Habitat and resource partitioning between abundant and relatively rare grazing ungulates

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Abstract

Species assemblages commonly include species persisting at low density alongside more abundant species, raising questions about the mechanisms enabling this coexistence. Relatively rare species may persist through (1) specializing on a narrow range of resource types that are sparsely but widely available or (2) precisely selecting patches where their favoured resources are concentrated that are only lightly exploited by more abundant species. Our study compared the habitat and resource use across a range of scales of relatively uncommon sable antelope with those of more abundant buffalo and zebra sharing a common preference for relatively tall grass. Buffalo occupied a wide range of habitat types, but shifted towards lowlands during the late dry season when water became limiting. Sable and zebra foraged year-round in upland regions, undertaking journeys to water. Zebra occupied mainly the prevalent habitat type on basaltic substrates. Sable more narrowly exploited habitats on quartzitic sandstone where green leaves persisted in grasslands through the dry season, and favoured the grass species that retained green leaves. Buffalo and zebra were tolerant of grass that was mostly brown. Hence, the coexistence of sable was enabled by their precise selection for the green foliage remaining in between the depletion zones generated by the more abundant grazers. Nevertheless, the local sable distribution had contracted following an influx of zebra, suggesting that resource use distinctions were insufficient to prevent the competitive displacement of sable from a wider region by zebra. Hence, niche breadth and resource availability concepts both have relevance.

Introduction

Species assemblages commonly include several uncommon species coexisting alongside species that appear to be competitively superior, as judged by their much greater abundance (Gaston, 1997). Such coexistence may be due to resource partitioning in either habitat or diet. According to niche breadth concepts, less common species specialize on a narrow range of resource types, while abundant species exploit a wide range of resources and habitat conditions (Brown, 1984). Alternatively, resource availability concepts suggest that relatively uncommon species have the capacity to exploit a wide range of resources, but are restricted to places where resources remain unused by superior competitors (Gaston & Kunin, 1997; Rosenzweig & Lomolino, 1997). Campbell, Grime & Mackey (1991) suggested that rarer plant species precisely exploit soil nutrients in between the depletion zones generated by more widespread and hence more tolerant species. This implies that species with low regional densities may be superior competitors under the narrow conditions for which they are specialized (see Gregory & Gaston, 2000, with respect to British birds). Heterogeneity in resources at different scales could facilitate coexistence among mobile animals with distinct responses to this heterogeneity (Hanski, 1983; Ritchie & Olff, 1999; Ritchie, 2002). Our aim is to evaluate the applicability of these concepts to three large mammalian grazers that similarly seek fairly tall grass, but differ somewhat in body size, digestive adaptations and abundance.

Niche separation among large herbivores has been explained as resulting from (1) digestive adaptations affecting the relative use of grass or browse as a food resource (Hofmann & Stewart, 1972; Hofmann, 1989), as well as

tolerance of the fibre component in this forage (Bell, 1971; Janis, 1976); (2) body size distinctions affecting metabolic requirements and hence how narrowly selective ungulates are for specific plant parts and growth stages (Bell, 1971; Jarman, 1974; Prins & Olff, 1998); (3) oral morphology affecting the grass height exploited most efficiently (Bell, 1969, as reported in Owen-Smith, 1982; Murray & Illius, 1996). Distinctions in habitat occupation can be recognized at various scales, from landscape regions through vegetation types to the composition of local resource patches (Senft et al., 1987). Differences in food resources can be identified at plant species level, or in terms of the local accessibility and nutritional value of plant parts or growth stages. Relevant features of resource heterogeneity at landscape scale include woody vegetation structure (Ferrar & Walker, 1974; Greenacre & Vrba, 1984) and soil fertility (East, 1984). Choice of feeding sites and plant species and parts consumed by herbivores is influenced by nutrient and fibre contents (Ben-Shahar & Coe, 1992; Bailey et al., 1996), dependent on grass height and relative greenness (Wilmshurst et al., 1999). Hence, coexistence among large herbivores may be enabled by distinctions in resource use at one or more of these scales, underlain by differences in body size and morphological adaptations.

Sable antelope *Hippotragus niger* are medium-sized ruminants (adult female body mass 220 kg) with relatively narrow muzzles (incisor arcade breadth 57 mm; Gordon & Illius, 1988) that enable them to graze tall grass (Skinner & Chimimba, 2005). Their highest recorded density is about three animals per km^2 (Grobler, 1974), but their local abundance within the Kruger National Park (KNP) where our study area was located did not exceed 0.5 animals per km^2 (Chirima et al., unpubl. data). African buffalo (*Syncerus caffer*) are large ruminants (adult female body mass 520 kg) with broad muzzles (incisor arcade breadth 93 mm), and are bulk grazers on tall grass. They attain a regional density of 1.5 animals per km^2 within KNP, and local densities of 3–5 animals per km^2. Plains zebra (*Equus quagga*) are medium-large non-ruminants (adult female body mass 310 kg) that tolerate quite tall and hence fibrous grass due to their hindgut digestion. They exhibit local and regional densities in KNP closely similar to those of buffalo. Differences in social groupings may also influence resource exploitation patterns. Buffalo form large herds generally numbering several hundred animals and zebra cohesive groups of 5–10 animals, while sable herds typically number 15–30 animals (Grobler, 1974; Sinclair, 1977; Skinner & Chimimba, 2005).

Our study was focused on the dry season when competition for diminishing resources was expected to be accentuated, and, hence, resource partitioning most evident. Global Positioning System (GPS) collars placed on adult female animals representing the three ungulate species enabled their locations and habitat use to be recorded in fine temporal and spatial detail, and allowed places where animals had recently been feeding to be located. Hence, we could record the resource use of all three species simultaneously across a comprehensive range of scales. Based on the concepts outlined above, we expected that:

1. Following the resource availability hypothesis, buffalo (because of their large size) and zebra (because of their hindgut fermentation) would occupy a wide range of habitat types, while sable would concentrate more narrowly in habitats less thoroughly exploited by the two more abundant competitors.

2. In accordance with the niche breadth hypothesis, sable would (1) select foraging areas where grass was greener than in the broader landscape, whereas zebra and buffalo would more broadly exploit areas offering abundant but predominantly brown grass; (2) precisely select feeding sites retaining green grass; (3) selectively feed on grass species regarded as relatively palatable because of high leaf : stem ratio, while buffalo and zebra would accept wider range of plant species.

3. Dietary overlap between sable and buffalo or zebra would diminish over the course of the dry season as zebra and buffalo widened their tolerance for the lower quality resources that remained abundantly available, while sable concentrated their resource use in places where some green grass remained.

Materials and methods

Study area

KNP covers almost 20 000 km^2 along South Africa's northeastern border adjoining Mozambique. Our study area extended from Punda Maria camp in the far north of KNP (22°68′S, 31°018′E) towards the Mphongolo River, encompassing about 500 km^2. This area formerly supported among the highest local densities of sable antelope in KNP. However, sable numbers had decreased from a peak of 150–200 animals prior to 1988 to only around 25 animals at the time of our study. Zebra numbers in the study area declined from around 600 to approximately 200 animals over the same period, while around 400 buffalo were present, up from the low of under 200 animals counted following the 1991/2 drought. Other grazers included about 700 Impala *Aepyceros melampus*, 50 Waterbuck *Kobus ellipsiprymnus* and fairly numerous African elephant *Loxodonta africana*. Wildebeest (*Connochaetes taurinus*) were absent. Buffalo and zebra constituted 90% of the regional grazer biomass, excluding elephant which feeds somewhat differently. Following Venter (1990), we distinguished the following habitat types, based on underlying geology and, hence, soils, vegetation composition and structure: (1) open bush savanna comprising *Pterocarpus rotundifolius*, *Combretum collinum* and *Combretum apiculatum* on mainly basalt-derived soils; (2) bush savanna comprising *Terminalia sericea*, *C. collinum* and *C. zeyheri* on mainly sandstone-derived soils; (3) open woodland of *Combretum* spp on coarser quartzitic sandstone; (4) tree to bush savanna consisting of *Colophospermum mopane*, *C. apiculatum* and *P. rotundifolius* on granitic sands; (5) tree savanna dominated by *C. mopane* on clayey soils formed from shale and mudstone; (6) riparian woodland on alluvial soils fringing the Mphongolo River. Rainfall recorded at Punda Maria camp averaged 560 mm per year (1960–2007). Rainfall over the seasonal cycle (July–June) was 33% above the long-term mean in 2005/6, and

25% below the mean in 2006/7. In 2006, the first spring rains were delayed until early November, whereas in 2007, the first rain of the wet season was received at the end of September. Surface water availability became restricted to pools in the Mphongolo River by mid-August, apart from artificial sources near the western border fence and the tourist camp in the north.

Research design and data collection

In May 2006, GPS/GSM collars (Africa Wildlife Tracking; http://www.awt.co.za) were placed on three adult females representing the sole sable herd of about 20 animals, four female zebra in separate herds of 5–7 animals and two female buffalo present in a single herd of about 400 individuals, later commonly split into two subgroups. In June 2007, collars were replaced on one of the previously collared sable and buffalo, and placed on female zebra representing two new herds, to extend the study period through September 2007. Animal capture was carried out by South African National Parks staff using immobilizing drugs injected from a helicopter, following their ethical guidelines. No animal fatalities were recorded.

Field observations covered two dry seasons (June–October 2006 and May–September 2007). Habitat use through the wet season (December 2006–April 2007) was provided by the GPS tags. GPS collars recorded herd locations routinely every 6 h, at 8:00 and 20:00 representing foraging times during the day, and at 2:00 and 14:00 representing resting times. To facilitate observations at feeding sites, GPS tags on selected herds were temporarily re-set to provide hourly locations. Places where these animals had been present during the morning (6:00–10:00) and late afternoon (16:00–20:00) foraging periods were visited on 2 days per species each week. Feeding sites were identified from fresh hoof prints and signs of recent grazing, generally found within 5 m of the GPS location. Sites with signs of recent use by other grazers were discarded, but represented less than 1% of sites visited. One to five feeding sites were sampled to represent either the morning or afternoon foraging session.

In the area surrounding each feeding site, the habitat features recorded included (1) topographic location as lowland, slope or upland; (2) tree (>2.5 m in height) and shrub (<2.5 m) canopy cover within a 25-m radius, estimated in the following classes: 0%, 1–10%, 11–25%, 26–50% and 51–75%; (3) tree canopy height, estimated as short (≤5 m), medium (6–10 m) or tall (>10 m); (4) prevalent grass height within a 25-m radius, estimated in the following classes (ignoring emergent culms): short (≤10 cm), medium (11–20 cm), medium-tall (21–40 cm), tall (41–80 cm) and very tall (>80 cm); (5) greenness of the grassland within a 25-m radius estimated as the proportion of green leaves in the following classes: 0%, 1–10%, 11–25% and >25%.

To assess food selection, a 0.7 × 0.7 m quadrat was placed at the first identified sign of recent grazing at each feeding site. A further eight quadrats were placed systematically 2 m apart, two along each of the four cardinal directions. Within each quadrat, all grass species present were scored as grazed or ungrazed. The amount grazed was estimated by counting the

number of bites taken from each grass species, representing each bite by the area covered by a fist. For each grass species, the proportion of green leaves was estimated. The leaf height of ungrazed tufts assumed to represent those that had been grazed was measured and grouped into the same categories used at the feeding site level. The number of stems per tuft was classified as no stems, few stems (1–2) or many stems (≥3). Grass species identification and nomenclature followed van Oudtshoorn (1999).

Data analysis

Based on patterns of rainfall and grass green leaf retention, the dry season was subdivided into the early (June–July 2006 and May–July 2007) and late (August–October 2006 and August–September 2007) divisions. For some analyses, we combined data for the same season from different years, because grass greenness in feeding sites did not differ substantially between the 2 years in the monthly divisions used. Habitat occupation was assessed for the wet season of 2006/7 from GPS locations.

The collared sable and buffalo represented all of the herds of these species present in the study area, while the collared zebra herds represented 10–20% of the zebra herds in the study area, depending on the periods over which different collars functioned. The proportional availability of habitat types within the study area was determined for each herbivore species by amalgamating all GPS locations from collared animals to obtain the 100% minimum convex polygon ranges. GPS locations of each ungulate species at the time of day when foraging was the prevalent activity (8:00 and 20:00) were assigned to habitat types using the map developed by Venter (1990).

Each morning or afternoon, foraging period with 1–5 feeding sites was considered to be an independent sample of habitat features at foraging sites. Log-linear analysis in Systat 11.0 for Windows (Systat Software, Inc., Richmond, CA, USA) was used to distinguish habitat features between pairs of herbivore species during each stage of the dry season. Habitat types were pooled into fewer categories to increase the sample size because some categories were inadequate. Accordingly, the following categories were used for statistical analyses: topography – upland or non-upland; tree and shrub cover – more open (≤10%) or less open (>10%); tree height – short (≤5 m) or medium-tall (>5 m); grass greenness – mainly brown (≤10%) or fairly green (>10%); and grassland height – medium (≤40 cm) or tall (>40 cm). For graphical displays, we retained the finer categories recorded. Only the features with significant effects between pairs of herbivores were considered in building the full models. Because our measures of woody vegetation structure (tree cover, shrub cover and tree height) were all positively correlated (Spearman rank correlation $r >$ 0.4), we retained only tree cover in the full model. The relative support for models incorporating different combinations of habitat features was assessed using the Akaike Information Criterion (AIC; Burnham & Anderson, 2002). Following Agresti (1990), for categorical data, $AIC = G^2 - 2d.f.$, where G^2 is the deviance of each model or log likelihood ratio chi-square, and $d.f.$ refers to degrees of freedom.

To assess selection of grass species, we considered each feeding site (encompassing nine quadrats) to be an independent sample of food choice. Following Owen-Smith & Cooper (1987), the availability of each grass species was calculated as the proportion of feeding sites where each species was present within one or more quadrats. The site-based acceptance of each grass species present at ≥ 10 feeding sites for each herbivore species was obtained by dividing the number of feeding sites where each grass species was grazed in at least one quadrat by the total number of feeding sites where the grass species was present. Grass greenness was categorized as follows: <5%, 6–10%, 11–20% and >20%. For grass height, only two categories were used, because too few grass tufts were shorter than 20 cm or taller than 80 cm in the feeding sites. We also calculated acceptance ratings for grass tufts aggregated into greenness categories independently of the grass species represented for each herbivore species.

Log-linear analysis was used to compare structural and phenological features of the grass tufts grazed by sable with those grazed by buffalo or zebra. The change in model fit when the factor herbivore was removed from the model was evaluated using the likelihood ratio test (G^2) for $P < 0.05$. We examined z-scores to identify the cells of the contingency table that contributed most to the lack of fit of the reduced model, thereby identifying the main distinctions in grass species availability or acceptability between the herbivore species.

To estimate the dietary contribution by each grass species for each grazer, we assumed morning or afternoon foraging periods to be independent sampling units. The proportional dietary contribution was estimated by dividing the number of bites taken on tufts of each grass species by the total number of bites recorded at the feeding sites. The resulting proportions were averaged across foraging periods to obtain the monthly or seasonal diet contribution by each grass species.

Results

Habitat types

Sable favoured woodland savanna underlain by quartzitic sandstone in the wet season and early dry season (Fig. 1a). During the late dry season, bush savanna associated with finer-grained sandstone became most strongly favoured, along with increased use of *C. mopane* tree savanna on shale and mudstone, particularly in the wetter of the 2 years. Zebra strongly favoured the open bush savanna associated with basaltic soils, the most widely prevalent vegetation type, throughout the year (Fig. 1b). Buffalo showed a broadly distributed use of habitat types during the wet season, but concentrated strongly in the granitic region near the river during the dry season, most especially in the drier year (Fig. 1c).

Foraging localities

Both sable and zebra foraged mainly in upland regions of the landscape throughout the dry season (Fig. 2a). Buffalo concentrated in slope regions in the early dry season and made

greater use of lowland near the river during the late dry season. Sable and zebra entered this lowland only to drink from pools in the river.

The foraging areas of zebra were usually more open with shorter trees than those occupied by sable (Fig. 2b). However, tree canopy cover and height in the foraging areas of buffalo were very similar to those for sable. Grass height in foraging areas was generally in the range 41–80 cm for all three grazers, with no seasonal variation (Fig. 2c). The grassland tended to be greener than in the foraging areas of sable than in those of zebra and buffalo in the early dry season, but this distinction fell away during the late dry season when very little green grass remained (Fig. 2d).

The model incorporating both grass greenness and tree canopy cover best distinguished the foraging areas of sable from those zebra, although the model with greenness replaced by season was almost equally supported (Table 1a). For the sable–buffalo comparison, the best supported model included only grass greenness as a distinguishing feature, but with some support for an interaction with season (Table 1b). Either tree cover or topography was the most strongly supported distinction between the foraging areas of zebra and buffalo (Table 1c).

Feeding sites

Acceptance of the grass at feeding sites was more strongly influenced by grass greenness for sable than was the case for both zebra ($G^2 = 91.6$, d.f. $= 3$, $P < 0.001$) and buffalo ($G^2 = 116.0$, d.f. $= 3$, $P < 0.001$) (Fig. 3a). Zebra appeared somewhat indifferent to distinctions in greenness in their grass acceptance throughout the dry season, while buffalo showed an inconsistent response to grass greenness in the early dry season, and foraged solely in sites containing little or no green grass during the late dry season. During the late dry season, sites containing grass that was more than 10% green were present only in the feeding sites of sable.

Sable differed from both zebra ($G^2 = 94.08$, d.f. $= 2$, $P < 0.001$) and buffalo ($G^2 = 43.96$, d.f. $= 2$, $P < 0.001$) in the influence of grass height on acceptance. Sable strongly favoured grass taller than 40 cm, while zebra showed less preference for taller grass, and buffalo appeared indifferent in their grass height acceptance (Fig. 3b). The effect of stem number on grass acceptance by sable was unexpectedly positive, while stemminess had no consistent influence on grass selection by zebra and buffalo (Fig. 3c).

Grass species grazed

Generally, 4–5 grass species constituted about 75% of the diet of each herbivore in each season (Fig. 4). *Panicum maximum* was among the principle grass species of all three ungulate species throughout the dry season, but with sable showing the narrowest concentration on it. For zebra, *Setaria incrassata* was the top-ranked dietary component, while for buffalo, *Urochloa mosambicensis*, the species most frequently present in feeding sites, was as important as *P. maximum* in the diet. Sable made comparatively little use of *U. mosambicensis*,

a

b

c
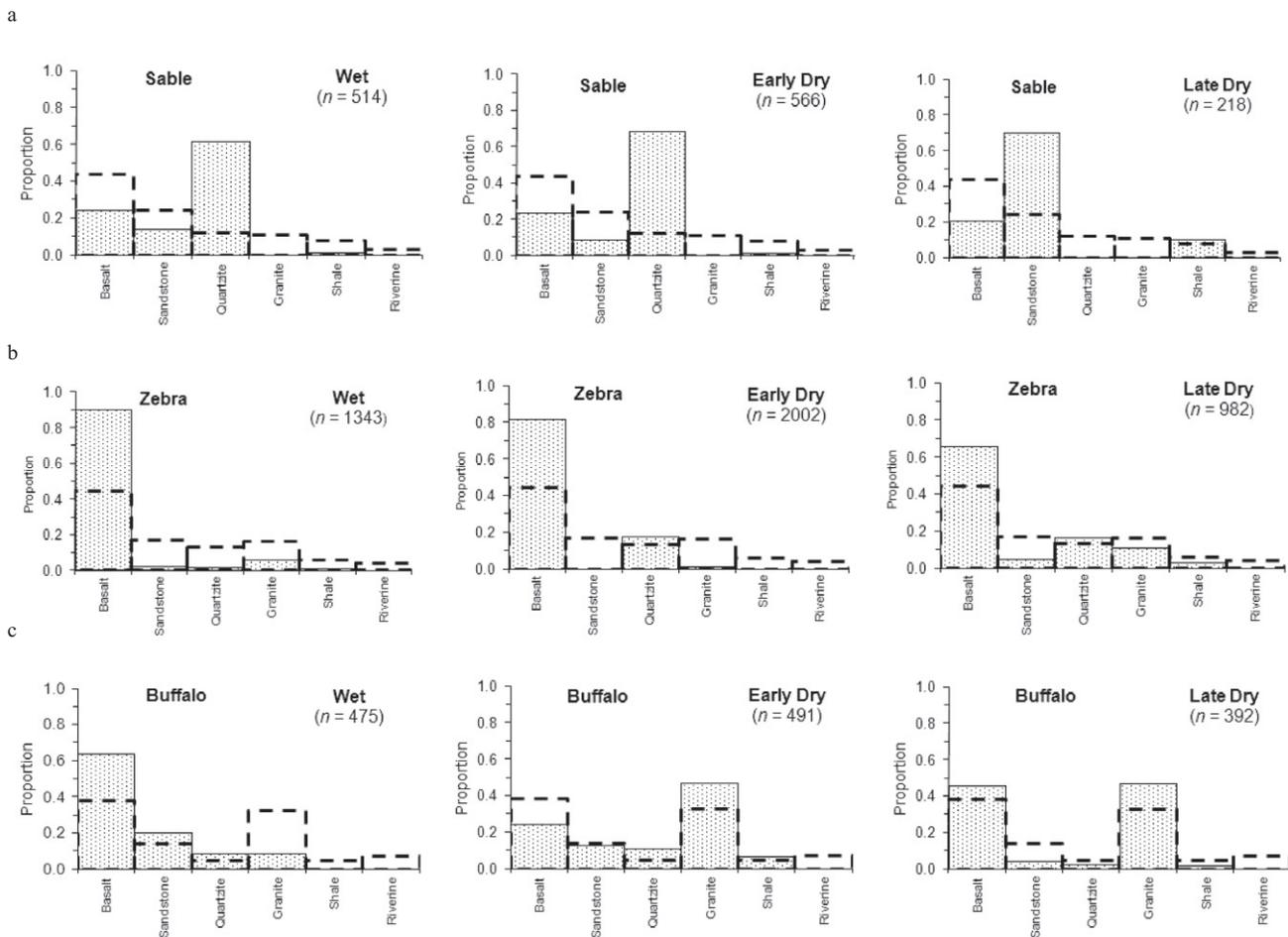
Figure 1 Relative use of land types distinguished by geological substrates by (a) sable, (b) zebra and (c) buffalo (filled bars), compared with the proportional availability of these land types in the Punda Maria study area (dashed outlines). Seasons distinguished are wet, early dry (EDry) and late dry (LDry). Sample n is number of Global Positioning System locations representing morning and evening foraging sessions.

especially during the late dry season. In this season, a set of uncommon grasses rarely recorded in the feeding sites of zebra or buffalo became prominent among the grass species consumed by sable.

Discussion

Distinctions were apparent in the habitat preferences of the sable, buffalo and zebra herds. Zebra concentrated mainly in the basaltic area characterized by relatively open woody cover and mostly short trees, which was the most widely prevalent habitat in the study area, throughout the year. The sable herd was most commonly located in the region underlain by quartzitic sandstone with taller and denser woody vegetation than that favoured by the zebra during the wet season and early dry season. The shift by this herd towards mixed woodland on fine-grained sandstone in the late dry season seemed largely related to gaining closer access to remaining surface water (Cain, Owen-Smith & Macandza, 2012). The buffalo herd

broadly exploited all habitats during the wet and early dry seasons, shifting to the proximity of the river where granite adjoined the basalt in the late dry season. The contrast in diversity of habitat types occupied between sable and buffalo matches the relationship with body size identified by du Toit & Owen-Smith (1989) for browsing ruminants covering a body mass range from 11 to 800 kg (see Redfern, Ryan & Getz, 2006, and Cromsigt, Prins & Olff, 2009, with respect to other large herbivore guilds). This nested pattern of habitat use did not exclude substantial overlap in habitat use between sable and buffalo during much of the year. Moreover, the basaltic habitat favoured by zebra was second most important for sable in terms of the proportion of foraging records located in it.

At finer resource scales, the most striking pattern was strong selection by sable for foraging areas and feeding sites where grasses remained greener than in the places where zebra and buffalo grazed. Among grass species, sable concentrated most narrowly on *P. maximum*, which retained green leaves
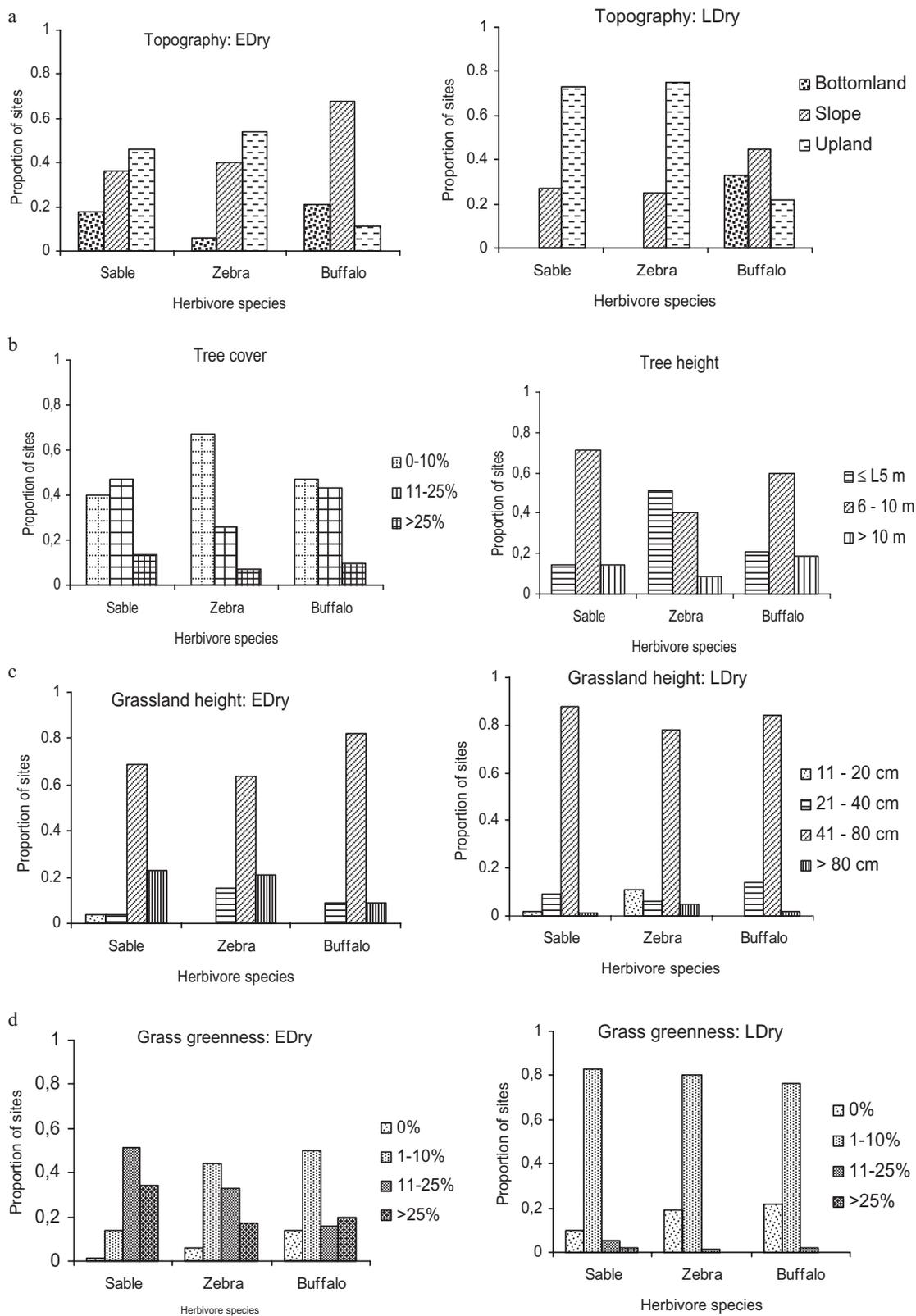
Figure 2 Prevalence of habitat features in feeding sites used by sable, zebra and buffalo, distinguishing early (EDry) and late (LDry) dry season periods when patterns differed substantially between them. (a) topography, (b) tree canopy cover and height, (c) grassland height and (d) grass greenness. Sample sizes, for early dry and late dry seasons, respectively, were sable 77, 94; zebra 72, 64; buffalo 44, 51 foraging sessions.

Table 1 Distinctions in habitat features at feeding sites of sable and zebra assessed using log-linear models

|	G^2	d.f.	AIC	Δ AIC
a. Sable versus zebra				
Herbivore × greenness × tree cover	149.63	14	121.63	0
Herbivore × season × tree cover	151.71	14	123.71	2.08
Herbivore × season × grassland height	152.54	14	124.54	2.91
Herbivore × grassland height × greenness	153.67	14	125.67	4.04
Herbivore × tree cover	156.24	15	126.24	4.61
Herbivore × grassland height × tree cover	160.44	14	132.44	10.81
Herbivore × grassland height	161.09	15	131.09	9.46
Herbivore × season × greenness	164.98	14	136.98	15.35
Herbivore × greenness	174.47	15	144.47	22.84
b. Sable versus buffalo				
Herbivore × greenness	37.49	15	7.49	0
Herbivore × season × greenness	35.75	14	7.75	0.26
Herbivore × season × topography	37.77	14	9.77	2.28
Herbivore × greenness × tree cover	37.78	14	9.78	2.29
Herbivore × topography	40.03	15	10.03	2.54
Herbivore × topography × greenness	42.24	14	14.24	6.75
Herbivore × tree cover	47.33	16	15.33	7.84
Herbivore × season × tree cover	45.16	14	17.16	9.67
c. Zebra versus buffalo				
Herbivore × tree cover	23	7	9	0
Herbivore × topography	23.4	7	9.4	0.4
Herbivore × season × tree cover	28.9	8	12.9	3.9
Herbivore × season × topography	29.2	8	13.2	4.2

AIC, Akaike Information Criterion.

into the dry season through occurring commonly under tree canopies. Towards the end of the dry season, sable exploited uncommon grass species that still retained green foliage through being associated with sites where soil moisture persisted, such as localized drainage sumps. They did not avoid grass species that were tall and stemmy, but rarely grazed grass that was shorter than 40 cm. Zebra and especially buffalo were tolerant of grasses that were predominantly brown by the late dry season, including the most common species in the study area, *U. mosambicensis*.

These patterns seem in accordance with the concepts of precision and tolerance in resource use advanced by Campbell *et al.* (1991) to explain coexistence between common and rare plant species. They are also consistent with niche breadth theory (Brown, 1984), with the narrower niche of sable being based mainly on their greater need for green leaf in their diet than the larger buffalo and non-ruminant zebra. Narrower specialization on higher-quality vegetation components is the basic feature of the niche separation among ruminant herbivores governed by body size identified by Bell (1971) and Jarman (1974). Due to this niche contraction, maximum population densities attained by ungulates decrease with diminishing body size below a pivotal female mass of 50 kg (du Toit & Owen-Smith, 1989; Owen-Smith, 2008), which is inconsistent with the general negative relationship between increasing abundance and body mass identified by Damuth (1981). Moreover, maximum population densities of certain ungulate species larger than 50 kg remain well below those attained by other species of about the same size. There is a huge contrast between the density of over 60 animals per km^2 attained by wildebeest in the Serengeti ecosystem (Mduma, Sinclair & Hilborn, 1999) and the highest density of three animals per km^2 recorded for sable antelope (Grobler, 1974).

The assumption that smaller ungulates are superior competitors for sparse resources because of their lower quantitative food requirements (Illius & Gordon, 1987; but see Owen-Smith, 2002: Chapter 12) is discordant with the declining trend of sable numbers in KNP as zebra and buffalo populations expanded (Owen-Smith & Mills, 2006). This brings aspects of the resource availability hypothesis (Gaston & Kunin, 1997) into contention, specifically whether rarer sable are restricted through competition to places where resources remain little utilized by abundant buffalo and zebra. Sable herds were formerly more numerous in northern KNP including the western basaltic region now dominated by zebra (Chirima *et al.*, unpubl. data), suggesting that competitive displacement had occurred during the extreme drought conditions that had prevailed after 1991. Evidently, sable herds had formerly occupied a broader range of habitats than the narrow concentration exhibited by the single surviving sable herd. The depression of the green leaf component in the basaltic grasslands following the increased local abundance of zebra, enabled by wider surface water provision (Owen-Smith & Mills, 2006), could thus have contributed to the sable population decline. However, the implication that non-ruminant zebra with less effective digestion displaced a supposedly more efficient ruminant is contrary to generally perceived relationships between these alternative digestive strategies (Duncan *et al.*, 1990). Wider evidence indicates that an increase in the abundance of lions in the sable range following the increased availability of zebra as prey contributed to the sable population decline (Owen-Smith & Mills, 2006; Owen-Smith *et al.*, 2012, in press). Moreover, there is insufficient information on vegetation changes to exclude the possibility that less green grass persists through the dry season in northern KNP following the prolonged drought conditions experienced into the 1990s. But it does not seem credible to extend the latter mechanism to the moister southwestern region of KNP where the local sable sub-population also declined drastically (Chirima *et al.*, unpubl. data).

Nevertheless, the sable herd that we studied had survived despite the pressures and restrictions from shifting competition, predation and habitat conditions. They did so by
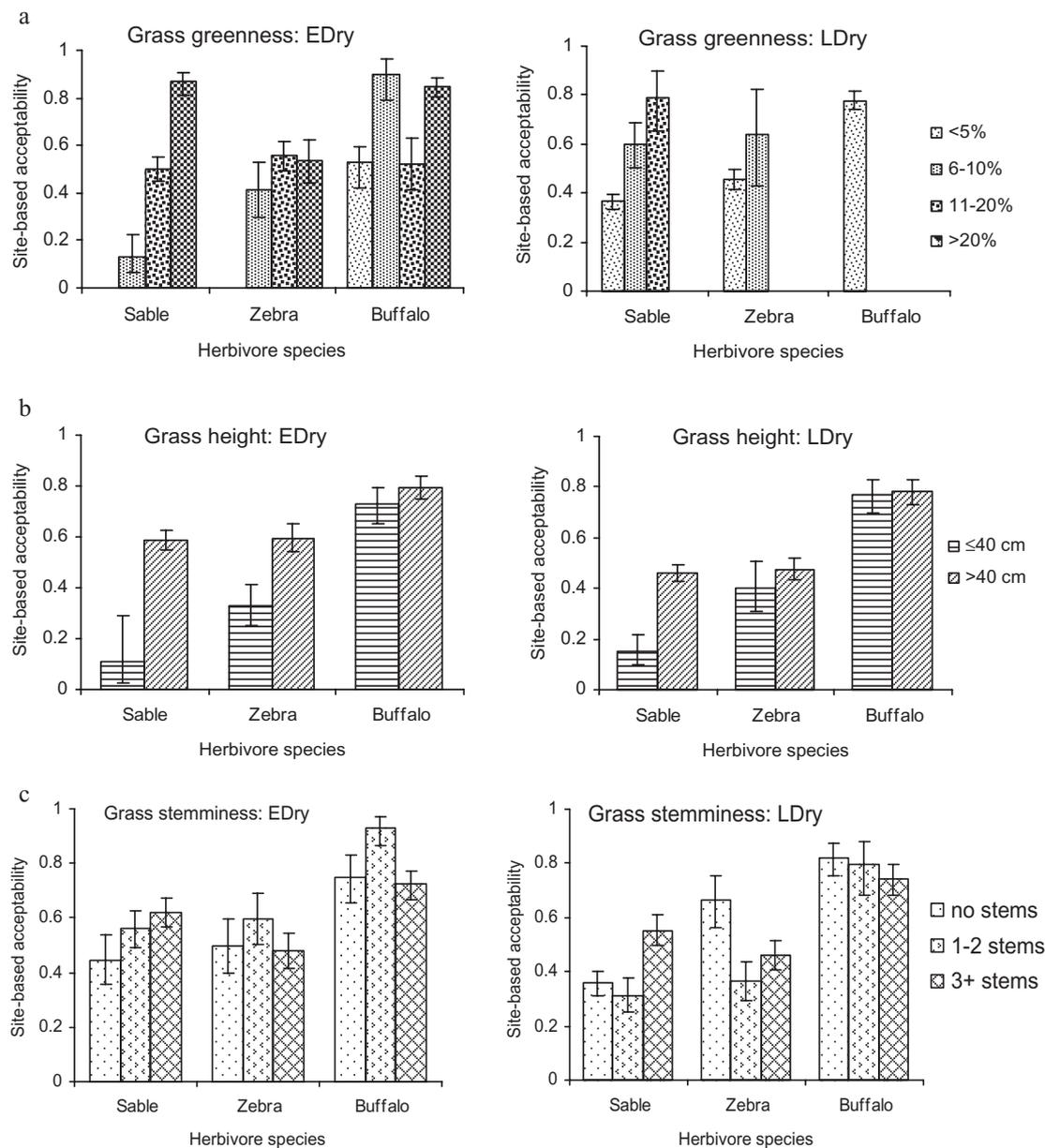
Figure 3 Relationship between grass features presented and the frequency of acceptance of sites for feeding by sable, zebra and buffalo. (a) grass greenness, (b) grass height and (c) stem categories at feeding sites of during the early dry seasons (EDry) and late dry seasons (LDry) of both years combined. Bars denote 95% binomial confidence intervals.

precisely locating patches in the heterogeneous landscape where some green grass remained despite the grazing pressure from more numerous buffalo and zebra. Spatial separation from buffalo was achieved dynamically by exploiting localities not yet grazed by the buffalo herd, facilitated by the shift by the buffalo to near the river where pools of water remained in the late dry season (Macandza et al., 2012, in press). Competitive overlap in resource use with small and hence more numerous zebra herds could not readily be avoided, and probably contributed to the greatly reduced abundance of sable in the study area.

Chapters in Kunin & Gaston (1997) revealed few common features distinguishing rare from common species across the variety of taxa covered, especially with regard to competitive dominance. A subsequent review by Gregory & Gaston (2000) with regard to the relationship between local abundance and regional distribution, specifically for breeding birds in Britain, found much support for the resource availability hypothesis, but little for the niche breadth hypothesis. In particular, birds that tended to use resources atypical of the broader environment tended to be rarer and thinly distributed, while those using more generally available resources were both common
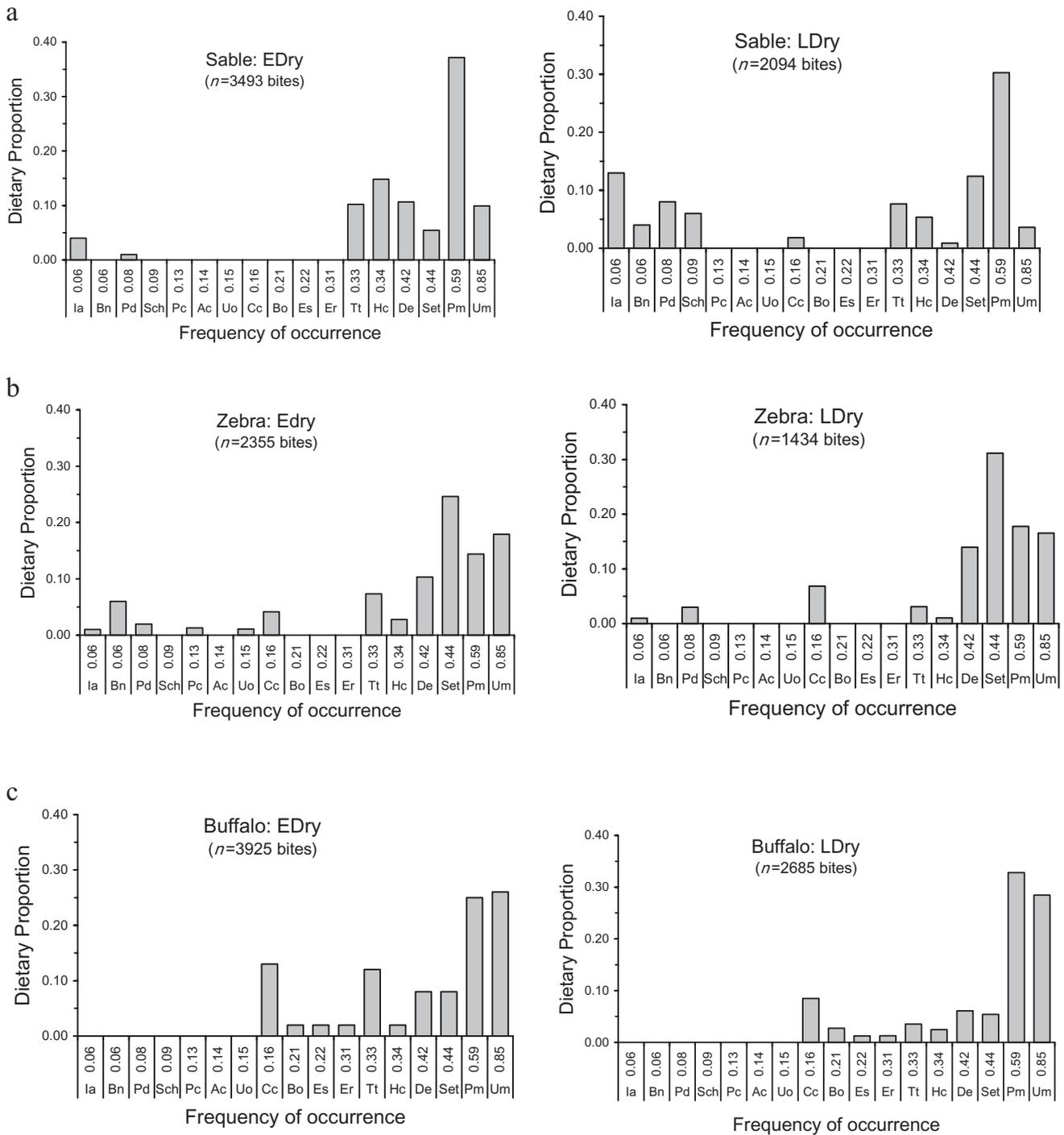
Figure 4 Relationship between the proportional dietary contributions of grass species and their overall frequency of occurrence in feeding sites of all three ungulate species combined, for the early (EDry) and late dry (LDry) season months. (a) sable, (b) zebra and (c) buffalo. Grass species labels: Ac, *Aristida congesta*; Bn, *Brachiaria nigropedata*; Bo, *Bothriochloa* spp; Cc, *Cenchrus ciliaris*; De, *Digitaria eriantha*; Er, *Eragrostis rigidior*; Es, *Eragrostis superba*; Hc, *Heteropogon contortus*; Ia, *Ischaemum afrum*; Pc, *Panicum coloratum*; Pm, *Panicum maximum*; Pd, *P. deustum*; Tt, *Themeda triandra*; Set, *Setaria incrassata*; Sch, *Schmidtia pappophoroides*; Um, *Urochloa mosambicensis*; Uo, *Urochloa oligotrricha*.

and widely distributed. Our findings suggest that low-density herbivore species can coexist alongside more abundant species by precisely exploiting the specific localities where their particular resource requirements are met.

Acknowledgements

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