DIETS OF HARTEBEEST AND ROAN ANTELOPE IN BURKINA FASO: SUPPORT OF THE LONG-FACED HYPOTHESIS

JAMES R. SCHUETTE, DAVID M. LESLIE, JR., ROBERT L. LOCHMILLER, AND JONATHAN A. JENKS

Project Nazinga, Association de Développement de l’Élevage de la Faune Africaine, B.P. 5570, Ouagadougou, Burkina Faso (JRS)
United States Geological Survey, Biological Resources Division,
Oklahoma Cooperative Fish and Wildlife Research Unit, Department of Zoology, Oklahoma State University, Stillwater, OK 74078 (DML)
Department of Zoology, Oklahoma State University, Stillwater, OK 74078 (RLL)
Department of Wildlife and Fisheries Sciences, South Dakota State University, Brookings, SD 57007 (JAl)
Present address of JRS: Florida Game and Fresh Water Fish Commission, 551 N. Military Trail, West Palm Beach, FL 33415

Diets of hartebeest (Alcelaphus buselaphus) and roan antelope (Hippotragus equinus) were assessed at the Nazinga Game Ranch in southern Burkina Faso, West Africa. Microhisto­
logical analysis of feces indicated that dietary overlap was high during the rainy (X = 73.7%) and cool-dry (68.2%) seasons, low during the hot-dry season (48.2%), and lowest during the last month of the hot-dry season (31.5%). As the hot-dry season progressed and food presumably became less available, diets of the two antelopes diverged. Hartebeest maintained a high percentage of grass in their diet, but roan antelope switched from being predominantly grazers (>95% grass) to mixed feeders (<50% grass). As grass feeders, both antelopes have skeletal features that facilitate acquisition and grinding of highly fibrous diets, but 11 of 12 mass-relative indices of the skull morphology of hartebeest exceeded those of roan antelope. Because of those differences in skull morphology, and in keeping with the “long-faced” hypothesis, hartebeest were apparently more capable than roan antelope of acquiring and masticating scarce regrowth of perennial grasses when availability of forage was lowest. Such divergence within a single foraging class of African bovids, such as grass feeders, should reduce competition and perpetuate coexistence.

Key words: Alcelaphus buselaphus, hartebeest, Hippotragus equinus, roan antelope, competition, diets, dietary overlap, skull morphology, Burkina Faso, West Africa

Considerable research has focused on beh­
avioral, physiological, and ecological fac­
tors that permit coexistence in diverse as­
semblages of Bovidae throughout Africa (Bell, 1971; Gordon and Illius, 1996; Hof­
mann, 1968; Jarman and Sinclair, 1979; Murray and Brown, 1993). Most research has been conducted in East and South Af­
rica; few empirical data are available from West Africa. Spencer (1995) demonstrated that quantitative differences in size, stature, and mandibular and vertebral morphology existed among African Bovidae, which fa­
cilitated dietary divergence and thus coex­
istence. Following Greaves (1991), Spencer (1995:461) suggested that bovids with a long snout, such as hartebeest (Alcelaphus buselaphus), have improved cropping abil­
ity to acquire grasses and enhanced bio­
mechanical ability to masticate grasses be­
cause their “lengthened jaw increases forc­
es at the cheek toothrow.” Thus, long-faced bovids can exploit a feeding niche that is not useable at all times of the year by other bovids—even those generally classified as grass feeders—because of morphological constraints associated with food acquisition, mastication (Spencer, 1995), and digestion.
We evaluated the long-faced hypothesis with monthly observations of diet selection by West African hartebeest and roan antelope (*Hippotragus equinus*)—two sympatric ungulates that inhabit secondary grasslands (Vesey-Fitzgerald, 1972) and prefer a diet of monocotyledons. Although both species generally are classified as grass feeders (Lamprey, 1963), the face of the roan antelope is not as elongated as that of the hartebeest (Spencer, 1995). Following the long-faced hypothesis, hartebeest should eat grasses to a greater extent throughout the year than do roan antelope. Dietary divergence between the two species should be most pronounced when availability of succulent grasses decreases, rendering necessary both enhanced mastication of senescent grasses, which are rich in silica and lignin, and efficient acquisition of scarce, but readily digestible, regrowth of grasses (McNaughton and Georgiadis, 1986). Following the conventional theory of competitive exclusion (Hardin, 1960; Zaret and Rand, 1971), dietary overlap between these two sympatric antelopes was expected to be minimized during times of limited resource availability.

**Materials and Methods**

**Study area.**—Our study was conducted on the Nazinga Game Ranch (Projet Pilote pour l'Utilisation Rationnelle de la Faune a Nazinga), located between Pô and Léo along the southern border of Burkina Faso in West Africa (11°10'N, 1°35'W). Game ranching is not new to Africa (Dasmann, 1964; Parker and Graham, 1971; Skinner, 1989), although most efforts have been in East and South Africa. Nazinga was a prototype game ranch for West Africa (Spinage, 1983), but because data for West African antelopes were extremely limited, basic information on the natural history of important target species was needed to maximize production of some of the secondary biomass.

Nazinga encompassed ca. 940 km² of uninhabited and relatively undisturbed Sudan savanna between 270 and 326 m above mean sea level. Tropical ferruginous soils varied from gravel-rock to silt-clay; clay content usually increased with depth. In some areas, soils were indurated on the surface and were composed of ironstone and rocky outcrops of laterite, quartz, and Precambrian granite (Buckle et al., 1983). Nazinga received an average annual rainfall of 876 mm from 1982–1987. June through September received >76% of the total, and no precipitation was recorded in December or January. Maximum daytime temperatures ranged from 18.1 to 45.5°C throughout the year. March and April had the highest daily temperatures (X = 38.5°C); August had the lowest (29.4°C—E. Johnson, in litt.). Night-time temperatures occasionally declined to 7°C in December and January (C. G. Lungren, in litt.). We divided the year into three climatic periods of 4-month duration. The rainy season occurred from June through September and ended abruptly. The cool-dry season occurred from October through January. Widespread fires signaled the beginning of the hot-dry season from February through May; it ended with the return of the rains in June.

Savanna was the most common vegetation type at Nazinga, and dominant woody species included: *Acacia, Afxelia africana, Combretum, Detarium microcarpum, Gardenia, Pilostigma thomningii, Pteleopsis suberosa, Terminalia, and Vitellaria paradoxa*. Grass cover was dominated by *Andropogon ascioides, A. gayanus bisquamatus, Aristida kerstingii, Hyparrhenia involucrata, Laudetiopsis kerstingii, and Schizachyrium sanguineum*. Riparian areas were the second most common vegetation type and were composed of *Albizia chevalieri, Anogeissus leiocarpus, Daniellia oliveri, Khaya senegalensis, Mitragyna inermis, Andropogon gayanus gayanus, Hyparrhenia involucrata, Pennisetum subangustum, Sporobolus pyramidalis, and Vetiveria nigriana* (A. van Boxtel and W. Lokhorst, in litt.).

Common herbivores at Nazinga (M. O'Donoghue, in litt.) included elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*), roan antelope, hartebeest, waterbuck (*Kobus defassa*), reedbuck (*Redunca redunca*), bushbuck (*Tragelaphus scriptus*), warthog (*Phacochoerus africanus*), oribi (*Ourebia ourebi*), and Grimm's duiker (*Sylvacarpa girma*). Viable populations of predators were limited to the small carnivores, including genets (*Genetta*), African civets (*Viverra civetta*), mongooses (*Herpestes athel*).
Samples were collected throughout the month, samples were collected monthly for each antelope species from May 1986 through June 1987. Fifteen fresh (i.e., still moist internally) fecal samples were collected randomly with an eyedropper. The four coverslips per fecal sample until 25 fragments were hit and identified as grass or non-grass. This procedure yielded a monthly sample size of 1,500 fragments for each antelope species (four coverslips X 25 identified fragments of grass and non-grass X 15 fecal samples per antelope). It also reduced the bias of differential fragmentation and identification between grasses and non-grasses. Ratios derived from all identified fragments in a field-of-view could have overestimated the non-grass component because dicotyledons are usually more identifiable to species with fewer cells than monocotyledons (Johnson et al., 1983; Stewart, 1967).

Fragment counts were used to quantify species composition of grasses and non-grasses in individual fecal samples (Stevens et al., 1987; Stewart and Stewart, 1970). Fragments were defined as possessing at least two identifying characters (Field, 1972; Scotcher, 1979) and were located by systematically traversing each of the four coverslips in alternate vertical rows to avoid duplication of individual fragments. Fifteen grass and 15 non-grass fragments were identified to species on each of the two slides for a total of 30 grass and 30 non-grass fragments per fecal sample. By doing this for every plant fragment viewed in the fecal samples, a monthly sample of 450 grass fragments and 450 non-grass fragments was obtained for each antelope species. If a sample contained <5% non-grass species or diets included items that reduced fragment clarity (i.e., after salt lick use or consumption of burned vegetation), <30 grass or non-grass fragments may have been identified.

Data analyses.—Monthly differences in the proportion of grasses and non-grasses in diets of hartebeest and roan antelope were tested with a two-way analysis of variance of ranked values (Conover and Iman, 1981). Tukey's multiple range test was used to identify monthly differences in grass consumption between the two antelope species and therefore did not affect relative comparison between species.

Point intercept frequencies were used to quantify the ratio of grass: non-grass fragments in individual fecal samples (Casebeer and Koss, 1970; Stewart, 1967). A group of four points on a microscope ocular was moved systematically over each coverslip by traversing it horizontally; one field-of-view separated sampling fields, both vertically and horizontally. The field-of-view was moved on each of the four coverslips per fecal sample until 25 fragments were hit and identified as grass or non-grass. This procedure yielded a monthly sample size of 1,500 fragments for each antelope species (four coverslips X 25 identified fragments of grass and non-grass X 15 fecal samples per antelope). It also reduced the bias of differential fragmentation and identification between grasses and non-grasses. Ratios derived from all identified fragments in a field-of-view could have overestimated the non-grass component because dicotyledons are usually more identifiable to species with fewer cells than monocotyledons (Johnson et al., 1983; Stewart, 1967).

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telope species (Steel and Torrie, 1980). Percentage of each grass species in individual fecal samples was determined by adjusting the percentage that a grass species contributed to the total grass component (as determined by fragment counts) by the percentage of grass in that sample (as determined by point intercept frequencies). Percentage of each non-grass species in individual diets was determined in the same manner.

Dietary overlap was determined with composite diets. Monthly composite diets of hartebeest and roan antelope were calculated by averaging the percent contribution of each plant species in individual fecal samples for each month. Numerous approaches have been used to assess dietary overlap (Gauch, 1973; Hansen et al., 1973; Horn, 1966). Our approach was straightforward (Hurlbert, 1978), and overlap ranged from 0 (no overlap) to 1 (identical diets):

\[
\text{Overlap} = \sum_{i=1}^{\text{species}} \min(P_{r,i}, P_{h,i}),
\]

where \(P_{r,i}\) = the proportion of plant species \(i\) from roan antelope fecal samples; \(P_{h,i}\) = the proportion of plant species \(i\) from hartebeest fecal samples; and \(\min(P_{r,i}, P_{h,i})\) = the lesser of the two proportions \(P_{r,i}\) and \(P_{h,i}\).

As grass feeders, both hartebeest and roan antelope have evolved skeletal and muscular features that facilitate acquisition and grinding of highly fibrous diets (Spencer, 1995). We speculated, albeit a posteriori from determining composition of diets, that a way for the two species, apparently occupying a similar feeding niche, to avoid dietary overlap was divergence in morphological features of their skulls, rendering one species more capable of thoroughly exploiting grasses (via acquisition and mastication) throughout the year than the other species. In keeping with the long-faced hypothesis, hartebeest should possess such features.

We used skull measurements from Spencer (1995, appendix I) and calculated 95% CI to compare hartebeest and roan antelope. No single measurement is ideal for allometric scaling (Mosimann and James, 1979), and Spencer (1995) already used length of the upper molar row as a size adjustor, reasoning that it demonstrated differences in shape rather than size (Mosimann and James, 1979). In doing so, she was able to classify African bovids into groups based on their forage-type selection; hartebeest and roan antelope were grouped together. To further separate hartebeest and roan antelope, we used the average body mass of each species to allometrically scale skull measurements. We reasoned that if evolutionary divergence in skull morphology had not occurred, average skull measurements from both sexes, adjusted by the average body mass of each species, would be similar. To evaluate this hypothesis, percent differences between 12 mass-relative skull measurements were calculated, assuming average mass of 170 kg for hartebeest and 240 kg for roan antelope (Walker, 1975).

**RESULTS**

**Dietary comparisons.**—Grass consumption varied by month \((F = 14.403, d.f. = 13,390, P < 0.001)\) and species of antelope \((F = 48.490, d.f. = 1,390, P < 0.001)\). During the rainy season in 1986, both hartebeest and roan antelope ate >95% grass (Fig. I). With the exception of May 1986 for hartebeest and October 1986 for roan antelope, grass consumption in the dry seasons never exceeded 95%. Although composite diets for hartebeest never contained <80% grass in the hot-dry season, six of nine dry-season diets of roan antelope contained <80% grass. Diets of hartebeest had less grass during the cool-dry season than during other times of the year. Percentages of grass in diets of roan antelope varied to a greater extent than in diets of hartebeest. Peaks in the percentage of browse in diets of both antelopes occurred at the end of both the cool-dry season and the hot-dry season (Fig. 2).

After analyzing 418 fecal samples, we concluded that typical forage classifications that include grasses, browse, and forbs (Anthony and Smith, 1977; Leslie et al., 1984) were not appropriate for our study, mainly because of the predominance of grasses in diets throughout the year (Fig. 1). Therefore, eight forage categories were defined, based on plant taxonomy, physiognomy, and histology (Table I).

Grasses consumed by hartebeest and roan antelope during the rainy season were dominated by short *Andropogon* (mostly *A. as-
Fig. 1.—Mean monthly percentages of grass in diets of hartebeest and roan antelope and dietary overlap relative to monthly rainfall during this study (1986–1987) and mean monthly rainfall (1982–1987) at the Nazinga Game Ranch, Burkina Faso. Significant differences in the percentages of grass occurred between the two antelope species in March, April, and May 1997 (Tukey's multiple range test, $P < 0.001$).

cinodis) and Hyparrhenia (Fig. 2). Increased use of grass culms and inflorescences occurred during flowering of grasses, was followed by peak use of tall Andropogon in October or November (Fig. 2), and was matched by the reduction of all other grass leaves to $<10\%$ of the diet. Diets after fires in December and January were similar to those during the rainy season, although culms and Jasminium kerstingii occurred in diets of both antelopes in greater proportions than in the rainy season. As the hot-dry season progressed, hartebeest ate $>50\%$ grass leaves; roan antelope ate $<15\%$ grass leaves (Fig. 2). Roan antelope shifted from regrowth of perennial grasses to legumes. The return of the rains in June coincided with a reduction in culms and legumes in both diets, but J. kerstingii increased from $<2\%$ for both antelope in May 1987 to 13$\%$ and 20$\%$ for hartebeest and roan antelope, respectively, in June 1987.

Dietary overlap.—Overlap indices suggested a high plant-specific similarity between diets of hartebeest and roan antelope during the rainy and cool-dry seasons (Fig. 1). Diets became more dissimilar from the cool-dry season through the hot-dry season when forage availability presumably was most limited. Dietary overlap at the end of the hot-dry season was less than one half of the levels recorded during the rainy season when forage availability was greatest.

Comparative skull morphology.—Because of the smaller size of hartebeest, we expected absolute measurements of skulls to be greatest in roan antelope. Contrary to
FIG. 2.—Mean monthly percentages of eight forage categories identified in the diets of a) hartebeest and b) roan antelope at the Nazinga Game Ranch, Burkina Faso, 1986–1987 (the solid line depicts percentages of monocotyledons in diets).

TABLE 1.—Characteristics of eight forage categories used to describe diets of hartebeest and roan antelope at the Nazinga Game Ranch, Burkina Faso, West Africa, 1986–1987.

<table>
<thead>
<tr>
<th>Forage category</th>
<th>Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grass</td>
<td>Exhibit silica bodies</td>
</tr>
<tr>
<td>Tall Andropogon</td>
<td>All perennial bunchgrasses</td>
</tr>
<tr>
<td></td>
<td>Inflorescences &gt;3 meters tall</td>
</tr>
<tr>
<td></td>
<td>Exhibit multiple papillae</td>
</tr>
<tr>
<td>Short Andropogon</td>
<td>Perennials and annuals</td>
</tr>
<tr>
<td>Hyparrhenia</td>
<td>Inflorescences &lt;3 meters tall</td>
</tr>
<tr>
<td>Culms</td>
<td>Perennials and annuals</td>
</tr>
<tr>
<td></td>
<td>Very large papillae</td>
</tr>
<tr>
<td></td>
<td>Very large stomata</td>
</tr>
<tr>
<td>Miscellaneous leaves</td>
<td>Silica-suberose couplets</td>
</tr>
<tr>
<td>Non-grass</td>
<td>No papillae</td>
</tr>
<tr>
<td>Legumes</td>
<td>Both identified and unidentified</td>
</tr>
<tr>
<td></td>
<td>No silica bodies</td>
</tr>
<tr>
<td>Jasminium kerstinii</td>
<td>Abaxial side with papillae</td>
</tr>
<tr>
<td></td>
<td>Adaxial side featureless</td>
</tr>
<tr>
<td>Miscellaneous leaves</td>
<td>Segmented trichomes</td>
</tr>
<tr>
<td></td>
<td>Heavy striations</td>
</tr>
<tr>
<td></td>
<td>Both identified and unidentified leaves and stems</td>
</tr>
</tbody>
</table>
Table 2.—Mean lengths and mass-relative indices of the skull morphology of roan antelope and hartebeest.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Roan antelope</th>
<th>Hartebeest</th>
<th>Mass-relative difference¹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>X̄ (mm)</td>
<td>Mass-relative index¹</td>
<td>X̄ (mm)</td>
</tr>
<tr>
<td>Diastema length</td>
<td>103.12</td>
<td>0.430</td>
<td>106.23</td>
</tr>
<tr>
<td>Mandibular depth</td>
<td>55.22</td>
<td>0.230</td>
<td>52.80</td>
</tr>
<tr>
<td>Mandibular width</td>
<td>24.34</td>
<td>0.101</td>
<td>21.06</td>
</tr>
<tr>
<td>Paracondylar process</td>
<td>58.99</td>
<td>0.246</td>
<td>55.55</td>
</tr>
<tr>
<td>Snout position</td>
<td>1.01</td>
<td>0.004</td>
<td>19.94</td>
</tr>
<tr>
<td>Glenoid height</td>
<td>58.39</td>
<td>0.243</td>
<td>53.13</td>
</tr>
<tr>
<td>Molar row length</td>
<td>70.90</td>
<td>0.295</td>
<td>64.42</td>
</tr>
<tr>
<td>Premolar row length</td>
<td>48.38</td>
<td>0.201</td>
<td>33.12</td>
</tr>
<tr>
<td>Predental length</td>
<td>132.45</td>
<td>0.552</td>
<td>141.68</td>
</tr>
<tr>
<td>Premaxillary width</td>
<td>26.75</td>
<td>0.111</td>
<td>26.23</td>
</tr>
<tr>
<td>Palatal width</td>
<td>64.03</td>
<td>0.267</td>
<td>57.91</td>
</tr>
<tr>
<td>Skull length</td>
<td>405.91</td>
<td>1.691</td>
<td>390.13</td>
</tr>
</tbody>
</table>


That prediction, interspecific comparisons of 95% CI of skull measurements from Spencer (1995:469–471, appendix I) indicated that 1) eight of 12 measurements of male hartebeest and roan antelope did not differ between species or were greater for hartebeest and 2) nine of 12 measurements of female hartebeest and roan antelope did not differ between species or were greater for hartebeest. Spencer’s (1995) measurement of snout position was greater in both male and female hartebeest than roan antelope, which attested to the long-faced character of the hartebeest. Eleven of 12 mass-relative indices of the hartebeest’s skull morphology exceeded those of the roan antelope by 22% to 2,825% (Table 2). Only mass-relative length of the premolar row was comparable between hartebeest and roan antelope.

**DISCUSSION**

*Dietary comparisons.*—Hartebeest and roan antelope consumed grasses when they were fresh and plentiful during the rainy season. As grasses reached senescence during the dry seasons, the proportion of non-grasses in diets of both antelopes increased, but that trend was most pronounced for roan antelope. After grasses had dried out, fires during the middle of the cool-dry season removed the old growth and promoted regrowth of some perennial grasses. Because regrowth of grass was initially fresh and abundant, the proportion of grasses in diets of both antelopes increased, although grasses did not comprise as large a percentage of diets of roan antelope as they did in diets of hartebeest. As the hot-dry season progressed, the proportion of browse in the diet of roan antelope increased, but hartebeest maintained their use of grasses.

Proportions of grasses in diets of both antelopes were less variable during the rainy season than during other seasons (Schuette, 1991). During the dry seasons, differences in phenology and availability may have caused more variance in the proportions of grasses in diets. Localized rain and fire produced a mosaic of phenological stages (potentially separated by >1 month) throughout the landscape at Nazinga, which probably was reflected in diets of antelopes because fecal samples were collected from
relatively disjunct areas throughout the ranch (and likely from different herds of animals).

During the rainy season, diets of hartebeest and roan antelope were influenced by abundance of different grasses. The increase in culm material and decrease in leaf material of specific grasses in diets in September (the month that grasses put out their reproductive shoots) support this contention (Fig. 2). Increased use of tall *Andropogon* in October to the near exclusion of most other grass material, except culms, could not be explained simply by changes in abundance. Based on our general field observations, tall *Andropogon* had a low ratio of reproductive shoot:vegetative shoot, which meant that there were fewer stalks to physically inhibit ungulate use of tall *Andropogon* leaves than was the case for short *Andropogon*. Combined with this, vegetative shoots tended not to senesce as early as reproductive shoots, which made them more palatable.

Fires in November and December caused a decrease in the use of tall *Andropogon*, which was not due entirely to reduced availability because these grasses did regrow. Proportions of short *Andropogon* in diets of both antelopes increased. Eight to 12 weeks after the fires, both antelopes switched from short *Andropogon* to tall *Andropogon*. Sen and Macey (1965) showed that concentrations of crude protein in *A. gayanus* (a tall *Andropogon*) in Ghana were higher in 8- to 12-week-old fresh material than fresh 4-, 16-, or 24-week-old material. That peak in the concentration of crude protein after the fourth week differed from a general trend of decreasing concentration of crude protein with age (Sen and Macey, 1965) and indicated that dietary shifts by antelopes may have been because of changes in forage quality.

The last 2 months of the hot-dry season caused the regrowth of perennial grasses to wither and become less abundant. Diets of hartebeest had high proportions of grasses during the hot-dry season (Fig. 2), attesting to their apparent ability to acquire scarce regrowth of tall and short *Andropogon*. Nevertheless, diets of hartebeest contained low-quality culm material, which could result in dietary stress (Gwynne and Bell, 1968) unless enhanced mastication (Spencer, 1995) permitted them to obtain sufficient nutrients to sustain themselves. Roan antelope switched from using grass-leaf regrowth to browse species, especially legumes that produced new leaves and started flowering in March and April when most other browse species were still dormant (M. K. Johnson, in litt.). The notable decrease of browse (except *Jasminium kerstingii*) in diets of both antelopes when rains returned in June suggested that browse was not a preferred forage but one of necessity and further attested to the classification of both species as grass feeders (Lamprey, 1963; Spencer, 1995).

*Jasminium kerstingii* was an important part of diets of both hartebeest and roan antelope during two times of the year: 1 month after fires moved through an area and immediately after rains returned in June. Although *J. kerstingii* was locally abundant, it never made up >2% of the rainy-season cover in any of the vegetation types found at Nazinga (A. van Boxtel and W. Lokhorst, in litt.). Both antelope species used patches of *J. kerstingii* heavily, which suggested that it was highly preferred.

Dietary overlap and comparative skull morphology.—Although the best examples of interspecific competition come from small animals observed and manipulated under experimental conditions (Neill, 1975; Park, 1962), several attempts have been made to document competition for food among ungulates under natural conditions (Hansen and Reid, 1975; Hudson, 1976; Leslie et al., 1984; Schwartz and Ellis, 1981; Singer, 1979). Considerable research has been conducted on ungulates in East and South Africa (Bell, 1971; Lamprey, 1963; McNaughton, 1985; Murray and Brown, 1993; Sinclair, 1985; Sinclair and Norton-Griffiths, 1982) and the possibility
of niche overlap, a prerequisite to interspecific competition (Pianka, 1976), is theoretically high among Africa's rich and varied ungulate fauna (Jarman and Sinclair, 1979).

There were three times as many roan antelope \( (n = 2,172) \) as hartebeest \( (n = 753) \) at Nazinga (M. O'Donoghue, in litt.). These grass feeders commonly occurred in mixed herds and were comparable in stature, although roan were ca. 50% heavier than hartebeest. Bell (1971:90) hypothesized that "if two species of different size have the same food supply (all other parameters being equal), the larger species will displace a smaller one" due to their lower relative energy requirements and higher digestive efficiency. These factors, combined with the high levels of dietary overlap, suggested that interspecific competition for food could occur between hartebeest and roan antelope, unless factors such as seasonal dietary divergence, mediated perhaps by differences in skull morphology and mass-relative intake requirements, permitted one species to exploit a unique or rare food resource and thereby minimize competition.

Some have speculated that, to foster coexistence and minimize interspecific competition, diets diverge most in times of limited resources (Colwell and Futuyma, 1971; Sale, 1974), although the opposite has been recorded among some ungulates in North America (Jenkins and Wright, 1987; Leslie et al., 1987; Schoener, 1982; Schwartz and Ellis, 1981). In support of our hypothesis, diets of hartebeest and roan antelope diverged to the greatest extent during the hot-dry season (Fig. 1) when browse was more plentiful than drying regrowth of perennial grasses.

Dunham (1994) noted that prolonged dry periods had the greatest effect on populations of grazing ungulates in Zambezi riverine woodlands in Africa due to reduced availability of perennial grasses. During the hot-dry season, roan antelope selected more browse than during other seasons or than did hartebeest. Continued use of widely spaced, short tufts of the regrowth of perennial grasses by the smaller hartebeest during the hot-dry season supported our hypothesis that they have evolved means to acquire and subsist on a limited forage base during the period of greatest potential competition from roan antelope. Competition with other bovids on Nazinga during the hot-dry season appeared to be minimized by divergent food choice (e.g., Grimm's duiker and bushbuck primarily eat dicots) and divergent use of habitat (e.g., reedbuck and waterbuck occurred in riparian areas).

Murray and Brown (1993) also concluded that specialization on different growth stages of grasses separated dietary niches of resident African antelopes such as hartebeest and topi \( (Damaliscus lunatus) \) in the Serengeti. Such specialization provides managers of game ranches such as Nazinga the opportunity to promote (e.g., with prescribed burning) vegetative conditions favorable to a particular antelope (Murray and Brown, 1993).

Foraging ecology of African bovids, as it relates to their coexistence, has been described in several ways: for example, simple contrasts of forage-type selection (i.e., grass versus dicot feeders—Lamprey, 1963; Spencer, 1995), differences in digestive capabilities (i.e., concentrate versus bulk-roughage feeders—Hofmann, 1968, 1989; Hofmann and Stewart, 1972), and contrasts of mass-dependent digesta kinetics (Gordon and Illius, 1996). Across tribes of ungulates, grass feeders, in general, have shorter premolar rows than mixed-grass or dicot feeders, which has been attributed to the need for enhanced mastication of the highly fibrous materials that they prefer to consume (Spencer, 1995). Regardless of the classification scheme, however, one might expect, given the richness of assemblages of sympatric bovids in Africa, further divergence in food selection and morphology within a particular feeding group because of interspecific competitive pressures on food resources. Observations from our study suggest that the long face of the hartebeest permits it to exploit a feeding niche that is
not usable by roan antelope — and likely other bovids— during times of the year when forage is least available. Divergence in a single foraging class such as grass feeders should minimize potential competition and perpetuate coexistence.

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