

Selective feeding by a megaherbivore, the African elephant (*Loxodonta africana*)

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The metabolic rate–body size relationship suggests that the African elephant (*Loxodonta africana*) should be least selective among mammalian herbivores in its diet. However, selection among plant species needs to be distinguished from selection for plant parts or other features. We investigated seasonal variation in the selective utilization and dietary contribution of woody plant species, parts, and height classes to vegetation consumed by elephants in the Kalahari sandveld region of Chobe National Park, Botswana. Only 30% of 27 common woody species were moderately or highly acceptable to elephants in the wet season, increasing to more than 50% in the hot dry season. Six woody species remained mostly or entirely rejected by elephants throughout the year. Most of the browse consumed during each season came from 1 or 2 common shrub species. Leaves and leaf-bearing shoots constituted 80% of the material consumed from woody plants during the wet season, but only 45% during the cool dry season. Stem, bark, and root tissues contributed 50% of the woody plant component of the diet in the cool dry season, increasing to 94% in the hot dry season. Hence, despite their narrow selection for plant species, large size coupled with hindgut digestion enables elephants to exploit a wide range of plant parts, including fibrous stems, bark, and roots. Accordingly, elephants occupy a dietary niche distinct from browsing or grazing ruminants.

Key words: African elephant, body size, Botswana, browsing, Chobe National Park, dietary niche, *Loxodonta africana*, megaherbivores, vegetation impacts

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In an influential paper, Jarman (1974) suggested that larger ruminants should be less selective in their dietary choice than smaller species because they have lower nutrient requirements per unit of body mass. Furthermore, Bell (1971) pointed out that nonruminants should tolerate lower dietary quality than ruminants of similar body mass because, as hindgut fermenters, their faster digestive passage more than compensates for lowered digestive efficiency on fibrous diets (see also Janis 1976). For carnivores (Sinclair et al. 2003) and herbivorous insects (Chambers et al. 1996; Futuyma 1976), dietary selectivity is generally assessed in terms of the range of prey or host species eaten. In contrast, Jarman (1974) described how small antelope are narrowly selective for new leaves, flowers, and fruits, whereas larger ruminants accept a greater proportion of supporting stem tissues in their diets (documented in Owen-Smith 1988:86, figure 6.3). This implies that, among these mammalian herbivores, selective feeding is expressed mainly in terms of plant parts consumed, rather than the species diversity of the diet. Nevertheless, confusion still persists in the literature about how concepts relating to the

breadth of the dietary niche apply to large herbivores. All consumers are selective in their dietary range in some way; the fundamental issue is which resource features govern the narrowness or breadth of diet.

According to the concepts outlined by Bell (1971) and Jarman (1974), the African elephant (*Loxodonta africana*) should be least selective among herbivores in its dietary range because it is a hindgut fermenter in addition to being the largest extant herbivore. Large size coupled with generalist feeding enables elephants to have a destructive effect on trees (Laws 1970; Owen-Smith 1988), potentially transforming savanna woodlands into almost treeless grasslands (Dublin et al. 1990), or monotonous shrublands (Laws et al. 1970). However, these consequences depend on the woody plant species affected as well as the plant parts and size classes impacted.



In addition to fiber content, another factor affecting the selective utilization of plant parts and species by herbivores is the content of secondary metabolites in particular tissues. These chemical defenses can have an overriding influence on diet selection by browsers (Bryant and Kuropat 1980; Cooper et al. 1988). Larger herbivores should be better able to accommodate the diluting effect of secondary chemical contents on nutritional value than smaller ones. Furthermore, ruminants should be more capable than nonruminants of dealing with potentially toxic chemicals through degradation via forestomach fermentation (Alexander 1993). This capability is claimed to be one of the benefits promoting the origin of ruminant digestion (Langer 1988).

Our study on the diet selection patterns of elephants was conducted in a region of Botswana supporting more than 80,000 elephants within a total range of 100,000 km² at that time (Craig 1990; Gibson et al. 1998). Dry-season concentrations near the Chobe River amounted to 4–6 elephants/km². Vegetation in the riparian fringe and adjoining alluvial terrace had been transformed from woodland to shrubland through the feeding impacts of these elephants (Mosugelo et al. 2002). However, the Kalahari sandveld savanna stretching southward from the river had been much less affected. Vegetation growing on such nutrient-deficient soils typically shows a greater prevalence of chemical defenses than plants associated with nutrient-rich soils (Coley et al. 1985; Owen-Smith 1993; Owen-Smith and Cooper 1987b). Accordingly, we expected that selection by elephants at the plant species level would be more strongly expressed in the sandveld savanna than elsewhere. Other studies in this region on the patterns of food selection by the elephants have been restricted to the hot dry season (Stokke 1999; Stokke and du Toit 2000), or to the riparian zone (Makhabu 2005). The consequent damage caused to woody plants was assessed in riparian woodlands by Wackernagel (1993) and Teren and Owen-Smith (2010) and more broadly in northern Botswana by Ben-Shahar (1998).

The aim of our study was to establish factors governing the selective utilization of woody plants by elephants, taking into account seasonal variation. The specific questions addressed were which woody species are favored or rejected as food in particular seasons; which woody species and parts constitute the bulk of the dietary intake during each season; which plant height classes contribute most of the food consumed; and what are the implications of these patterns for vegetation changes induced by elephants? Selective neglect of certain plant species or size classes by elephants would indicate that a compositional or structural change in the woodland is a more likely outcome of the damage caused by elephant feeding activities than elimination of most of the woody plant component. Last, we consider how our findings illuminate the dietary niche distinguishing elephants from browsing ruminants.

MATERIALS AND METHODS

Study site.—Our study was conducted in the northeastern section of Chobe National Park and adjoining parts of the Kasane Forest Reserve and its extension in northern Botswana

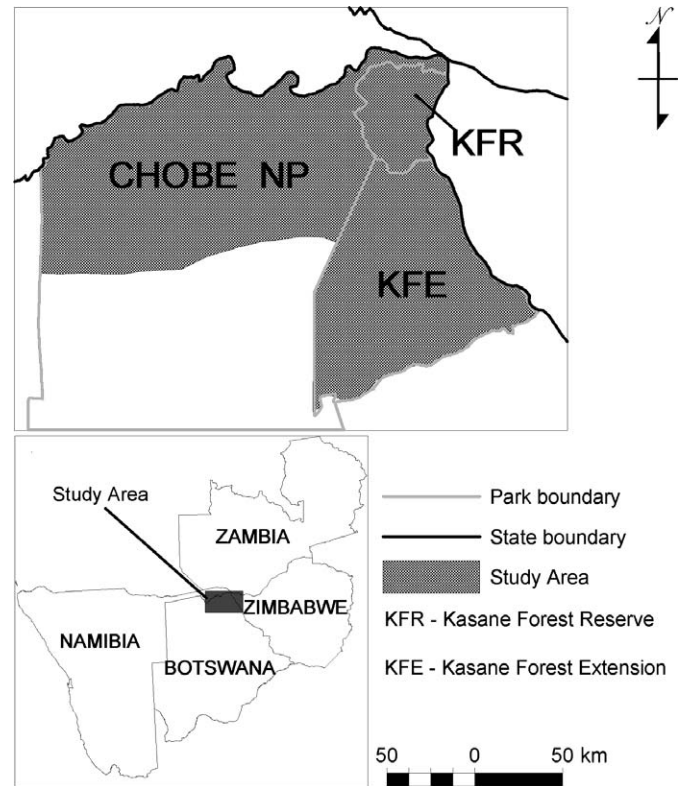


FIG. 1.—Map showing the study area encompassing a section of Chobe National Park and the adjoining Kasane Forest Reserve (KFR) and Kasane Forest Extension (KFE) in northern Botswana.

(17°46'–18°15'S, 24°43'–25°15'E; see Fig. 1). Mean annual rainfall in Kasane town is about 700 mm, received mostly between November and March. Monthly temperatures range between a mean daily maximum of 35°C in October and a mean daily minimum of 10°C in June.

Vegetation in the region can be subdivided structurally between riparian fringe woodland, shrubland on the adjoining alluvial terrace, and Kalahari sandveld savanna extending southward from the river front. The sandveld woodland is characterized by *Baikiaea plurijuga* trees on deeper sand and *Burkea africana* trees on shallower sand. Other common tree species include *Erythrophleum africanum*, *Guibourtia coleosperma*, *Brachystegia boehmii*, *Terminalia sericea*, and *Pterocarpus angolensis*. Common species in the shrub layer are *Ochna pulchra*, *Diplorhynchus condylocarpon*, *Bauhinia petersiana*, *Baphia massaiensis*, *Combretum apiculatum*, *C. collinum*, *C. fragrans*, and *C. zeyheri* (plant nomenclature follows Gibbs-Russell et al. 1984).

Data collection.—Observations commenced in August 1992 and ended in July 1993, thus spanning 1 full year. Three seasons were distinguished, based on rainfall and temperature patterns: wet (November–April); cool dry (May–July); and hot dry (August–October). Because of the restricted road network, sufficient direct observations on feeding elephants were obtained only in the alluvial shrubland, and only during the hot dry season when elephants concentrated within this region in adequate numbers. Hence, the results reported here are

restricted to the sandveld savanna, and were gathered using plant-based observations.

Tracks of elephants crossing roads were located in the early morning, and interpreted as fresh feeding tracks if discarded plant parts had not dried out. These tracks were followed away from the road, either in the same or opposite direction to that travelled by the elephant group. The location of the 1st sample patch was selected by multiplying the fractional random number generated by a scientific calculator by 200 m, this distance approximating the maximum length of feeding track sampled. Within a 10-m radius of this initial point, each woody plant was examined for evidence of fresh feeding by elephants. Consumption of the following plant parts was recorded: leaves; shoots including terminal stems plus leaves; woody stems only; roots; bark of stems; bark of roots; fruits; and other plant parts such as flowers or fallen leaves. Grazing was not recorded because our focus was on impacts on the tree and shrub components. An additional 4 sample patches were placed systematically 50 m apart along the feeding track, on either side of the initial patch. Together these 5 patches constituted 1 feeding site.

Data analysis.—For our index of selection, we used the behavior-based measure of acceptance described by Owen-Smith and Cooper (1987b), adapted for plant-based observations. The acceptance of a food type is the proportional frequency with which it was eaten (used) when encountered. The corresponding availability measure is the frequency with which the food type was encountered along the foraging pathway. Both measures can be assessed at different scales of aggregation, from individual plants or plant parts of particular species to feeding patches or foraging sites. Fine-scale measures provide more precise differentiation of use among food types, but feeding decisions governing acceptance are not independent when plants are encountered in clusters. In these circumstances, statistical assessments need to fall back on site-based acceptance frequencies, provided these sites are sampled independently. This approach avoids some of the problems encountered in interpreting selection from ratios between proportional use and availability estimated independently: arbitrary decisions about what is effectively available within some broad foraging area; spurious divisions between positively and negatively selected food types; and unbounded upper values of such ratios (see Owen-Smith and Cooper 1987a). Acceptance frequencies take values with the range 0–1, and natural clustering of these values indicates divisions between food types that are favored (frequently eaten when encountered), neglected (rarely eaten when encountered), or rejected (never eaten when encountered—see Owen-Smith 1994; Owen-Smith and Cooper 1987b).

We calculated the availability of each woody species along the foraging pathway indicated by the elephant tracks followed by dividing the number of patches where the species was present by the total number of patches sampled. The acceptance of each woody species was calculated by dividing the number of patches where feeding on the species was evident by the number of feeding patches where the species

was present. Patch-based measures were chosen for display because they differentiate the relative availability and use of more common woody species better than the corresponding site-based measures. However, we also tabulate the site-based records for each species needed for statistical assessments. Furthermore, results are presented only for species present in ≥ 10 feeding sites sampled in at least 1 season. Based on inspection of the distribution of values (see Fig. 2), plant species with patch-based acceptance frequencies > 0.4 were interpreted as highly favored, those with values in the range 0.2–0.4 as moderately favored, those with values 0.001–0.2 as neglected, and those with zero acceptance as rejected.

A measure of the dietary contribution by each plant species was derived by multiplying the number of records of consumption of each plant part for that species by the product of the availability and acceptance frequency per site. This approximation was used because it was difficult to quantify objectively the actual dietary contribution by mass of the wide range of available plant species and parts. The relative dietary contribution was then calculated by dividing the dietary contribution of each species by the summed dietary contributions across all species consumed. Similar calculations were used to estimate the relative dietary importance of particular plant parts and height classes. For measures of use, 95% confidence intervals were calculated, assuming sites to be replicate samples.

RESULTS

Sample sizes.—In total, 27 independent feeding sites were sampled in the wet season, 34 in the cool dry season, and 60 in the hot dry season. The sites comprised 135 feeding patches in the wet season, 164 in the cool dry season, and 300 in the hot dry season.

Species acceptance.—During the wet season, 8 of the 27 sandveld tree and shrub species with adequate samples were highly or moderately favored by elephants, of which 3 species showed acceptance frequencies > 0.4 and thus appeared highly favored (Fig. 2; see Appendix I, online; file can be found online at <http://dx.doi.org/10.1644/11-MAMM-S-350.S1>). During the cool dry season, 4 species appeared highly acceptable and an additional 6 moderately acceptable. During the hot dry season, the number of highly acceptable species increased to 8, and a further 7 species were moderately acceptable. At this time of the year *B. petersiana* was leafless, and appeared somewhat less acceptable than in the seasons when it retained leaves. In contrast, *B. massaiensis* showed its lowest acceptability in the cool dry season. The species most favored during the cool dry season was *D. condylocarpon*, whereas *C. fragrans* and *Combretum elaeagnoides* remained highly favored throughout the dry season. *C. zeyheri*, *C. collinum*, and *T. sericea* became highly favored only during the hot dry season and were accepted much less frequently at other times of the year. All of the species that were highly favored in 1 or more seasons grow as shrubs rarely exceeding 5 m in height, except for *T. sericea*. Commonly available species that were completely rejected in all seasons included

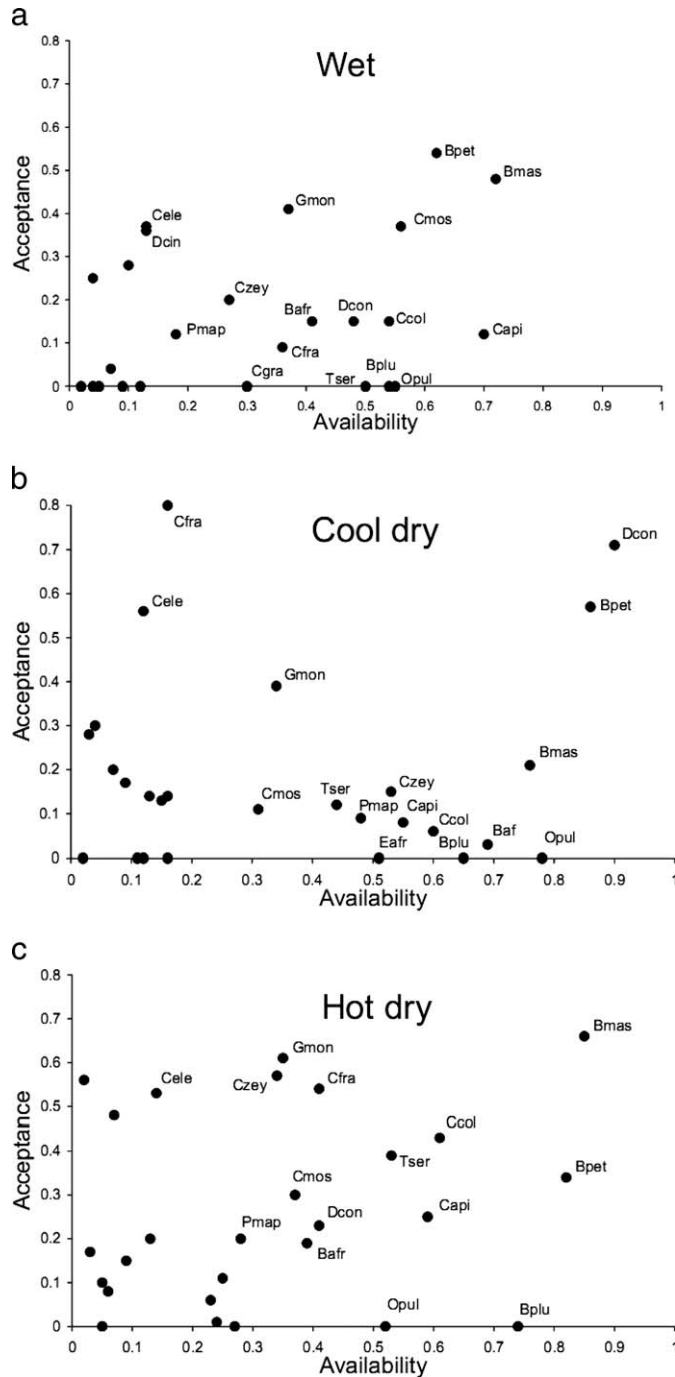


FIG. 2.—Patch-based acceptance frequency versus availability for 27 woody plant species with adequate samples for a) wet season, b) cool dry season, and c) hot dry season. Species acronyms: Bafr = *Burkea africana*; Bmas = *Baphia massaiensis*; Bpet = *Bauhinia petersiana*; Bplu = *Baikiaea plurijuga*; Capi = *Combretum apiculatum*; Ccol = *Combretum collinum*; Cele = *Combretum elaeagnoides*; Cfra = *Combretum fragrans*; Cgra = *Croton gratissimus*; Cmos = *Commiphora mossambicensis*; Czey = *Combretum zeyheri*; Dcin = *Dichrostachys cinerea*; Dcon = *Diplorhynchus condylocarpon*; Eafr = *Erythrophleum africanum*; Gmon = *Grewia monticola*; Opul = *Ochna pulchra*; Pmap = *Pseudolachnostylis maprouneifolia*; Tser = *Terminalia sericea*.

B. plurijuga, *O. pulchra*, *Croton gratissimus*, and *E. africanum*.

Dietary contribution.—During the wet season, more than 60% of the estimated dietary contribution from woody plants was constituted by *B. massaiensis* and *B. petersiana*, whereas in the cool dry season, *B. petersiana* and *D. condylocarpon* together made up almost three-fourths of the estimated dietary contribution (Fig. 3; see Appendix II, online; file can be found online at <http://dx.doi.org/10.1644/11-MAMM-S-350.S1>). In the hot dry season, *B. massaiensis* made up close to 40% of the estimated diet, whereas no other species contributed much more than 10%. Six woody species made up more than 90% of the estimated diet during the wet season, 4 species during the cool dry season, and 8 species during the hot dry season.

Plant part contributions.—During the wet season, leaves contributed 45% and shoots 25% to the estimated intake of plant parts by the elephants from trees and shrubs (Fig. 4). The bulk of the leaves stripped came from *B. massaiensis* and *B. petersiana*, whereas most of the shoots were provided by *B. petersiana* together with a range of other species. In the cool dry season, about 45% of the estimated intake of plant parts was composed of stems, followed by leaves (24%) and shoots (21%). Much of the stem component was provided by *D. condylocarpon*. Elephants stripped off and discarded the leaves of this species, as well as those of several *Combretum* spp., before ingesting the stems. The leaves and shoots consumed came primarily from *B. petersiana*, which also contributed the small proportion of fruits eaten at this time. In the hot dry season, stems comprised the bulk of the diet (55%), mainly from *B. massaiensis*, together with the bark of stems (25%) and roots (14%). Most of the root intake came from *C. zeyheri*, *B. petersiana*, *Commiphora mossambicensis*, and *T. sericea*, mostly from plants under 2.5 m in height except in the case of *T. sericea*. Leaves and shoots contributed only 1% each. Overall, plants 1–2.5 m in height contributed approximately 45% of the estimated diet in all seasons.

DISCUSSION

Our findings show that, at the plant species level, the elephants fed selectively on a subset of the woody species available to them in the Kalahari sandveld savanna. Approximately two-thirds of the 27 woody species that were frequently encountered by the elephants in at least 1 season were either neglected or rejected as a food source during the wet and early dry seasons when foliage remained abundantly available, including some very common species. Moreover, 40–70% of the estimated food consumption from woody plants during each season was constituted by just 1 or 2 favored and abundant shrub species. Elephants widened the range of woody plant species that they accepted for feeding during the hot dry season when little foliage remained available, but certain species remained completely rejected year-round.

From observations restricted to the alluvial terrace adjoining the Chobe River, Makhabu (2005) found that *C.*

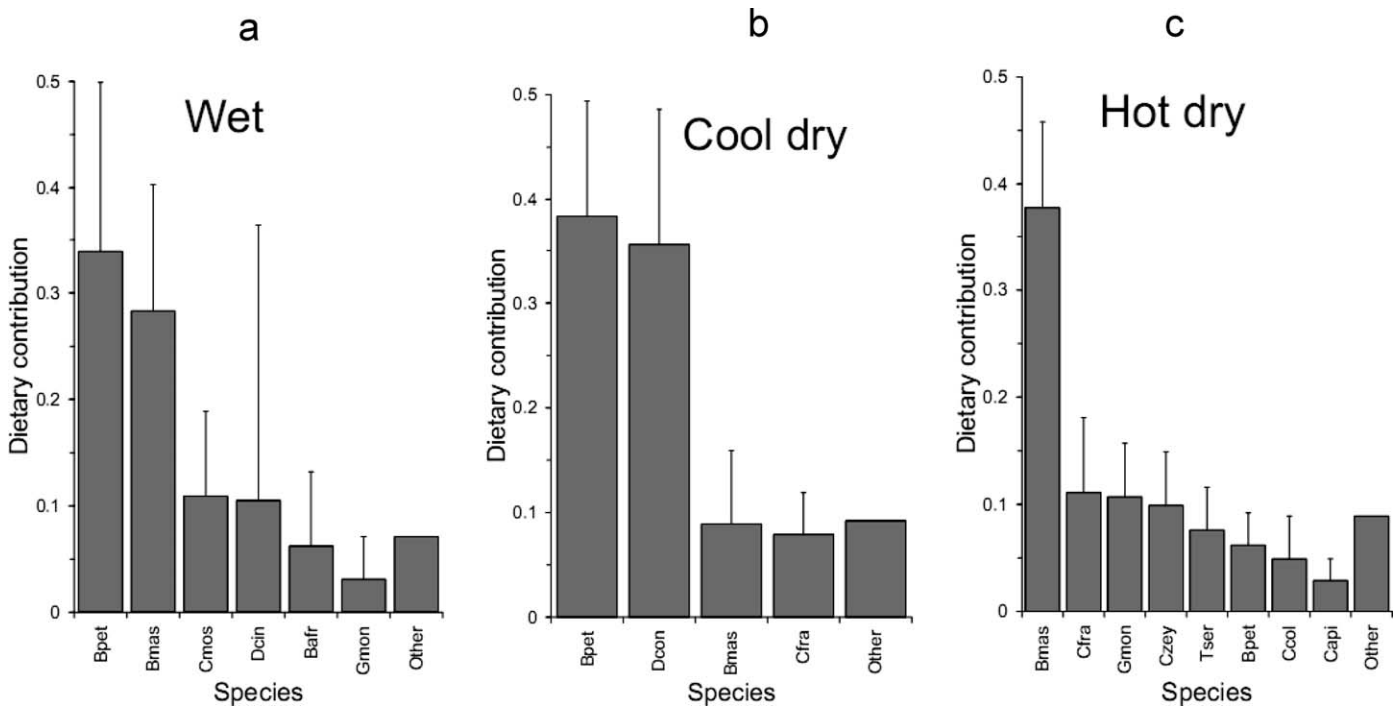


FIG. 3.—Ranking of the dietary contribution of woody plant species constituting in total >90% of the estimated woody plant component of the diet during the a) wet season, b) cool dry season, and c) hot dry season. Acronyms are as in Fig. 1; upper 95% confidence limits are indicated.

elaegnoides made the greatest contribution to the dietary intake of elephants throughout the year, followed by *Croton megalobotrys*, which was consumed mainly during the dry season, and *Dichrostachys cinerea*, contributing more during the wet season than the dry season. He recorded very little use by elephants of the widespread shrub *Combretum mossambicense* and the abundant woody scrambler *Capparis tomentosa*. Our direct observations on elephants feeding in this region during the hot dry season showed a very similar pattern. The findings of Stokke and du Toit (2000) on plant species selection cannot be easily compared to ours because their observations covered a wider section of Chobe National Park, while being restricted to the hot dry season. In Ruaha National Park in Tanzania, Barnes (1982) recorded a similarly narrow concentration on certain woody plant species by elephants, with 2 or 3 species contributing much of the food intake during the dry season, and grasses predominating in the diet in the wet season.

For giraffe (*Giraffa camelopardalis*), the largest browsing ruminant, Pellow (1984) documented strongly positive selection for 6 woody species and moderately positive ratings for an additional 6 species in the Serengeti region when assessed year-round. None of the 20 species listed was completely rejected by the giraffe, whereas 3 woody species made up 55% of the diet of these giraffe during both the wet and dry seasons. For kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*) observed in a savanna with nutrient-poor sandy soils, 62% of 29 woody species were classified as palatable through remaining highly or moderately acceptable throughout the year, and all of the remaining species were eaten at some stage of the seasonal cycle (Owen-Smith and Cooper 1987b). The 6 woody species

that were mostly commonly eaten constituted 40% of the wet-season diet of the kudu (Owen-Smith and Cooper 1989).

Restrictions on the species range of woody plants consumed by mammalian browsers have been related to the presence of plant secondary metabolites functioning as toxins or digestion inhibitors (Bryant et al. 1991). For browsing ruminants, condensed tannins appeared to be the primary chemical deterrent, and woody species with high contents of other phenolics, including hydrolyzable tannins, were readily consumed (Cooper et al. 1988; Owen-Smith 1994). In particular, species in the Combretaceae commonly show high contents of total polyphenols, but relatively little condensed tannin, in their foliage (Owen-Smith 1993). Elephants completely rejected 1 species in this family (*C. mossambicense*), and sometimes discarded the leaves of other *Combretum* species to feed on the stems. Leaves of the *Combretum* spp. rejected or discarded by elephants are readily consumed by browsing ruminants, including giraffe, kudu, and impala observed in the Chobe riparian region (Makhabu 2005) and elsewhere (Owen-Smith and Cooper 1987b; Sauer et al. 1982). Elephants also mostly stripped off leaves before feeding on the stems of *D. condylocarpon*, in the family Apocynaceae, which includes some notoriously poisonous plants. Among the species rejected by elephants, *B. plurijuga* and *E. africanum* are in the legume subfamily Caesalpinioideae; however, so is *B. petersiana*, with highly favored foliage. Distinctions in plant species favored result in some degree of resource partitioning between elephants and browsing ruminants in the Chobe River region (Makhabu 2005).

Hence, instead of showing higher tolerance for secondary chemicals than did smaller ruminants, elephants avoided

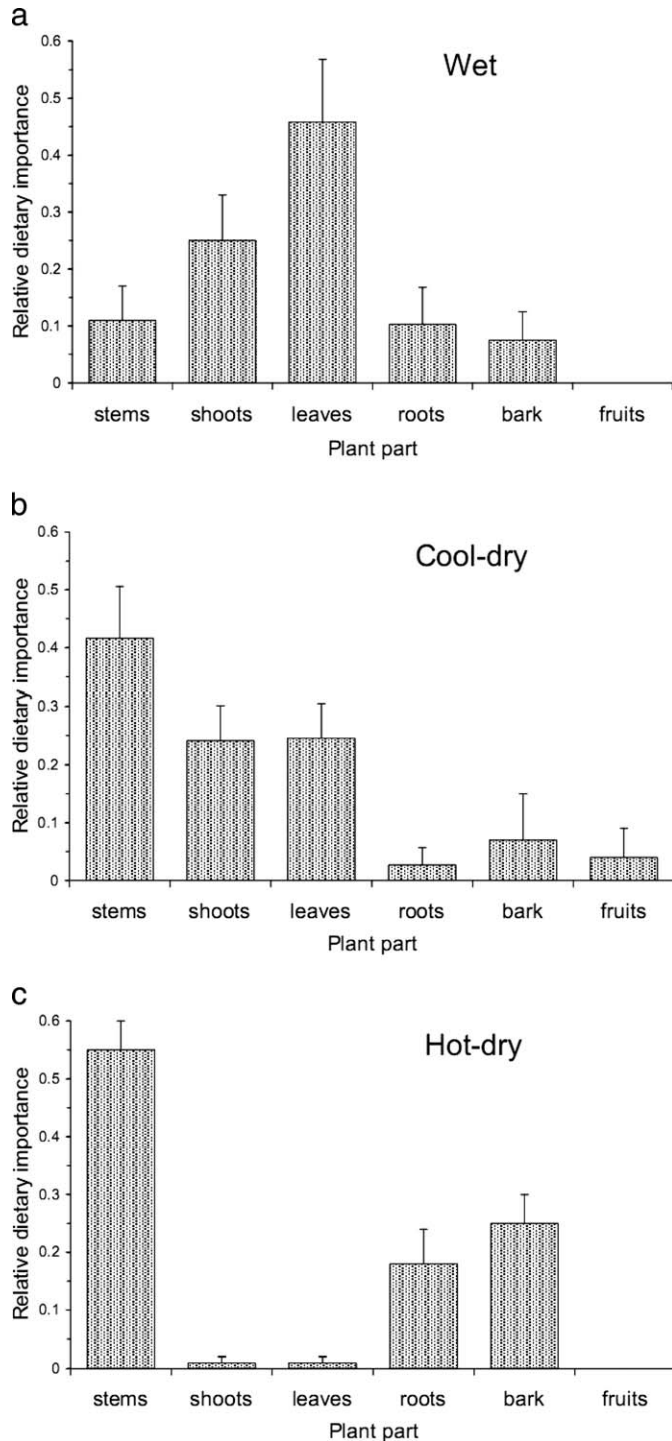


FIG. 4.—Estimated relative dietary contribution of plant parts during the a) wet season, b) cool dry season, and c) hot dry season (upper 95% confidence limits are indicated).

consuming the phenolic-rich leaves of many of the *Combretum* spp. commonly eaten by ruminants. It is unclear whether this intolerance could be due to retarded potential for detoxification in the liver as a consequence of the lowered metabolic rate associated with larger body size (Freeland 1991), or to relatively rapid digestive throughput (Clauss et al. 2003, 2007) allowing less potential for bacterial detoxification

in the gut. Perhaps elephants have simply not evolved the relatively large livers typifying true browsers (Hofmann 1989) because of their lean-season dependence on plant parts defended by fiber rather than toxins.

The woody species that were highly favored by elephants in Chobe were predominantly shrubs, seldom growing taller than 5 m, and thus mostly occurring within the 1- to 2.5-m height range. Tree saplings within this size class were generally less favored (e.g., *B. africana* and *T. sericea*), or even avoided completely (*B. plurijuga* and *E. africanum*) in our study area. Nevertheless, elephants also browsed small plants of the favored shrub species under 0.5 m in height, thereby potentially suppressing growth to taller size classes by these species.

The selective concentration by elephants on certain woody plant species could potentially eliminate these favored species from the woody plant layer. However, shrubs prevalent in Kalahari sandveld typically exhibit substantial underground biomass (Childes and Walker 1987), and seemed able to withstand the leaf stripping and pruning that were the predominant forms of damage imposed by elephants, through growing back strongly during the wet season. Although no instances of tree felling were recorded at the feeding sites we sampled, elsewhere we encountered situations where localized tree felling by elephants had occurred in circumstances where food availability in the shrub layer had been reduced by fire or frost (Chafota and Owen-Smith 2009). Nevertheless, several of the most common tree species showed little or no feeding or other damage by elephants, even in the vulnerable sapling stage. Hence, this species-selective utilization by elephants is likely to engender changes in woodland composition rather than structural transformation of the sandveld savanna into open grassland or shrubland. This may be a general feature of savanna woodlands associated with nutrient-deficient soils where most woody species seem to have chemically defended foliage. The situation may be different on more fertile soils, where the *Acacia* species that are commonly predominant in the tree canopy incur heavy utilization by elephants (Dublin et al. 1990; Western 2007). The structure and composition of the vegetation growing on the alluvial terrace and riparian woodland adjoining the Chobe River have been radically transformed by the impacts of elephants, largely through the elimination of *Acacia* trees (Mosugelo et al. 2002).

Turning now to plant part use, a very different pattern emerges. Elephants consumed an exceptionally wide range of plant tissues, with almost nothing being rejected at this level when food became sparse during the late dry season. The estimated dietary intake of elephants in our study area shifted from 80% leaves or leaf-bearing shoots in the wet season to 94% twigs, bark, and roots during the hot dry season. Barnes (1982) recorded a similar pattern in Ruaha National Park, with the dietary intake of elephants shifting from 95% leafy tissues (including grasses) in the wet season to more than 50% woody tissues by the dry season and more than 80% woody tissues toward the end of this season in a dry year. We did not estimate the contribution made by grasses, which would have elevated the foliage contribution during the wet season, but

probably made very little difference during the dry season. Stable isotope ratios indicated a range in the contribution of C4 grasses to the diets of elephants in different parts of Kenya from 44% at Amboseli to less than 10% year-round in other regions (Cerling et al. 2007). In Kruger Park, the grass contribution indicated by this method decreased from approximately 50% during the wet season to 10% in the southern region of the park during the dry season (Codron et al. 2006). Our impression was that elephants consumed little or no grass during the hot dry season in our study area, probably because grasses growing in the sandveld savanna were dry and hence very low in nutritional value during this period. In Ruaha, the high level of woody part intake was associated with a decline in body condition of the elephants (Barnes 1982). In contrast, the elephant population in our study region was expanding with little indication of malnutrition.

The dietary intake of the elephants in our study area and in Ruaha comprised a much broader range of plant parts than is typical of browsing ruminants in Africa, especially in the substantial contribution made by twigs, bark, and roots in addition to leaves and fruits. For giraffe, stem material amounted to less than approximately 10% of rumen contents, whereas for other African ruminants this proportion was less, even during the dry season (Owen-Smith 1988:86, figure 6.3). In contrast, moose (*Alces alces*) consume mostly twig tips plus the needlelike leaves of evergreen conifers during the winter period (Bergstrom and Danell 1987; Risenhoover 1989). By concentrating on stem and bark, elephants avoid the secondary chemicals that seem to be present primarily in foliage. They cope with the high fiber content in woody plant parts through rapid digestive throughput rather than high digestive efficiency (Clauss et al. 2003).

The dependence of elephants on woody tissues during the critical period of the late dry season, as well as their narrowed selection among woody plant species during the wet season and early dry season, reduces their dietary overlap with other browsing ungulates. Resource partitioning among these large herbivores may be based largely on distinct tolerances for particular secondary chemicals, with feeding by ruminants such as kudu deterred by condensed tannins (Cooper and Owen-Smith 1985; Cooper et al. 1988), but not by other forms of polyphenols prevalent in the leaves of Combretaceae (Makhabu 2005; Owen-Smith 1993). Through these mechanisms, the competitive effect of plant utilization by elephants on browsing ruminants is greatly reduced, despite the large fraction of primary production that elephants consume. Hence the negative relationship between the abundance of elephants and that of browsing ruminants reported by Fritz et al. (2002) may be more a result of this fundamental niche distinction rather than direct competitive displacement, considering in particular the distinct dry-season resources supporting these populations.

Dietary niche separation among large herbivores has been related primarily to relative proportions of grasses versus woody plants or nongraminaceous herbs consumed (Hofmann and Stewart 1972), especially during the winter or dry-season bottleneck in food availability (Owen-Smith 1997). A secondary axis has been recognized distinguishing herbaceous brows-

ers dependent largely on leaves from frugivorous browsers consuming mainly fruits, supplemented by fallen leaves (Bodmer 1990; Owen-Smith 1997). Although commonly classified as mixed feeders along the grass-browse continuum, savanna-inhabiting elephants are distinct from all coexisting ruminants in their dependence on bark, twigs, and roots rather than foliage or fruits during lean times in the seasonal cycle. In this feature, their digestive strategy resembles that of rodents and lagomorphs, also adapted through hindgut digestion to tolerate high dietary fiber contents (Bryant et al. 1983; Fryxell and Doucet 1993), rather than grazing or browsing ruminants dependent more narrowly on foliage. Our findings reinforce Jarman's (1974) contention that niche separation among large mammalian herbivores is governed more fundamentally by differential use of plant parts than by distinctions in the plant species utilized.

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