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Ecological Separation among Browsing Ungulates in Tsavo East National Park, Kenya

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Summary. Data on food habits and habitat preferences of four browsing herbivores (black rhinoceros, giraffe, gerenuk and lesser kudu) were analyzed to assess niche width for each species and niche overlap between pairs of species. All four species depended heavily on woody plants as food, and overlap in the utilization of different plant types (trees and shrubs, herbs, grasses, etc.) was very great in three of six species pairs. When individual plant species were considered, markedly less overlap was apparent. Three of the four ungulate species preferred the most densely wooded vegetation type. Overlap in habitat preferences tended to be least in those pairs of species with the greatest dietary overlap, which resulted in some degree of ecological separation. This was further increased by differences in browsing level. Seasonal variations in the browsing level of the giraffe had the effect of reducing overlap with the other species in the dry season, when food was in relatively short supply. Whether or not actual competition existed among the four ungulate species could not be established; in any event, it would probably be less important than possible competition exerted by the elephant, the dominant herbivore by far in the ecosystem. The ecological separation evident among the four browsing species probably permitted them to coexist in the area before the elephant reached its present dominant position and started altering the original vegetation.

Introduction

A striking feature of African herbivore communities is the relatively large number of species with similar ecological requirements that often coexist in the same area. This has led to a number of studies on ecological separation, i.e. the mechanisms reducing interspecific competition and preventing possible 'competitive exclusion' (e.g., Lamprey, 1963; Jarman, 1971; Hirst, 1975). A

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large body of data has been collected on food habits, particularly of grazers (e.g., Field, 1972; Gwynne and Bell, 1968; Bell, 1970), where studies have been facilitated by the development of identification techniques for plant particles in stomachs and faeces (Stewart, 1965). For browsers, little information was available until recently, at least partly because of greater difficulties in identifying and quantifying the different components of their diets.

In the framework of research on the "Tsavo elephant problem" and its ramifications (e.g., Napier Bax and Sheldrick, 1963; Laws, 1969; Leuthold, 1969, 1978a) studies were conducted on the populations of various ungulates and on the food habits of several browsing herbivores, viz. the black rhinoceros (*Diceros bicornis* (L.); Goddard, 1969, 1970), the gerenuk (*Litocranius walleri* (Brooke); Leuthold, 1970, 1978b), the lesser kudu (*Tragelaphus imberbis* (Blyth); Leuthold, 1971, 1978a) and the giraffe (*Giraffa camelopardalis* (L.); B. and W. Leuthold, 1972, 1978). Collectively, these data permit at least a preliminary evaluation, which is presented in this paper, of ecological separation among the four browsing ungulates mentioned.

The Study Area

The research was conducted in the southern part of Tsavo East National Park in southeastern Kenya, in the area lying to the south of the Galana River (for details see W. and B. Leuthold, 1976; Leuthold, 1978a). In this paper, only data from the area between the Voi and Galana Rivers (ca. 2800 km²) have been used.

Mean annual rainfall varies locally between 250 and 500 mm. Most of it falls in two rainy seasons, in March-May and November/December, but its spatial and temporal distribution is highly irregular. June through October constitutes a long, though relatively cool, dry season which, exacerbated by desiccating winds, is the main period of nutritional stress for herbivores.

The vegetation consists of remnants of formerly extensive *Commiphora-Acacia* woodlands that have been destroyed or at least thinned out by elephants (*Loxodonta africana* (Blumenbach)). Densities of trees and shrubs are generally lowest near rivers, except for local patches of riverine forest or fringes of trees along water courses; the largest belt of riverine forest exists along the Voi River (see Figs. 1 and 2 in Leuthold, 1978a).

Methods

1. Food Habits

The food habits of gerenuk, lesser kudu, and giraffe were investigated in three relatively small study areas near the Voi River, which overlapped substantially—though not totally—and thus contained essentially the same vegetation types. Feeding animals were observed with the aid of 10 × 50 binoculars; plants eaten were either identified visually in the field or collected and checked against herbarium specimens. Feeding records were expressed as frequencies of animals feeding on each plant species (in % of all food records); they probably do not represent actual quantities ingested (cf. Leuthold, 1970, 1978a; Jarman, 1971).

Food plants were divided, according to growth form, into five categories: (1) Trees and shrubs = woody plants normally growing to > 1 m in height; (2) dwarf shrubs = woody plants normally < 1 m tall; (3) creepers and climbers = herbaceous or lignified climbing plants (vines); (4) herbs = dicotyledons with little or no lignification; (5) grasses. A further category (6) comprised fruits and root tubers, which the animals collected and ate in a different manner than other plant parts.

2. Habitat Preferences

Data on distribution and densities were collected in six road strip counts between December 1970 and August 1971 (W. and B. Leuthold, 1976). Perpendicular distances from the road of all animals sighted were measured with a range-finder and densities calculated according to the following formula (Gates et al., 1968; Gates, 1969):

$$D = \frac{n}{2L \left(\frac{n \bar{y}}{n-1} \right)}.$$

where D = density, L = length of transect (road strip), n = number of animals counted, $\bar{y}$ = mean of all sighting distances.

The vegetation was classified into four categories of increasing density of woody plants (not quantified) as follows: A = open grassland with scattered trees; B = grassland with light shrub cover; C = medium bush with incoherent grassy understorey; D = dense bush or woodland. A fifth category ("riverine"), mainly along roads following river courses, was rather heterogeneous, generally quite open, but sometimes included patches of riverine forest. Treating the data for each vegetation type separately, I obtained vegetation-specific densities for each animal species in each season (two counts in the "green", four in the dry season). From these, I derived relative frequencies (in % of each season's sample) of each animal species in each vegetation type. Also, I calculated a "preference index" (PI) for each vegetation type by dividing the number of animals recorded in it by the number expected if animals were distributed regardless of vegetation type (significance checked by χ^2-test).

3. Analysis of Data

A useful way of assessing ecological separation (or similarity) is to calculate *niche widths* of different species and *niche overlap* among them (e.g., Pianka, 1973; May, 1975). Niche width is expressed as $W = 1/\Sigma p_i^2$, where p_i is the proportion of the i-th resource utilized. For comparisons, it is more convenient to use a relative niche width: $W_{rel} = W/N$, where N is the number of different resources within a resource category. W_{rel} can assume values between $1/N$ and 1.

To compare resource utilization among the ungulate species considered, I calculated indices of overlap as follows:

$$\alpha_{jk} = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum p_{ij}^2 \sum p_{ik}^2}}$$

where α_{jk} = mutual overlap between the j-th and k-th species, and p_{ij}, p_{ik} = the proportions of the i-th resource utilized by the j-th and k-th species, respectively (Pianka, 1973). This index of overlap, which can range between 0 and 1.0, gives an indication of the potential for competition between two species.

As an alternative measure of dietary overlap, I calculated the percentages of individual plant species common to the diets of two herbivore species, following Jarman (1971). In the present context, this method provides a more refined, and possibly more realistic, assessment of dietary similarity, as it considers individual plant species, not just plant categories as defined above.

Both food habits and habitat preferences are evaluated for the green and dry seasons separately. However, the irregularity of rainfall made delimitation of the seasons difficult, and subjective judgement had to be used at times. Also, distinction of only two seasons is an oversimplification, but any further subdivision would have created even greater problems.

Results

From the original data given in the papers quoted in the Introduction I calculated relative niche widths, for each species in each season, for the following

niche dimensions ($\approx$ resource types): *food* (utilization of different food plant categories), *browsing level* (height above ground, data for giraffe only) and *habitat* (selection of vegetation types). Results for each niche dimension are first presented separately (sections 1–3, Tables 1–4) and then related to each other by means of the indices of overlap derived from them (section 4, Table 5).

1. Food Habits

a) Utilization of Different Plant Categories. Whereas the data for gerenuk, lesser kudu, and giraffe are fairly directly comparable, those for the black rhinoceros were collected in a slightly different manner and in different areas. For present purposes I chose data from the areas that appeared to have the most similar vegetation to my own study areas (rhino data combined from study areas 4 and 5 of Goddard, 1970). As only plant categories are considered here, I feel that the differences in data collection do not invalidate comparisons with other species.

Table 1 shows the frequencies with which the different ungulates utilized the different plant categories defined above in different seasons, and relative niche widths calculated from them. The following points are noteworthy:
– While the lesser kudu is the only species utilizing all six types of food plants, niche width is slightly greater in the rhinoceros, mainly because no single plant type predominates as much in its diet as in the other herbivores.
– The giraffe shows the narrowest niche because of its near-exclusive dependence on trees and shrubs.
– Most niches tend to be somewhat narrower in the dry than in the green season. This is largely a consequence of seasonal changes in availability of the different plant types: many creepers, herbs, and grasses are either unavailable or unpalatable in the dry season. They all show markedly reduced frequencies in dry-season diets, with corresponding increases in the proportions of trees and shrubs.

– Overall, there appears to be considerable overlap of diets among the four ungulate species, all of which depend heavily on woody plants. The overlap is greater in the dry season because of the decreased diversity of food plants then available. If competition does occur, this is most likely to be in the dry season.

b) Utilization of Different Plant Species. Because of the differences in data collection, the black rhinoceros is not considered here.

Table 2a presents seasonal frequencies of a few selected trees and shrubs in the diets of the other three herbivores and percentage overlap in pairs of these, calculated after Jarman (1971), and Table 2b gives total dietary overlap in the three pairs of herbivore species. In Table 2a, the first three plant species are deciduous shrubs eaten primarily in the green season (the dry-season value for *Premna resinosa* in the gerenuk's diet appears unrealistically high, probably because of a fortuitous preponderance at some stage of data collection). The following two are deciduous shrubs which, however, provide edible parts throughout most of the year but are utilized rather differently by the three ungulate species. The last three plant species are evergreen trees and shrubs eaten in quantity only in the dry season; they could be considered as "dry-season staples".

The data in Table 2a indicate considerable differences in the utilization of different trees and shrubs, between as well as seasonally within herbivore species. These differences are largely "masked" in the records in Table 1, where all trees and shrubs are lumped together. Real dietary overlap among the three herbivores may thus be less than is suggested by the data in Table 1. Percentage overlap in pairs of species varies between about 30 and 50% (Table 2b), increasing in the dry season – as expected – in two pairs; overlap between lesser kudu and giraffe, however, decreases in the dry season, contrary to expectation.

The exact significance of these values of percentage overlap is difficult to assess but, overall, they suggest a certain degree of ecological separation in diets that is not evident from the data on utilization of plant types (Table 1).

2. Browsing Level

The giraffe is generally said to feed mainly on trees and shrubs too tall to be reached by smaller browsers and thus to avoid competing with them (e.g., Darling, 1960; Astley Maberly, 1960). Observations specifically directed at this question showed this assumption to be only partially valid: about 50% of giraffe browsing in Tsavo East occurred below 2 m above ground, i.e. at levels that gerenuk and lesser kudu could reach, too (Table 4 in B. and W. Leuthold, 1972). In the present context, seasonal differences in browsing level are of particular interest: in the green season 67% of giraffe browsing was below 2 m versus only 37% in the dry season. From these data I calculated relative niche widths with respect to browsing level (two "resources": above and below 2 m) as follows:

Table 1. Utilization of different food plant categories by browsing herbivores in Tsavo East National Park. – Figures = % of total feeding records in each season

Species	Season	Trees + shrubs	Dwarf shrubs	Creepers, climbers	Herbs	Grasses	Fruits	Relative niche width
Lesser kudu	Green	71.19	8.79	11.63	7.14	1.03	0.22	0.31
	Dry	78.18	13.31	1.63	0.89	0.07	5.87	0.26
Gerenuk	Green	68.57	0.87	25.87	–	–	4.68	0.31
	Dry	93.72	1.00	2.97	–	–	2.28	0.19
Giraffe	Green	95.16	0.11	4.80	–	–	...	0.18
	Dry	99.55	0.05	0.05	–	–	0.30	0.17
Rhinoceros[a]	Green	27.87	65.57	0.10	6.46	–	–	0.33
	Dry	34.30	63.91	0.25	1.54	–	–	0.32

[a] Data from Goddard (1970), "station" data of habitats 4 and 5 combined

Table 4. Vegetation-specific densities (animals/km²), relative frequencies (% of seasonal sample) of occurrence in, and preference indices (*PI*) for the four vegetation types, and relative niche widths derived from them. — Significance of *PI*: + = preferred, − = avoided; 1 symbol: $P < 0.05$, 2 symbols: $P < 0.01$, 3 symbols: $P < 0.001$

Species	Season		Vegetation type				Relative niche width
			B	C	D	Riv.	
Kudu	Dry	Density	0.098	0.570	0.962	0.354	
		frequency (%)	4.9	28.7	48.5	17.8	
		PI	0.24	1.39	2.33	0.86	0.71
		Significance	− − −	+ +	+ + +	n.s.	
Gerenuk	Green	Density	1.231	1.132	0.363	1.041	
		frequency (%)	32.7	30.1	9.6	27.6	
		PI	1.21	1.12	0.36	1.03	0.88
		Significance	n.s.	n.s.	− −	n.s.	
	Dry	Density	1.413	0.937	0.296	1.264	
		frequency (%)	36.1	24.0	7.6	32.3	0.84
		PI	1.34	0.89	0.28	1.20	
		Significance	+ +	n.s.	− − −	+	
Giraffe	Green	Density	0.090	0.392	0.366	0.060	
		frequency (%)	9.9	43.2	40.3	6.6	
		PI	0.43	1.89	1.76	0.29	0.69
		Significance	− −	+ + +	+	− − −	
	Dry	Density	0.011	0.361	1.074	0.535	
		frequency (%)	0.6	18.2	54.2	27.0	
		PI	0.03	0.94	2.81	1.40	0.62
		Significance	− − −	n.s.	+ + +	+ + +	
Rhinoceros	Dry	Density	0.192	0.152	0.356	0.106	
		frequency (%)	23.8	18.9	44.2	13.1	
		PI	1.24	0.98	2.28	0.68	0.82
		Significance	n.s.	n.s.	+ +	−	

relatively large), partly quite different (gerenuk). However, for two species sufficient data on habitat preferences are available only for the dry season; green-season records might possibly reveal a somewhat different picture. On the other hand, the situation in the dry season is ecologically more important, as the potential for competition over food is greatest at that time (see above, section 3a).

4. Niche Overlap

Using the data presented above on food habits (Table 1), habitat preferences (Table 4), and browsing level, both real and assumed (Table 3 and text, section 2), I calculated niche overlap between pairs of species according to the

Table 5. Indices of overlap (α) in the three niche dimensions considered, and combined overlap, among pairs of the four herbivore species, in green and dry seasons. — The index of combined overlap is the product of the indices in the three dimensions. Data for assumed browsing levels are those listed in Table 3

Species pair	Season	Niche dimension				Combined overlap	
		Food	Habitat	Browsing level		Browsing level	
				Actual	Assumed	Actual	Assumed
Kudu/gerenuk	Green	0.97	−	1.0	1.0	−	−
	Dry	0.99	0.56	1.0	1.0	0.55	0.55
Kudu/giraffe	Green	0.98	−	0.90	0.67	−	−
	Dry	0.98	0.97	0.51	0.32	0.48	0.31
Gerenuk/giraffe	Green	0.95	0.68	0.90	0.67	0.58	0.43
	Dry	0.999	0.50	0.51	0.32	0.26	0.16
Kudu/rhino	Green	0.50	−	1.0	0.78	−	−
	Dry	0.61	0.93	1.0	0.86	0.57	0.49
Gerenuk/rhino	Green	0.38	−	1.0	0.78	−	−
	Dry	0.48	0.69	1.0	0.86	0.33	0.28
Giraffe/rhino	Green	0.39	−	0.90	0.21	−	−
	Dry	0.47	0.89	0.51	0.16	0.21	0.07

formula given under "Methods". Indices of overlap (Table 5) are given for each niche dimension separately, and an index of combined overlap in all three dimensions, obtained by multiplying the three separate indices, is also shown, where sufficient data are available. Multiplication of the three separate indices ("product α"; May, 1975) presupposes that the niche dimensions involved are independent of each other, which is almost certainly not true, strictly speaking. Total interdependence of niche dimensions, on the other hand, is even less likely to obtain in the cases considered here; it would call for the arithmetic means of the three separate indices to be calculated, as a maximum value of possible overlap ("summation α"; May, 1975).

The six possible pairs of species can readily be grouped into two sets of three each on the basis of their food overlap. The first set comprises all "pure-ruminant" pairs, showing very high overlap (with the provisos set out in section 1 b); the second set includes the three combinations of the rhinoceros with another species, in which diets overlap much less. Conversely, overlap with respect to habitat is greater in the second set than in the first one, with one exception (kudu/giraffe). In the latter case, the great overlap in both food and habitat is "offset" by separation in browsing levels.

Use of the assumed browsing levels listed in Table 3 has the effect of reducing combined overlap in all cases but one (kudu/gerenuk; whether an overlap of 1.0 for browsing level in these two species adequately reflects reality must remain an open question).

Discussion

While the methods of data collection could undoubtedly have been improved upon in various respects, they were the same for all species considered (except for food habits of rhinoceros), and the results obtained offer some insights into the mechanisms that bring about ecological separation among browsing herbivores. One of these, apparently, is a certain degree of intercompensation among different niche dimensions. Pairs of species with great food overlap tend to show some separation in habitat preference and/or in browsing level, and vice versa (Table 5). Whether this is a general principle remains to be seen, but similar results have emerged from other studies (e.g. Lamprey, 1963; Schoener, 1968). In this context, the seasonal differences in browsing level of the giraffe are particularly interesting. While they may result, in part, from seasonal differences in availability of such deciduous shrubs as *Premna* spp. (Table 2a), their overall effect is to reduce overlap with lesser kudu and gerenuk in the dry season, i.e. at the time when the potential for competition is highest because of the decreased variety and abundance of food resources. The hypothetical, though probably realistic, differentiation of browsing levels (Table 3) has the effect of further separating five of the six species pairs in this niche dimension. Additional separation in other dimensions could possibly have resulted from a more refined classification of vegetation types (see, e.g., Hirst, 1975) and from feeding records reflecting the actual amounts ingested rather than only the frequencies with which certain plants were eaten. Also, there are undoubtedly further niche dimensions on which no data were obtained in the studies considered here (possibilities: dependence on water, tolerance of heat stress, extent of daily and seasonal movements, susceptibility to predation). The values for combined overlap in Table 5 are thus likely to be relatively too high with respect to real niche overlap, even though they are minimal with regard to the three dimensions considered, being "product αs".

The absolute values of combined niche overlap that are "tolerable", i.e. do not result in severe competition, are difficult to determine. Actual competition, of course, occurs only when the resources in question are in short supply. Whether or not this is the case is always difficult to establish unequivocally in the field. A pointer, however, is the fact that the highest value of combined overlap in Table 5 concerns the green season, in the only species pair for which complete data are available in both seasons (gerenuk/giraffe). Greater overlap may be "permissible" in the green season, when food is likely to be overabundant. The reduced overlap in the dry season may, at least partly, be "enforced" by the reduced quantity and variety of food then available. Actual shortage of food was almost certainly the main cause of recent die-offs of both black rhinoceros (Goddard, 1970) and elephants (Corfield, 1973). This suggests that food resources in Tsavo may, at times, fall below the level required to maintain existing herbivore populations (cf. Phillipson, 1975), but no evidence relating to species other than elephant and rhinoceros is available.

In the specific circumstances of Tsavo National Park, the following considerations may further be important in assessing ecological relationships among different herbivore species:

(a) By the time the studies reported here began (1967-1969), the original vegetation of Tsavo had already been modified extensively. This had resulted in a considerable reduction of woody plants, particularly trees, a trend that continued until recently (Leuthold, 1977). While this may have produced a greater variety of habitats, at least initially, the diversity of woody plants has almost certainly declined overall. Conceivably, this could be reflected in present-day diets of browsing herbivores, and perhaps even in their habitat preferences, both of which might therefore show greater overlap than was the case formerly. In other words, ecological strategies that were adapted to the original conditions may no longer be fully adequate under the circumstances prevailing now.

(b) Jarman (1971) found that dietary overlap between two herbivore species was inversely related to their relative biomass, i.e. overlap was least in species contributing the greatest proportions to the biomass. In the Tsavo study area, the four species considered here constituted the following proportions of total herbivore biomass (13 species): black rhinoceros 6.1%, giraffe 4.0%, lesser kudu and gerenuk 0.3% each (Table 4 in W. and B. Leuthold, 1976). The data in Table 5 are in line with Jarman's hypothesis, at least if the three niche dimensions considered here are viewed in conjunction: the two species with the highest biomass (giraffe and rhino) show by far the least combined overlap, while gerenuk and lesser kudu, with the lowest biomass, show the second-highest value (dry season only), and the highest if assumed browsing levels are used.

Herbivore biomass in the Tsavo study area is dominated overwhelmingly by the elephant (72.3%). This, in conjunction with the visible effects that elephants have had on the Tsavo vegetation, suggests that competition between any two of the browsing species considered here may be of far less consequence than competition from the elephant, or possibly from the elephant and other species combined ("diffuse competition"; Mac Arthur, 1972). If this is so, one might ask why ecological separation has arisen at all among the four browsers considered. Various historical accounts suggest that, formerly, elephants were much less numerous in Tsavo than they are today (references in M. Corfield, 1974). With little or no competition from elephants, possible competition among the other browsing ungulates could have been relatively much more important, and the ecological separation documented in this paper may have enabled them to coexist in the Tsavo area in its original condition.

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