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# Seasonal diet and foraging preference of greater kudu *Tragelaphus* strepsiceros in the Llano Uplift of Texas

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The greater kudu Tragelaphus strepsiceros, a large African herbivore, occupies the browser trophic niche. This species has been introduced into selected areas of Texas inhabited by the white-tailed deer Odocoileus virginianus, a native browser. Based on similar trophic function, potential interspecific competition could exist between these two species. The objectives of our study were to: 1) describe the seasonal diets of greater kudu in Texas and 2) determine if greater kudu show preference for plants that might create competition with white-tailed deer. We documented the seasonal diet and forage preference of greater kudu at Mason Mountain Wildlife Management Area from 15 May 2001 to 25 February 2002 by identifying epidermal fragments of plants in faecal pellets. We identified and quantified 49 species of plants eaten by greater kudu. Annually, browse made up 80.2% of the diet, while 7.6% mast, 6.5% grasses, 3% forbs and 2.7% unidentified material comprised the remaining parts of their diet. Important browse species included Texas/blackjack oak Quercus buckleyi/Q. marilandica, plateau live oak Q. fusiformis, Ashe juniper Juniperus ashei, mesquite Prosopis glandulosa, prickly pear Opuntia sp., flameleaf sumac Rhus lanceolata, and Texas persimmon Diospyros texana. We measured availability of forage plants by quadrat and line intercept methods concurrent with faecal pellet collection. We compared plant use (dietary composition) with plant availability and assessed forage preference by greater kudu using loglikelihood  $\chi^2$ -tests with Bonferroni corrected confidence intervals and Manly's alpha indices. We detected statistically significant differences between plant use and availability (P < 0.05). Purple horsemint Monarda citriodora, Canada wildrye Elymus canadensis, mesquite, flameleaf sumac, Texas/blackjack oak and Ashe juniper were preferred species. Relative preference of general forage categories by greater kudu in Texas was similar to that reported from Africa. Based on our findings, greater kudu could compete with white-tailed deer for browse forage.

Key words: diet, food habits, greater kudu, Texas, Tragelaphus strepsiceros

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Texas has the most diverse, widespread and abundant populations of non-indigenous ungulates in the United States (Teer et al. 1993). The establishment of nonindigenous ungulates is a controversial ecological issue because of their potential role as invasive species and competitors with indigenous species (Samuel & Demarais 1993). In central Texas, two or more classes of domestic livestock plus wildlife species forage on most rangelands. This region has the highest-density white-tailed deer Odocoileus virginianus population in conjunction with exotic species in the world (Ramsey 1969, Baccus 2002). This abundance of herbivores on rangelands with historic high-impact grazing has resulted in species packing in the herbivore trophic niche and increased the potential for interspecific competition with and reduction of the realized niche of indigenous white-tailed deer (Baccus et al. 1984).

The greater kudu Tragelaphus strepsiceros, a large African herbivore, occupies the browser trophic niche in southern Africa (Wilson 1965, 1970, Conybeare 1975, Owen-Smith 1979, Owen-Smith & Cooper 1985, Owen-Smith & Cooper 1989). The white-tailed deer is the primary native browser in the Edwards Plateau Ecological Region of Texas (McMahan 1964, Bryant et al. 1981, Waid et al. 1984); therefore, dietary overlap and competition between greater kudu and whitetailed deer could exist. Based on the size of greater kudu (adult male weight: 290-315 kg) compared to white-tailed deer (adult male weight: 45-59 kg), the greater kudu might limit forage available to whitetailed deer, depending on the extent of dietary overlap. Dietary overlap and competition for limited forage resources have been the most often cited causal mechanisms of potential competition between white-tailed deer and non-indigenous ungulates (Demarais et al. 1998). Although the estimated population of greater kudu in Texas is low (186 in 1994), this ungulate occurs on several ranches in central and southern Texas as reproducing, nutritionally independent herds with the potential for significant increases (Traweek 1995); however, basic dietary information for the species is lacking for Texas and North America. Such knowledge is essential to assess the potential for dietary competition with native and other non-native herbivores. The objectives of our study were to: 1) describe the seasonal diets of greater kudu in Texas and 2) determine if greater kudu show preference for plant species that might create competition with white-tailed deer.

# Material and methods

## Study area

We conducted our research at Mason Mountain Wildlife Management Area (MMWMA), Mason County, in the Llano Uplift Ecological Region of Texas (Sellards et al. 1932). The Llano Uplift, embedded in the Edwards Plateau Ecological Region, encompasses about 800,000 ha, with rolling to hilly topography ranging in elevation within 251-686 m a.s.l. Granitebased sandy loams are the most widespread soil types in the region (Carter 1931). The average annual precipitation is 76 cm, with peaks in May through June and September. The average annual temperature is 19.6°C (Carter 1931) with a 9.3°C minimum in January and a maximum of 29.5°C in July (Whitehouse 1933). During our study the annual average precipitation amounts for 2001 and 2002 were 63.6 cm and 68.9 cm, respectively, which were slightly below the long-term average annual precipitation, with March, May and November 2001 receiving nearly 50% of the precipitation (United States Department of Commerce 2001, 2002).

MMWMA is owned and managed by Texas Parks and Wildlife Department and is a 2,120-ha area of oak thickets and savannahs divided into seven pastures by 2.4-m high game-proof fences. Our study was conducted in the Turkey (709 ha; 30°51'N, 99°13'W) and South Voca (243 ha; 30°50'N, 99°11'W) pastures. In addition to greater kudu, white-tailed deer, axis deer *Axis axis*, blackbuck antelope *Antilope cervicapra*, sable antelope *Hippotragus niger*, scimitar-horned oryx *Oryx dammah*, and impala *Aepyceros melampus* inhabited these pastures. Of eight major plant communities (Diamond 1993) identified by Texas Parks and Wildlife personnel on MMWMA, seven (plateau live oak Quercus fusiformis, mesquite Prosopis glandulosa-white brush Aloysia gratissima, mixed oak Ouercus sp., Texas oak O. bucklevicanyons, blackjack oak Q. marilandica-post oak Q. stellata, xeric slopes, and grassland) occurred in our study pastures. Browse plants that dominated these habitat types were oaks and mesquite along with Texas persimmon Diospyros texana, agarita Berberis trifoliolata, prickly pear Opuntia sp., Ashe juniper Juniperus ashei, devil'sshoestring Nolina lindheimeriana, and twisted-leaf vucca Yucca rupicola. Grassland sites were dominated by curlymesquite Hilaria belangeri, little bluestem Schizachyrium scoparium, purple threeawn Aristida purpurea, hairy grama Bouteloua hirsuta, sideoats grama B. curtipendula, and Texas wintergrass Stipa leucotricha. These grasses also were associated with other habitats. Dominant forbs in most habitats were prairie coneflower Ratibida columnaris, wild carrot Daucus pusillus, broomweed Amphiachyris dracunculoides, one-seed croton Croton monathogynus, plantain Plantago sp., hairy wedelia Wedelia hispida, filaree Erodium sp., sida Sida filicaulis, and western ragweed Ambrosia psilostachya.

#### **Faecal collection**

Due to the small size of the greater kudu herd on MMWMA and the value of the animals, faecal analysis was used to assess annual and seasonal diets. Faecal analysis has many advantages including noninterference with habits and movements of animals, virtually unlimited sample size, and ease of sampling. The major disadvantage to faecal analysis is differential digestion of consumed plants (Storr 1961, Smith & Shandruk 1979, Holechek et al. 1982). However, other dietary investigations of other herbivores have found little difference between faecal analysis and other methods such as esophageal samples or rumen samples (Casebeer & Koss 1970, Anthony & Smith 1974, Johnson & Pearson 1981, Mohammad et al. 1995, Chapuis et al. 2001).

We collected faecal samples from 196 freshly deposited pellet groups (20 pellets per sample) during spring (15 May - 6 June 2001), summer (25 July - 19 August 2001), autumn (13 October - 10 November 2001), and winter (19 January - 25 February 2002). We collected 50 faecal samples each season with the exception of spring when 46 samples were collected. Collections came from freshly deposited faeces (soft and covered by mucus; Green 1987) immediately after observed defecation by greater kudu to eliminate the possibility of collecting faecal pellets of other ungulates. In the

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laboratory, we air-dried faecal pellets in paper sacks with paradichlorobenzene to deter mould growth and insect damage (Scott & Dahl 1980).

#### **Faecal analysis**

We ground 2.0-2.5 g (3-4 pellets) from each faecal sample in a Wiley Mini-Mill using a 0.425 mm screen delivery tube to standardize fragment size (Litvaitis et al. 1996). We soaked ground samples in undiluted 5% sodium hypochlorite for 15-20 minutes to remove pigments (Holechek & Valdez 1985) and washed them with water over a 0.074 mm screen (Sparks & Malechek 1968). We prepared two slides from each faecal sample by evenly spreading enough processed faecal material to insure that at least three large epidermal fragments occurred per field of view (Hansen & Reid 1975, Scott & Dahl 1980). We used Mount-Quick aqueous mounting medium for preservation (Daido Sangyo Co., Ltd., Japan). After air drying for two hours, we sealed the edges of the cover slips with Permount mounting medium.

We identified plant epidermal cells to species in five randomly selected fields of view per slide using a compound binocular microscope (Nikon Alphaphot YS, Nikon USA, Melville, New York) at  $100 \times$  or  $400 \times$ . Weidentified the plant epidermal fragment nearest the ocular lens pointer in each field of view to the lowest possible taxon (Sparks & Malechek 1968). A reference collection of microhistological slides made from leaves, stems, flowers and fruits of potential forage plants gathered from our study pastures, as well as photographs and dichotomous keys (Scott & Dahl 1980, Green et al. 1985) were used in identifying epidermal fragments. Diagnostic anatomical plant characteristics used in identifications included trichomes, silica cells, cork cells, stomata size and shape, guard cells, cell size and cell wall configuration. We pooled the identified plant epidermal fragments from samples within each season and across seasons.

Because of difficulty in distinguishing Texas and blackjack oak foliage, we combined them as a Texas/ blackjack oak category in analyses. Also, due to the difficulty in identifying most browse shoots (young sprouts or shoots of browse species) to species, we combined them as a browse shoots category.

#### **Vegetation sampling**

We randomly selected 16 points as the origin for sampling transects from more than 50 points on previously established grids covering our study pastures. At each point, we randomly selected an azimuth for a 100-m transect. Along each transect, we recorded herbaceous plant species and percent cover by species at 10 randomly selected locations using a  $100 \times 25$  cm frame (Daubenmire 1959) and used the line-intercept method to estimate percent woody plant cover by species (Gates 1949). Dekker (1997) found that greater kudu had a 2-m maximum browsing height; therefore, we used a 2-m pole to identify woody plants available to greater kudu. We classified living leaves, stems, flowers or fruits of woody plants intercepted at or below the top of the 2-m pole as available. We sampled herbaceous plants in 160 Daubenmire frames for all seasons and woody plants on 1,500 m of line intercept in spring 2001 and winter 2002 to estimate availability of herbaceous and woody plant species, respectively.

#### Plant use

We defined use as the percent occurrence of each plant species in pooled faecal samples (Sparks & Malechek 1968, Holechek & Gross 1982a, 1982b). We designated a plant as a principal food item if percent occurrence in the diet during any season was  $\geq 3\%$ . We derived this cut-off point because plants with a percent occurrence of  $\geq 3\%$  collectively composed 88% of the annual diet. We also pooled plant species into forage classes such as browse (leaves and shoots of woody plants, mast (fruits and seeds of woody plants), forbs, grasses and 'other' for analyses. The 'other' category combined a mixture of species contributing < 3%during all seasons, unidentified fragments and supplemental food. We used this category in analyses of the seasonal diet but not for forage preference. Plants contributing < 3% to the diet included mistletoe Phoradendron tomentosum, green milkweed vine Matelea reticulata, poison ivy Toxicodendron radicans, Carolina buckthorn Rhamnus caroliniana, shin oak Quercus sinuata, redbud Cercis canadensis, netleaf hackberry Celtis reticulata, wafer ash Ptelea trifoliata, sweet mountain grape Vitis monticola, lotebush Ziziphus obtusifolia, kidneywood Evsenhardtia texana, greenbriar Smilax bona-nox, spiderwort Tradescantia sp., ratany Krameria lanceolata, day flower Commelina erecta, yarrow Achillea millifolium, one-seed croton Croton monahthogynus, Indian blanket flower Gaillardia pulchella, Mexican hat flower Ratibida columnifera, prairie fleabane Erigeron modestus, sideoats grama Bouteloua curtipendula, Texas grama B. rigidiseta, little bluestem Schizachyrium scoparium, plains lovegrass Eragrostis intermedia, hairy tridens Erioneuron pilosum, wheat Triticum aestivum, cedar sedge Carex planostachys, purple threeawn Aristida purpurea, buffalograss Buchlöe dactyloides, and plains bristlegrass Setaria leucopila.

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**Foraging preference** 

If an animal has access to a variety of food items, it will show preference for some and avoidance of others (Krebs 1999). Preference can be measured by comparing usage to the availability of food items in the environment. We used a log-likelihood  $\chi^2$ -test with estimated proportions of available resources to test whether greater kudu consumed plant species in proportion to their estimated availability (Manly et al. 1993). We calculated availability for each herbaceous plant species as the percentage of Daubenmire frames in which the species contributed  $\geq 5\%$  of the cover (C.J. Krebs, pers. comm.). We defined woody species availability as the percentage of 10-m intercept intervals in which the plant contributed  $\geq 5\%$  of the intercept length.

We also assessed preference or avoidance of a plant species by constructing 95% confidence intervals with a Bonferroni correction (Neu et al. 1974) for plants in faecal material (observed use) compared to their availability in the habitat (expected use). When confidence intervals for use of a plant exceeded and did not overlap with availability confidence intervals, we classified the species as preferred. If the confidence intervals for a species fell below and completely outside the confidence intervals of availability, we listed the species as avoided. We designated species with overlapping confidence intervals of availability as used in proportion to its availability. We also used Manly's alpha preference index (constant prey formula; Manly et al. 1972) to determine preference and avoidance of plants. An index score with a value of > 1/m (m = total number of plants species available) indicated preference, while an index value of < 1/m indicated avoidance. We determined that a food was preferred or avoided only if both techniques agreed. In cases where the results of the two methods conflicted, we concluded the item was used in proportion to availability. Our intent in using and comparing these two methods of analysis was to be conservative when assigning a designation of preference to any food item.

# Results

## Annual diet

We characterized the annual diet of greater kudu in central Texas based on 1,960 plant epidermal fragments. Seasonal data consisted of 460 fragments for spring and 500 fragments for the other three seasons. The annual diet of greater kudu at MMWMA conTable 1. Percent occurrence of plant species consumed by greater kudu at Mason Mountain Wildlife Management Area during 2001-2002. The asterisk (\*) indicates that the browse shoots in winter 2002 were live oak shoots.

	Season					
Plant species	Spring 2001	Summer 2001	Autumn 2001	Winter 2002	Annual	
Texas/blackjack oak	32.0	50.0	39.6	0.0	30.4	
Plateau live oak	3.3	0.0	0.6	39.0	10.9	
Ashejuniper	0.0	0.0	0.0	31.2	8.0	
Mesquite	11.5	14.6	4.4 0.0		7.6	
Browse shoots	5.4	8.6	6 6.8 2.2*		5.8	
Flameleaf sumac	3.0	0.8	11.4	0.0	3.8	
Prickly pear	0.2	2.0	0.0	9.4	3.0	
Devil's-shoestring	3.0	0.2	0.2	4.6	2.0	
Elbowbush	4.3	1.8	0.2	0.0	1.5	
Texas persimmon	1.3	2.6	0.8	0.2	1.2	
Skunkbush sumac	3.3	1.0	0.6	0.0	1.2	
Twisted-leaf yucca	0.2	0.0	0.4	3.4	1.0	
Other browse (no of species)	10.0(11)	4.4 (6)	2.0(3)	0.0	3.8 (14)	
Total browse	77.6	86.0	67.0	90.0	80.2	
Prickly pear seeds	0.0	0.0	13.0	0.0	3.3	
Prickly pear fruit	0.0	0.0	3.2	0.0	0.8	
Texas persimmon fruit	0.0	4.8	0.0	0.0	1.2	
Texas persimmon see	0.0	4.0	0.0	0.0	1.0	
Other mast (no of species)	2.6 (4)	0.0	2.4(3)	0.0	1.3 (6)	
Total mast	2.6	8.8	18.6	0.0	7.6	
Canada wildrye	5.2	0.0	0.0	1.0	1.5	
Texas wintergrass	0.0	0.0	0.0	6.0	1.5	
Milo	0.0	3.8	0.0	0.0	1.0	
Other grass (no of species)	1.7 (6)	1.2 (3)	5.0(7)	2.0 (4)	2.5 (10)	
Total grasses	7.0	5.0	5.0	9.0	6.5	
Purple horsemint flowers	5.7	0.0	0.0	0.0	1.3	
Other forbs (no of species)	6.7 (8)	0.0	0.4(2)	0.2(1)	1.7 (9)	
Total forbs	12.4	0.0	0.4	0.2	3.0	
Unknowns species (no of species)	0.4 (2)	0.2(1)	4.8(1)	0.8(1)	1.6(4)	
Whole corn	0.0	0.0	4.2	0.0	1.1	
Total other	0.4	0.2	9.0	0.8	2.7	

sisted of 49 species of browse, mast, forbs and grasses (Table 1). By forage class, the annual diet consisted of 80.2% browse, 7.6% mast, 6.5% grass and 3% forbs (see Table 1, Fig. 1). A combination of seven browse species (Texas/blackjack oak, plateau live oak, Ashe juniper, mesquite, prickly pear, flameleaf sumac and Texas persimmon) composed > 70% of the annual diet (see Table 1). Primary grasses consisted of Texas wintergrass, Canada wildrye and milo *Sorghum vulgare*. The primary forb in the annual diet of greater kudu was purple horsemint (flowers; see Table 1).

#### Spring diet

Browse made up 77.6% of greater kudu diet in spring (see Table 1 and Fig. 1) with Texas/blackjack oak, mesquite, elbowbush *Foresteria pubescens*, skunk-

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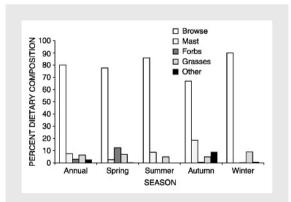


Figure 1. Relative composition of forage classes in the annual and seasonal diets of greater kudu at Mason Mountain Wildlife Management Area during 2001-2002.

bush sumac *Rhus aromatica*, plateau live oak, flameleaf sumac and devil's-shoestring each representing  $\geq 3\%$  of the diet. Forbs composed 12.4% of the diet with purple horsemint (flowers) being the dominant component. Mast and grass forage contributed 2.6 and 7% to the spring diet, respectively.

Greater kudu were selective browsers in the spring (P < 0.001). Using 95% confidence intervals, Texas/ blackjack oak, mesquite, flameleaf sumac, purple horsemint (flowers), and Canada wildrye were preferred food species (Table 2). Elbowbush, skunkbush sumac and devil's-shoestring were used in proportion to their availability in the habitat. Greater kudu avoided plateau live oak. Manly's alpha index scores (see Table 2) indicated that mesquite, flameleaf sumac, purple horsemint (flowers) and Canada wildrye were preferred and Texas/blackjack oak, elbowbush, skunkbush sumac, plateau live oak and devil's-shoestring were avoided.

The results of our analysis were in agreement in that mesquite, flame-leaf sumac, purple horsemint and Canada wildrye were preferred species and plateau live oak was avoided. Ambiguous or conflicting results were detected for Texas/blackjack oak, elbowbush, skunkbush sumac and devil's shoestring.

#### Summer diet

The summer diet was composed of 86% browse (see Table 1 and Fig. 1). Texas/blackjack oak dominated the diet followed by mesquite and Texas persimmon

(leaves). Mast (Texas persimmon fruits and seeds), forb and grass consumption collectively did not exceed 10% (see Table 1 and Fig. 1).

Greater kudu were selective browsers in the summer (P < 0.001). Using 95% confidence intervals, Texas/blackjack oak, mesquite and Texas persimmon (leaves, fruits and seeds) were preferred food species (see Table 2). Manly's alpha index scores indicated that greater kudu preferred Texas/blackjack oak, mesquite and milo, but avoided Texas persimmon (see Table 2).

The results of these analyses were consistent in suggesting Texas/blackjack oak and mesquite were preferred food species. Conflicting results were obtained for Texas persimmon and milo.

#### Autumn diet

During autumn, browse made up 67% of greater kudu diet with Texas/blackjack oak, flameleaf sumac and mesquite being the principal food items (see Table 1 and Fig. 1). Mast (18.6%) ranked as the second most used forage class with prickly pear (fruits and seeds) consumed the most. Grasses and forbs were insignificant components of the autumn diet (see Table 1 and Fig. 1).

Greater kudu were selective browsers in the autumn (P < 0.001). Using 95% confidence intervals, Texas/ blackjack oak, flameleaf sumac and prickly pear (fruits and seeds) were preferred food species (see Table 2). Manly's alpha index scores supported

Table 2. Seasonal forage preference of greater kudu at Mason Mountain Wildlife Management Area during 2001-2002, based on results of log-likelihood  $\chi^2$ -test and Manley's alpha preference index, indicating whether plants were preferred (P), avoided (A), neither preferred not avoided (N), or not present in the diet (-). The sample size was 50 in each season, except for spring when 46 samples were collected.

Plant species	Spring		Summer		Autumn		Winter	
	Log-Likelihood	Manley's	Log-Likelihood	Manley's	Log-Likelihood	Manley's	Log-Likelihood	Manley's
Texas/Blackjack oak	Р	Ν	Р	Р	Р	Р	-	-
Mesquite	Р	Р	Р	Р	Ν	Ν	-	-
Live oak	А	Ν	-	-	-	-	Р	Ν
Skunkbush sumac	Ν	Ν	-	-	-	-	-	-
Elbowbush	Ν	Ν	-	-	-	-	-	-
Flameleaf sumac	Р	Р	-	-	Р	Р	-	-
Texas persimmon	-	-	Р	Ν	-	-	-	-
Prickly pear	-	-	-	-	Р	Ν	А	Ν
Ashe juniper	-	-	-	-	-	-	Р	Р
Twisted-leaf yucca	-	-	-	-	-	-	Ν	Ν
Devil's shoestring	Ν	Ν	-	-	-	-	Р	Р
Milo	-	-	-	-	Ν	Ν	-	-
Canada wildrye	Р	Р	-	-	-	-	-	-
Texas wintergrass	-	-	-	-	-	-	А	Ν
Purple horsemint	Р	Р	-	-	-	-	-	-
Other	Ν	N	N	N	N	N	N	Ν

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greater kudus' preference for flameleaf sumac, but suggested avoidance for Texas/blackjack oak, mesquite and prickly pear (fruits and seeds).

Results of the two analyses agreed that flameleaf sumac was a preferred species. Conflicting results were noted for Texas/black jack oak, mesquite and prickly pear.

# Winter diet

The highest consumption of browse (90%) by greater kudu occurred in winter (see Table 1 and Fig. 1) with plateau live oak and Ashe juniper composing > 70% of the diet followed by lesser amounts of prickly pear, devil's-shoestring and twisted-leaf yucca. More grasses occurred in the winter diet (9.0%) than in any other season with Texas wintergrass being the most common. The only forb detected in the winter diet was yarrow *Achillea millifolium* (see Table 1). No mast occurred in the winter diet.

Greater kudu were selective browsers in the winter (P < 0.0001). Using 95% confidence intervals, plateau live oak, Ashe juniper and devil's-shoestring were preferred food species (see Table 2). Greater kudu consumed twisted-leaf yucca in proportion to its availability, whereas prickly pear and Texas wintergrass were avoided. Manly's alpha index also indicated that greater kudu preferred Ashe juniper, but avoided plateau live oak, prickly pear, devil's-shoestring, twisted-leaf yucca and Texas wintergrass.

The results of the two analyses concurred that Ashe juniper was a preferred food species and that prickly pear and Texas wintergrass were avoided. Conflicting results were obtained for plateau live oak, devil's shoestring and twisted-leaf yucca.

# Discussion

Greater kudu at MMWMA were principally browsers in all seasons, with seasonal use of forbs, grasses and mast. Greater kudus diets in southern Africa (Owen-Smith 1979, Owen-Smith & Cooper 1985, 1989) reflected patterns of forage class use similar to those found in our study. However, in our study browse consumption in all seasons (67-90%) exceeded the seasonal amounts (53-66%) reported from studies conducted in southern Africa. Mast, the second most frequently consumed food in our study, was consumed in similar amounts (4-23%) in southern Africa. Seasonal forb consumption (8-37%) in southern Africa contributed substantially more to the diet of greater kudu than in central Texas (0-12.4%).

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Seasonal grass ingestion was similar, although slightly higher, in Texas than in southern Africa (4-14%).

Seasonal use of all forage classes by greater kudu may be explained by plant availability. Although, browse was the major food item consumed in all seasons, a major shift in the use of browse by kudu occurred during winter. Texas/blackjack oak was the primary food in spring, summer and autumn. In the absence of this deciduous browse in winter, it was replaced in the diet with evergreen browse, such as Ashe juniper and plateau live oak. Mast likewise was a seasonal food. Texas persimmon, which ripens in summer, was the only mast item identified in summer. Prickly pear fruits that mature in autumn were consumed during the time of greatest abundance.

Forb consumption was almost exclusively a springtime phenomenon. Although forbs were available in every season, spring was the principle season for flowering in central Texas. We observed greater kudu eating flowers and found epidermal fragments of flower petals in faecal samples only during spring. Wilson (1965) noted a similar consumption of flowers in Africa.

Grass ingestion was minimal but consistent throughout the year with greatest occurrence in spring (7%) and winter (9%). Canada wildrye and Texas wintergrass, cool season grasses, were most frequently consumed in the spring and winter. The greater use of these grasses in winter may have resulted from a lack of deciduous browse species and the availability of more palatable forage (Scifres et al. 1982, Ortega et al. 1997).

Of nine foods preferred by greater kudu, seven were browse species (see Table 2). Even when not specified as preferred, browse composed the bulk of the diet during all seasons. Our study underscored the dependence of greater kudu on browse throughout the year and the potential competition of this species with white-tailed deer and other ungulates for this food resource. Browse in the diet of white-tailed deer under excellent range conditions in the Edwards Plateau Ecological Region was 61% (Bryant et al. 1981), 38% (Cross 1984), and > 75% on heavily grazed, 70% on moderately grazed, and 55% on ungrazed pastures (Baccus et al. 1984). Under poor range condition, the amount of browse in the diet was 56% (Waid et al. 1984). Greater kudu consumed many of the same plants, such as Texas oak (McMahan 1964), prickly pear (Everitt & Drawe 1974), Texas persimmon (Everitt & Drawe 1974), live oak (Bryant et al. 1981, Waid et al. 1984), and Ashe juniper (Bryant et al. 1981, Waid et al. 1984) found in white-tailed deer diets. McMahan (1964) described Texas oak as a preferred

white-tailed deer food. Greater kudu extensively fed on Texas oak/blackjack oak in all seasons except winter. Everitt & Drawe (1974) documented heavy use of prickly pear and Texas persimmon fruit by whitetailed deer. Greater kudu likewise fed on these plants but did not show selectivity for them. Bryant et al. (1981) and Waid et al. (1984) reported a reliance on live oak and Ashe juniper browse in the winter diet of white-tailed deer. These plant species had their highest percent occurrence in the diet of greater kudu in winter when greater kudu selected for them. Because of the scarcity of browse in winter and intensive use by greater kudu and white-tailed deer, there could be keen competition for these plant species in winter. In addition, Butts et al. (1982) suggested that axis deer, sika deer Cervus nippon, and fallow deer Dama dama might compete with white-tailed deer because of equal or higher content of browse in their seasonal diets. The potential for competition with white-tailed deer because of dietary overlap, as well as space and water requirements, must be considered by landowners and managers before stocking greater kudu on ranches. Further research on multispecies interactions among greater kudu, white-tailed deer and other nonindigenous species is warranted.

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