed by McNaughton & Georgiadis, 1986). Among grazers, body-size differences may result in available food being partitioned according to its nutritional quality (Gwynne & Bell, 1968; Bell, 1971; Jarman, 1974; Geist, 1974; Demment & van Soest, 1985). Among browsers, a standard explanation for coexistence is that, because of differences in body size, different species feed at different levels in the vegetation (Lamprey, 1963; Leuthold, 1978; McNaughton & Georgiadis, 1986). It has also been suggested for giraffe that competition between the sexes is avoided by males feeding above the level of females (Pellew, 1984b). Despite its wide acceptance, the hypothesis of feeding-height separation among browsers arises largely from qualitative field observations, and has not been adequately tested. Furthermore, although large browsers can clearly feed at levels in the vegetation that smaller browsers cannot reach, this will only reduce niche overlap if they do not also feed at levels that smaller browsers *can* reach. Hence, the aim of this study was to test the feeding-height separation hypothesis by measuring and comparing vertical distributions of feeding time, over the complete seasonal cycle, for giraffe, kudu, impala and steenbok. These four ruminants differ widely in body size but share a common food resource base (impala is a mixed feeder, the others are browsers) and have wide, overlapping distributions within the African savanna biome (Smithers, 1983).

Study area

The study was conducted between October 1984 and December 1986 in the Tshokwane region (24°47′S 31°52′E) of the Kruger National Park (KNP), South Africa. The two main landscapes in this region are *Sclerocarya birrea/Acacia nigrescens* savanna on a basaltic plain, and *Combretum apiculatum/Pterocarpus rotundifolius* scrub on hills composed of rhyolite and granophyre (Coetzee, 1983; Gertenbach, 1983). Annual rainfall averages 590 mm, with over 80% of this falling in the wet season from October to March.

Methods

Feeding observations

The continuous focal animal method (Altmann, 1974) of observation was used to record feeding behaviour of adult female steenbok, impala and kudu; and adult male and female giraffe. Focal animals were either radio-collared or else individually identifiable from natural markings (du Toit, 1988). Animals within the study area were habituated to vehicles, and feeding behaviour was recorded while slowly following focal animals in a 4-wheel drive vehicle. Observations were made through 7 × 50 binoculars, usually at distances of 10–20 m. Observation periods were usually 5 hours each, and were preplanned to cover all daylight hours during each month of the year.

Table 1. Feeding-height classes corresponding to neck angles*

Neck angle*	Class limit	Height of mouth above ground (m)			
		Giraffe	Kudu	Impala	Steenbok
45°	lower	0	0	0	0
	upper	1·7	0·7	0·4	0·25
90°	lower	1·8	0·8	0·41	0·26
	upper	2·7	1·1	0·7	0·4
135°	lower	2·8	1·2	0·71	0·41
	upper	3·7	1·7	1·15	0·6
180°	lower	3·8	1·8	1·16	0·61
	upper	4·5	2·0	1·45	0·9

*Subtended by the neck relative to the forelegs, in adult females of each species.

A portable microcomputer (Sharp PC-1500) equipped with 8K RAM was used for real-time recording of field observations. The microcomputer was affixed to a board that could be clipped to the vehicle dashboard, allowing operation with one hand. The data entry programme was designed for prompt-driven recording of time allocated to the first-order activity classes of feeding, moving, standing and lying, and lower-order classes within each of these (du Toit, 1988). Each entry was stored with a time-stamp, and a subsequent data processing programme on a minicomputer calculated the time elapsed (in seconds) between each successive entry.

Each event within the feeding activity class included the time between when the focal animal took its first bite at a particular height above ground from a particular plant part and species, and when that animal swallowed its last bolus before moving on or switching to feeding at a different height or plant part or species. During the course of the study, a total of 1094 h of field observations were recorded, broken down as follows: giraffe, 307; kudu, 381; impala, 207; steenbok, 199.

Feeding-height measurement

Feeding height was categorized into four classes, using the angle subtended by the focal animal's neck relative to its forelegs. The four classes included those feeding heights corresponding to neck angles closest to 45°, 90°, 135° and 180°, respectively. Neck angles were calibrated with height measurements for each species by separately measuring the height above ground of vegetation browsed within each neck-angle class, using a tape measure weighted at one end with a plumb-bob (Table 1). Mean feeding height above ground was calculated for each browser species during each month of the year as follows:

$$\text{Mean height} = \Sigma p_i h_i,$$

where p_i is the proportion of feeding time allocated to feeding in the ith neck angle class, and h_i is the median height above ground (in metres) of the ith neck angle class for the browser species in question.

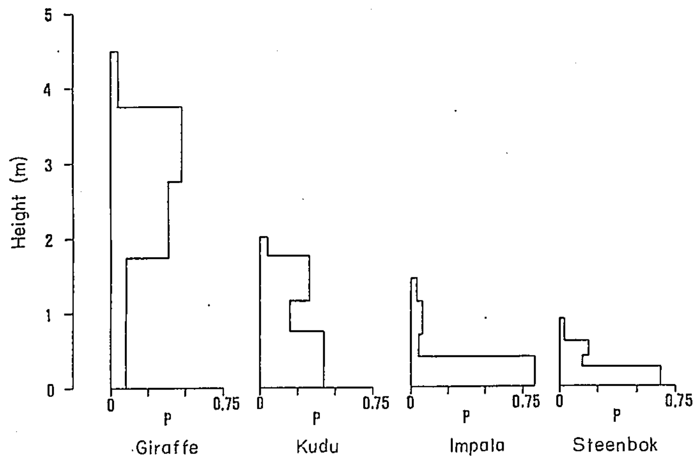

Fig. 1. Proportions (P) of feeding time allocated to height classes, which correspond to the four neck angle classes for each browsers species (see Table 1), calculated over the complete seasonal cycle.

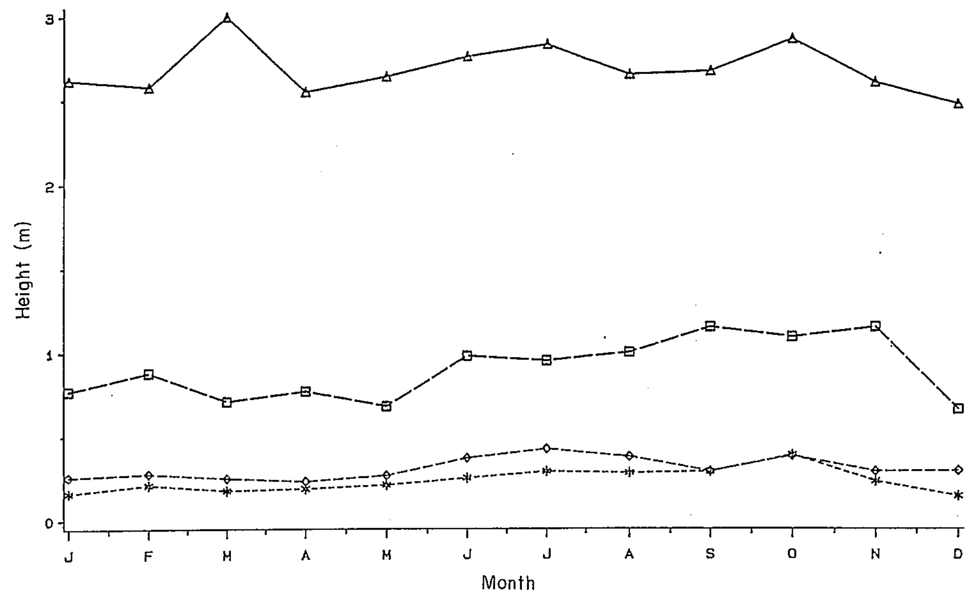

Fig. 2. Mean feeding heights of giraffe (triangles), kudu (squares), impala (diamonds) and steenbok (stars), plotted for each month of the year.

Results

Interspecific comparisons

On a mean annual basis, giraffe allocated almost 90% of feeding time to feeding above the height ranges of kudu, impala, and steenbok (Fig. 1). Kudu allocated 33% of their feeding time to the height range 1·2–1·7 m, which was little used by giraffe and impala, and is beyond the reach of steenbok. However, more than half of kudu feeding time was spent feeding below this level. In terms of mean feeding height, there was clear stratification throughout the seasonal cycle (giraffe > kudu > impala > steenbok; Fig. 2). Among kudu, impala and steenbok a common pattern

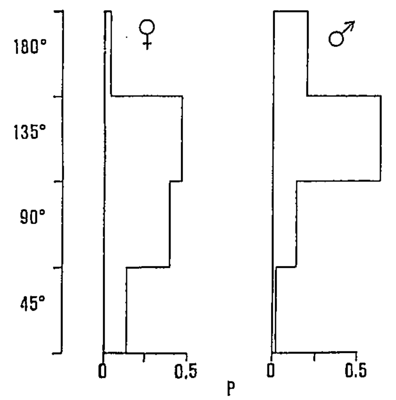

Fig. 3. Proportion (*P*) of feeding time allocated to each neck angle class, by female and male giraffe, respectively, over the complete seasonal cycle.

of increased mean feeding height was evident in the dry season (see June–October, Fig. 2). This is a reflection of the increased use of woody browse to compensate for the reduced availability of green forage in the herb layer during this period.

Giraffe cow/bull comparison (Fig. 3)

Giraffe bulls generally fed at a higher level than cows. Mean percentage of feeding time (± SEM) spent feeding above body height (neck angle >90°) was 84% (±4·0%) in bulls and 49% (±3·6%) in cows. The tendency for bulls to allocate a higher proportion of feeding time to the neck-angle classes 135° and 180° held consistently through the seasonal cycle (pair-wise Student's *t*-test, $P<0{\cdot}0005$, $n=7$ alternate months during which both sexes were studied, tested using arcsine-transformed data).

Discussion

This study showed that despite clear stratification of mean feeding levels among the browsers studied, there is considerable overlap among kudu, impala, and steenbok at the lower feeding levels. The significance of this overlap for inter-specific competition depends on forage production within this height range, browser population densities, habitat preferences, and feeding preferences. Nevertheless, from the results of this study, the assumption that browsers separate by using different feeding levels in the vegetation (Lamprey, 1963; Leuthold, 1978; McNaughton & Georgiadis, 1986) only really holds for the larger species, and not for those smaller than kudu. Overlap in feeding levels among the smaller species must be particularly high in riverine habitats of the northern KNP, for example, where kudu and impala are syntopic with nyala (*Tragelaphus angasi* Gray), bush-buck (*Tragelaphus scriptus* Pallas), and suni (*Neotragus moschatus* Von Dueben). Hence, the argument advanced here is that among savanna browsers, feeding-height stratification separates only giraffe from other species. Giraffe are also quite capable of feeding at lower levels though, so even this separation is not always complete. For example, in Tsavo East National Park, Kenya, giraffe have been found to allocate about 50% of feeding time to browsing below a height of 2 m (Leuthold & Leuthold, 1972). Elephants (*Loxodonta africana* Blumenbach) browse at low levels in the vegetation too, as found by Guy (1976) in the Sengwa

Wildlife Research Area, Zimbabwe. At that site 82% of mouthfuls of browse taken by elephants was from below 2 m, and 60% from below 1·2 m. Hence, among large herbivores exploiting the browse component of African savannas, the degree of overlap in feeding levels is perhaps more significant than the degree of separation (see also Walker, 1976).

An additional consideration is that while giraffe have exclusive access to the upper canopy of mature trees, these trees grow from saplings and seedlings, which are food to smaller browsers. If herbivory on saplings and seedlings was excessive then replacement of the mature canopy, where damaged by elephants for example, would be retarded. Hence, the possibility of long-term exploitative competition between the smaller browsers and giraffe must be considered. This type of competition is evident in the boreal forests of North America, where snowshoe hares (*Lepus americanus* Erxleben) can impact so heavily on preferred woody food plants that the abundance of browse used by moose (*Alces alces* Linnaeus) is severely reduced during peak hare densities (Wolff, 1980; Belovsky, 1984).

The finding that despite their ability to feed lower, giraffe feed almost entirely above the level of kudu (in the KNP at least) reflects the preference of giraffe for new, protein-rich shoots in the upper canopy (Pellew, 1984a; du Toit, 1988). This feeding preference could also explain why giraffe bulls in the KNP feed at a significantly higher level than cows, often with the neck stretched vertically upwards. In East Africa too, giraffe bulls usually feed at full neck stretch while cows prefer feeding at body or knee height (Sinclair & Norton-Griffiths, 1979; Pellew, 1983). Pellew (1984b), who used this difference in feeding posture as a means of sexing giraffe from a distance, proposed that it reduces competition between the sexes. In contrast, I suggest that it could in fact indicate the existence of such competition.

Clutton-Brock & Albon (1985) describe how, in sexually dimorphic large ungulate species, there is a tendency for increased mortality among adult males. They propose that skewed sex ratios could be associated with asymmetries in scramble competition which favour females. Giraffe bulls are bigger than cows ($\approx$0·5 m taller at the shoulder; Hall-Martin, unpubl., cited by Smithers, 1983) and so have a larger food bulk requirement, but spend less time feeding (Pellew, 1984a; du Toit, 1988). This is because giraffe are aseasonal breeders and so mature bulls have to allocate time throughout the year to searching for cows in oestrus and repelling other bulls. Hence, within the time available for feeding, it should be more profitable for bulls to feed on relatively abundant new shoots at full neck stretch than to search for remaining new shoots within the feeding height range of cows and sub-adult males. Feeding at full stretch might not be entirely beneficial, however, as it entails adopting a vulnerable posture. When feeding at full stretch the head is directed vertically upwards, which reduces vigilance, and the body is close up against the tree, which hampers rapid escape when alarmed (pers. obs.). Out of a sample of 559 adult giraffe sexed in the central NKP, du Toit (1988) found a bull:cow ratio of 1:1·6 (cf. 1:1·7 for the Serengeti – Pellew, 1983). Pienaar (1969) found that out of 93 adult giraffe killed by lions (*Panthera leo* Linnaeus) over a 2-year period in the KNP, the cow:bull ratio was 1:1·8—bulls are much more vulnerable to predation than cows. This can be partly accounted for by their solitary habits when wandering between herds in search of cows in oestrus, but feeding at full neck-stretch further increases their vulnerability. If there was no risk, then cows would be expected to feed at full neck-stretch too, but they very seldom do, and neither do kudu cows.

Acknowledgments

The author is grateful for advice and guidance from R.N. Owen-Smith at the University of the Witwatersrand, and assistance from research and management staff in the Kruger National Park. P. Retief wrote the data-capture software and P. Wolff provided valued input during fieldwork. Research funding was provided by the National Parks Board of South Africa, the CSIR, the South African Nature Foundation and the University of the Witwatersrand.

References

ALTMANN, J. (1974) Observational study of behaviour: sampling methods. *Behaviour* 49, 227–267.

BELL, R.H.V. (1971) A grazing ecosystem in the Serengeti. *Sci. Am.* 225, 86–93.

BELOVSKY, G.E. (1984) Moose and snowshoe hare competition and a mechanistic explanation from foraging theory. *Oecologia (Berl.)* 61, 150–159.

CLUTTON-BROCK, T.H. & ALBON, S.D. (1985) Competition and population regulation in social mammals. In: *Behavioural Ecology: Ecological Consequences of Adaptative Behaviour* (Eds R.M. Sibly & R.H. Smith). Blackwell Scientific Publications, Oxford.

COETZEE, B.J. (1983) *Phytosociology, Vegetation Structure, and Landscapes of the Central District, Kruger National Park, South Africa.* Dissertationes Botanicae, Cramer and Vaduz, Heidelberg.

DEMMENT, M.W. & VAN SOEST, P.J. (1985) A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *Am. Nat.* 125, 641–672.

DU TOIT, J.T. (1988) *Patterns of Resource Use Within the Browsing Ruminant Guild in the Central Kruger National Park.* PhD thesis, University of the Witwatersrand, Johannesburg.

GEIST, V. (1974) On the relationships of social evolution and ecology in ungulates. *Am. Zool.* 14, 205–220.

GERTENBACH, W.P.D. (1983) Landscapes of the Kruger National Park. *Koedoe* 26, 9–122.

GUY, P. (1976) The feeding behaviour of elephant (*Loxodonta africana*) in the Sengwa Area, Rhodesia. *S. Afr. J. Wildl. Res.* 6, 55–63.

GWYNNE, M.D. & BELL, R.H.V. (1968) Selection of vegetation components by grazing ungulates in the Serengeti National Park. *Nature (Lond.)* 220, 390–393.

JARMAN, P.J. (1974) The social organisation of antelope in relation to their ecology. *Behaviour* 48, 215–266.

LAMPREY, H.F. (1963) Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. *E. Afr. Wildl. J.* 1, 63–92.

LEUTHOLD, B.M. & LEUTHOLD, W. (1972) Food habits of giraffe in Tsavo National Park, Kenya. *E. Afr. Wildl. J.* 16, 1–20.

LEUTHOLD, W. (1978) Ecological separation among browsing ungulates in the Tsavo East National Park, Kenya. *Oecologia (Berl.)* 35, 241–252.

MCNAUGHTON, S.J. & GEORGIADIS, N.J. (1986) Ecology of African grazing and browsing mammals. *Ann. Rev. Ecol. Syst.* 17, 39–65.

OWEN-SMITH, R.N. (1982) Factors influencing the consumption of plant products by large herbivores. In: *Ecology of Tropical Savannas* (Eds B.J. Huntley & B.H. Walker). Springer-Verlag, Berlin.

PELLEW, R.A. (1983) The impacts of elephant, giraffe and fire upon the *Acacia tortilis* woodlands of the Serengeti. *Afr. J. Ecol.* 21, 41–74.

PELLEW, R.A. (1984a) The feeding ecology of a selective feeder, the giraffe (*Giraffa camelopardalis tippelskirchi*). *J. Zool. (Lond.)* 202, 57–81.

PELLEW, R.A. (1984b) Giraffe and okapi. In: *The Encyclopaedia of Mammals* (Ed. D. MacDonald). Allen and Unwin, London.

PIENAAR, U. DE V. (1969) Predator-prey relationships among the large mammals of the Kruger National Park. *Koedoe* 12, 108–176.

SINCLAIR, A.R.E. & NORTON-GRIFFITHS, M. (Eds) (1979) *Serengeti: Dynamics of an Ecosystem.* University of Chicago Press, Chicago.

SMITHERS, R.H.N. (1983) *The Mammals of the Southern African Subregion.* University of Pretoria, Pretoria.

WALKER, B.H. (1976) An assessment of the ecological basis of game ranching in southern African savannas. *Proc. Grassland Soc. Sth Afr.* 11, 125–130.

WOLFF, J.O. (1980) Moose-snowshoe hare competition during peak hare densities. *Proc. N. Am. Moose Conf.* 16, 238–254.

(Manuscript accepted 1 August 1989)