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Research Article

Experimental defaunation alters foraging behavior of a small antelope (Guenther's Dik-dik, *Madoqua guentheri*) in Kenya

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Abstract

African savannas are experiencing an array of human-induced changes, including reductions and extirpations of large mammalian herbivores. The outcomes of these changes will be at least partially dependent on the functional responses of species that persist, including changes to plant-herbivore interaction networks. However, experimental tests of how ecological context, season, and competition jointly regulate foraging behaviors of large mammals are sparse. Therefore, we combined dietary DNA metabarcoding and a long-term herbivore-exclusion experiment in semi-arid Kenyan savanna to understand how a small browsing antelope (Guenther's Dik-dik, *Madoqua guentheri*, ~5 kg) responds to the absence of larger herbivores across seasons (e.g., wet vs dry) and sites (e.g., mesic vs xeric). We hypothesized that: (i) dik-dik diets would differ from those of co-occurring large browsers due to size-based differences in forage selection and accessibility; (ii) exclusion of larger herbivores would increase dik-dik activity and enable them to select high-quality browse, consistent with competitive release; and (iii) this selective foraging by dik-dik would suppress the growth and recruitment of their preferred woody food species. Consistent with our hypotheses, dik-dik diets differed significantly from co-occurring—but much larger—mixed-feeders, including the African Savanna Elephant (*Loxodonta africana*) and Impala (*Aepyceros melampus*). Dik-dik foraged selectively according to plant nutritional properties, especially protein content, and they avoided long-spined *Acacia* species, particularly during dry seasons and at the xeric site. In the absence of larger herbivores, dik-dik activity increased >2-fold, and they increased selectivity for the most nutritious, least-defended *Acacia* species. Shifts in selectivity due to competitive release were strongest under resource-scarce conditions, including dry seasons and xeric environments, amplifying local impacts of large-herbivore losses on savanna plant communities. Finally, in the absence of larger browsers, dik-dik suppressed the growth of their preferred species (*Acacia mellifera*), but only at the xeric site. Together, these results provide strong evidence that dik-dik exhibit flexible foraging behavior in response to larger herbivores, especially in resource-scarce conditions. If large herbivores are extirpated, subsequent diet shifts by dik-dik may suppress long-term plant diversity in this savanna.

Keywords competition, foraging ecology, herbivory, niche partitioning, plant defenses

Savanna herbivores exert strong top-down control on plant communities, and large browsers have an especially strong influence on tree cover (Staver et al. 2021; Pringle et al. 2023). While interspecific competition is often assumed to be important in regulating savanna herbivore populations, foraging dynamics, and community composition (Pansu et al. 2022; Anderson et al. 2024), empirical evidence of competition is scarce (Cameron and du Toit 2007; Prins 2016; Kimuyu et al. 2017). Understanding how interspecific competition between

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large mammalian herbivores affects the diversity and composition of savanna vegetation is critical in light of anthropogenic impacts on these wildlife communities and the changing environments in which all of these trophic networks occur (Craigie et al. 2010; Guyton et al. 2020).

Anthropogenic defaunation is a size-biased process, often affecting the largest herbivores more than and prior to smaller species (Ripple et al. 2015; but see Owen-Smith et al. 2017). Diminished top-down control by the largest herbivores could release fast-growing, competitively dominant plants from suppression and/or enable less abundant, palatable species to escape herbivory (Bakker et al. 2006). However, these effects may be modified if smaller herbivores increase in density or activity in response to the loss of larger herbivores (Goheen et al. 2018). One possibility is that smaller herbivores benefit from shifting their diets to include plants that had been previously limited by larger herbivores, resulting in greater densities of small herbivores following competitive release and thus either diminishing or accelerating changes in the resulting plant community, depending on the degree to which smaller herbivores functionally replace larger species (Staver and Hempson 2020). Another possibility is that diet-switching by predators alters the behavior of smaller herbivores, perhaps causing them to take refuge in more protected habitats (Ford and Goheen 2015; Atkins et al. 2019). To understand how defaunation might impact savanna ecosystems, we need to understand whether and how populations of small browsers respond to the absence of larger species (Lagendijk et al. 2012).

Savanna ecologists have long grappled with the question of how different-sized browsers select foods and affect plant communities (Jarman 1974; Kartzinel et al. 2015; Potter et al. 2022). Smaller browsers tend to select the highest quality plant material, such as young green leaves and fruits (Owen-Smith and Novellie 1982), while megaherbivores require larger quantities of food and accordingly tend to have diets of lower mean nutritional quality (Bell 1971; but see Schmitt et al. 2016). Likewise, small browsers generally have narrower and more dexterous muzzles than large species, conferring greater ability to select high quality bites (Bell 1969). Different-sized browsers also partition food based on height; smaller browsers suppress the growth of high-quality foliage at and near ground level (Augustine and McNaughton 2004), whereas larger browsers can access foliage at taller heights (Cameron and du Toit 2007). The largest herbivores, including elephants, may also facilitate the foraging of smaller browsers by knocking down trees, which can increase the availability of browse at lower heights and create novel microhabitats in which a diversity of understory plants can thrive (Rutina et al. 2005; Valeix et al. 2011; Coverdale et al. 2016).

Climate and seasonality cause shifts in resource availability and thus can modulate the effects of large herbivores on smaller browsers. As physical stress decreases—as may occur along a gradient from less to more favorable climates—theory predicts a shift from relatively more facilitative interactions within a community to those that are relatively more competitive (Bertness and Callaway 1994; Goheen et al. 2018). Moreover, individuals should theoretically experience greater competition for food due to seasonal resource scarcity during dry seasons (Owen-Smith and Novellie 1982; Porter et al. 2022). The effects of seasonality on competitive dynamics may be exacerbated for specialized browsers that have high caloric intake requirements (Demment and van Soest 1985; McNaughton and Georgiadis 1986), but yet may not be able to seasonally switch feeding strategies as extensively as mixed-feeders do (Staver and Hempson 2020; but see, e.g., Kartzinel et al. 2019; Pansu et al. 2022).

The loss of large herbivores may lead to changes in the density, activity, and foraging behaviors of potential competitors such as smaller browsers (Bakker et al. 2006). Long-term field experiments coupled with dietary analyses provide a means of understanding how these changes occur (e.g., Ernest et al. 2016; Meserve et al. 2016; Goheen et al. 2018; Guyton et al. 2020). Here, we combined a large-herbivore exclusion experiment in Kenya with dietary DNA metabarcoding to determine whether and how a 5 kg browser (Guenther's Dik-dik) responds to the removal of larger herbivores (e.g., African Savanna Elephant, *Loxodonta africana*; Impala, *Aepyceros melampus*). We hypothesized that: (i) dik-dik diets would differ from those of co-occurring large browsers due to size-based differences in forage selection and accessibility; (ii) exclusion of larger herbivores would increase dik-dik activity and enable them to select high-quality browse, consistent with competitive release; and (iii) this selective foraging by dik-dik would suppress the growth and recruitment of their preferred woody browse species.

Methods

Herbivore-exclusion experiment

The research was performed at Mpala Research Centre, a ~200 km^2 conservancy in a semi-arid Kenyan savanna (0.3° N, 36.9° E, 1,650 m elevation). The region exhibits a weakly trimodal rainfall pattern, with longer rainy seasons from April to May and October to November and a third, shorter wet season in July or August that does not happen every year (Goheen et al. 2013). Mpala maintains a nearly complete community of native large mammalian herbivores (minus rhinoceros, *Diceros bicornis*, *Ceratotherium simum*), pastorally managed livestock herds (mainly cattle, *Bos indicus*), and the full suite of native predators, including painted dogs (*Lycaon pictus*), leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), lions (*Panthera leo*), and spotted hyenas (*Crocuta crocuta*; Goheen et al. 2013; Ford et al. 2014; Ford and Goheen 2015). The dominant large herbivores at Mpala in terms of biomass density are elephant (~3,000 kg), impala (~50 kg), and dik-dik (~5 kg). Dik-dik are by far the most numerically abundant of these species, with densities up to 140 individuals per km^2 (Augustine 2010), and their diets—like those of elephant, giraffe (*Giraffa camelopardalis*), and impala—are dominated by woody plants and forbs (herbaceous non-grasses). Dik-dik have a shoulder height of only ~0.36 m but—despite their short stature—routinely browse vegetation up to ~1 m by stretching their necks and/or standing on their hind legs, especially during wet seasons when they have been observed to eat a greater proportion of fresh leaves compared to fallen leaf litter (Manser and Brotherton 1995; Kingswood and Kumamoto 1996).

The Ungulate Herbivory Under Rainfall Uncertainty (UHURU) experiment was established at Mpala in 2008, using selective fencing to exclude herbivores of different size classes from replicated 1 ha plots on relatively infertile sandy clay loams (Goheen et al. 2013; Alston et al. 2022). We collected plant and dietary DNA data at 2 UHURU sites separated by 13 km, each with 3 replicated blocks (<0.5 km apart) of 3 contiguous herbivory treatments (9 plots per site × 2 sites = 18 plots; Goheen et al. 2013; Alston et al. 2022). Control plots are unfenced and permit all herbivores. Mesoherbivore-exclusion plots ("dik-dik-only") exclude all herbivores larger than dik-dik. Total exclusion plots exclude dik-dik and all other herbivores >2 kg (i.e., everything larger than hares). The plots are located at high-rainfall ("mesic") and low-rainfall ("xeric") sites along a north-south climatic gradient across Mpala. The 3 dominant woody plants across sites are

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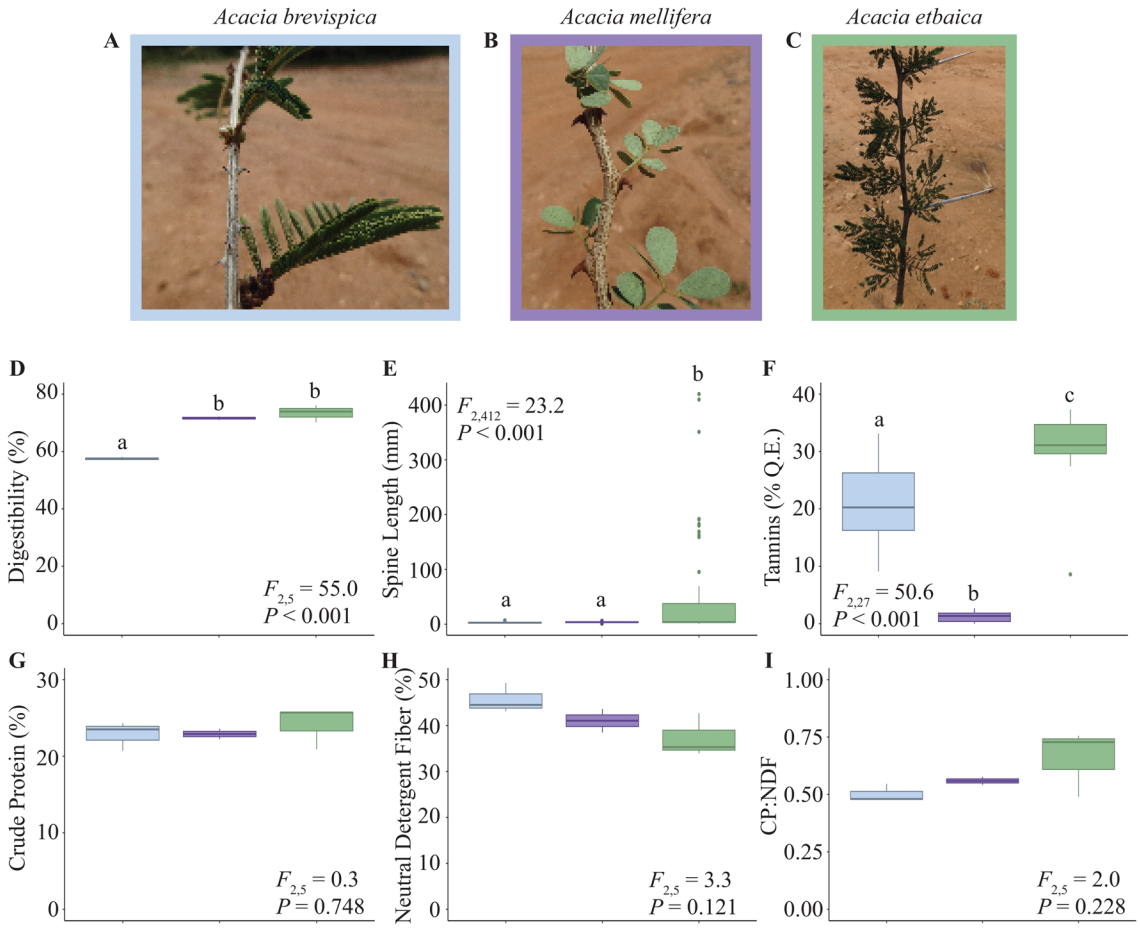

Fig. 1 A to C) Three *Acacia* species are the dominant woody plants at our study site and are prominent components of herbivore diets. D) *Acacia mellifera* and *A. etbaica* had significantly higher digestibility than *A. brevispica*, based on results from ANOVA. E) Spine length was an order of magnitude higher for *A. etbaica*, which has both long, straight spines and small, hooked spines. F) *Acacia etbaica* leaves have significantly higher tannin concentration (% Q.E.), followed by *A. brevispica*, then *A. mellifera*. However, these species did not differ significantly in (G to I) crude protein, neutral detergent fiber, or protein:fiber ratio. Boxes show the interquartile range, the middle line indicates the median, whiskers extend up to 1.5× the interquartile range, and points are shown for outliers that fall ≥1.5× outside the interquartile range. Letters for (D to F) indicate post hoc results from Tukey's honestly significant difference test.

Acacia (*Senegalia*) *brevispica*, *A.* (*S.*) *mellifera*, and *A.* (*Vachellia*) *etbaica* (Fig. 1A to C). On average, the mesic site has ~70% greater standing herbaceous biomass than the xeric site (Alston et al. 2022). To monitor the effectiveness of experimental treatments and quantify herbivore activity levels, our team performs quarterly dung surveys to count and identify all dung along 3 permanent parallel 60 m belt transects (spaced 30 m apart)—crushing each dung pile after identification to prevent recounting (Goheen et al. 2013; Alston et al. 2022).

To test our hypotheses about the effects of dik-dik and other large-herbivore exclusions on vegetation, we leveraged a combination of: (i) single-survey; and (ii) long-term census data from the UHURU experiment. First, to establish the cumulative impacts of herbivore exclusion on vegetation abundance and forage availability over the first ~10 yr of the experiment, we surveyed vegetation in 1 dry season (March 2017) and 1 wet season (December 2018). The goal of these surveys was to quantify the cumulative impacts of herbivore exclusion on both understory and overstory vegetation with a common currency using the canopy-intercept method. We accomplished this by placing an 8 m long telescoping pole (tall enough to extend through the tops of all trees) at each of 49 locations in a 60 × 60 m grid (10 m intervals) and recorded the height and taxonomic identity of all vegetation that touched the pole; we interpret the total number of "hits" per species as an index of relative forage abundance (see Kartzinel and Pringle 2020; Coverdale et al. 2021; Alston et al. 2022). Second, to determine the impacts of dik-dik and large-herbivore exclusion on *Acacia* species sapling abundance, we used long-term census data from the annual UHURU tree counts, in which we record the species and height of every tree along seven 10 × 60 m transects per plot (Alston et al. 2022).

Dietary analysis

We sampled large-herbivore dung in and around the UHURU experiment in consecutive wet (October 2014) and dry (March 2015) seasons, when the experiment had been running for about 7 yr. Dik-dik samples were collected from control (n = 36) and dik-dik-only (n = 46) plots at the same time as elephant (n = 41) and impala (n = 60) samples were collected from areas with similar vegetation surrounding the plots (Kartzinel et al. 2019). To obtain enough samples from wide-ranging elephant and impala near each experimental site, we collected samples for these 2 species in areas around the UHURU plots with similar environmental conditions to control plots, but not necessarily within

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them. The median distance of elephant and impala fecal samples from UHURU plots was ~3 km (range 0 to 8 km). Although dik-dik can move freely between control and dik-dik-only plots, they defecate repeatedly in territorial middens, so we assumed that fresh samples reflected recent foraging by individuals whose territories largely permit foraging inside the same plot.

We employed fecal DNA metabarcoding, which provides finer taxonomic and temporal resolutions than can be achieved using traditional field observations and which is amenable to considerably more replication (Nielsen et al. 2018). To characterize herbivore diets, dung samples were stored in lysis tubes with Zymo Xpedition Lysis/Stabilization Solution. They were homogenized with a vortex and then stored in a –80 °C freezer prior to DNA extraction, which we performed in small batches (12 to 24 samples per batch) using Zymo Xpedition Soil/Fecal MiniPrep kits. We amplified the chloroplast *trn*L-P6 loop using primers *trn*L(UAA)g and *trn*L(UAA)h (Taberlet et al. 2007; Kartzinel et al. 2015; 2019). Single-end sequencing was performed on an Illumina HiSeq 2500 (Supplementary Data SD1). We performed quality control steps using the DADA2 pipeline (Callahan et al. 2016) in R version 4.0.3 (R Core Team 2019) and then identified dietary sequences with reference to an Mpala-specific plant DNA reference library with barcodes for 438 local species (Gill et al. 2019; Freeman et al. 2022) as well as a global reference library downloaded from NCBI (Supplementary Data SD2) using "obitools" (Boyer et al. 2016). We required 100% sequence matching with 1 or both databases to ensure high taxonomic resolution and reliability (Deagle et al. 2019; Littleford-Colquhoun et al. 2022a, 2022b). We then rarefied samples to the minimum sequence read depth ($n = 4{,}845$) using "phyloseq" (McMurdie and Holmes 2013), resulting in the loss of 75 sequences with low relative abundances in the subset of samples in which they occurred. The final dataset consisted of 194 plant taxa and 183 diet profiles. Of these 194 plant taxa, 100% were identified unambiguously to family, 71% to genus, and 66% to species. For all dietary analyses, we calculated relative read abundance (RRA) for each taxon in each sample by dividing by the total number of sequences in each sample ($n = 4{,}845$). The use of RRA in dietary studies has been controversial because of the care required to validate methodologies and the potential for differences in digestibility and/or primer mismatches to skew the data relative to known intake proportions (Nakahara et al. 2015; Scasta et al. 2019; Malik et al. 2024), but recent laboratory and computational advances have consistently demonstrated that it remains useful in comparative studies based on well-established methods, extensive reference libraries, and large sample sizes (Deagle et al. 2019; Littleford-Colquhoun et al. 2022a, 2022b). At Mpala Research Centre, we have previously demonstrated that RRA is strongly correlated with independent measures of grass-browse consumption ratios based on carbon stable isotopes (Kartzinel et al. 2015) and that it can reliably recover both seasonal (Kartzinel et al. 2019) and geographic (Pansu et al. 2022) variation in the diets of diverse herbivores.

Forage quality analyses

To quantify foliar nutrition, we collected green leaf samples from 54 browse (understory and tree) species at Mpala that were found both in dik-dik diets and in the vegetation surveys. For woody plant species, samples were collected from branches at 1 m. Samples were collected across 2 bouts in September 2016 and August 2018. We air-dried the samples for analysis at CropNuts Laboratory in Nairobi, Kenya to quantify 3 traits related to forage quality: percent crude protein (CP) using sulfuric acid digestions (ISO 8968-1); percent neutral detergent fiber (NDF) using acid and alkaline digestion (ISO 6865); and percent neutral cellulase plus gammanase digestibility using near-infrared reflectance spectroscopy (Ramirez et al. 2015). Five of the 54 browse species analyzed could not be differentiated by the *trn*L-P6 marker and thus we attributed species-specific quality data to the first 49 plant taxa and averaged plant quality data from up to 3 closely related species for each of the 5 ambiguous *trn*L-P6 sequences prior to analysis.

We also compared chemical and physical defenses of the 3 dominant *Acacia* species by measuring the leaf tannin content and spinescence. For tannins, we collected mature leaves from branches ~1.5 m above the ground from 10 trees per species, air-dried them, and measured condensed tannin content using an acid-butanol protocol with quebracho as a standard (Ward and Young 2002). For spinescence, we counted the spines in the distal 10 cm of one branch about 1 m above the ground from 10 trees of each species and measured the length of each spine. To test for significant differences in forage quality among *Acacia* species, we ran separate ANOVAs with crude protein, neutral detergent fiber, CP:NDF, digestibility, tannins (% Q.E.), and spine length as the response variables.

Hypothesis testing

We tested the first hypothesis that dik-dik diet composition would differ significantly from those of the numerically dominant larger herbivores, both within and among sites and seasons. To quantify compositional dissimilarity, we calculated pairwise Bray–Curtis distances between each fecal sample using "vegan" version 2.6.4 (Oksanen et al. 2019) in R 4.0.3 (R Core Team 2019). To test for differences in diet composition among species, we performed permutational analysis of variance (perMANOVA) with species, season, and species × season interaction as main effects, including only the subset of dik-dik samples collected from control plots. We then tested whether the experimental exclusion of larger herbivores had a significant effect on dik-dik diet composition using perMANOVA with treatment + site + season as predictor variables.

Because *Acacia* spp. are the locally dominant woody plant taxa and dominant in the diets of browsers and mixed feeders, we tested for spatiotemporal variation in their contributions to herbivore diets at 2 levels. First, we tested for significant differences in the contribution of *Acacia* spp. to the diets of elephants, impala, and dik-dik through space and time. We began by logit-transforming the RRA data to achieve normality of the proportional data for the response variable. Then, we separately tested for significant differences in the RRA of each *Acacia* species in elephant and impala samples obtained in the vicinity of the experimental plots using 6 ANOVAs (1 for each *Acacia* and herbivore species) with the RRA of each *Acacia* species as response variables and with season as a fixed effect. Second, to test for significant differences in mean RRA of each *Acacia* species in dik-dik diets according to experimental treatment, we used a model-selection procedure. We constructed a set of 12 generalized linear mixed models (glmms). The first was a null model that correlated the response variable with 1, indicating no difference in slope or intercept after accounting for block. The other 11 models considered each possible combination of treatment, site, season, and pairwise and 3-way interactions. All models included the experimental block as a random effect. We used corrected Akaike's Information Criterion (AICc) to identify the top model(s) for each response variable based on a ΔAICc value ≤ 2 (Burnham and Anderson 2002). If the null model fell within these criteria, we concluded there was no significant support for a relationship between the model parameters.

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To test our second hypothesis that the absence of larger browsers would lead dik-dik to decrease selectivity for high-quality foliage, we calculated dietary selectivity using Jacobs' D index (Jacobs 1974). Jacobs' D ranges from –1 to 1, with negative values indicating that the food is underrepresented in diets based on its availability in the environment and positive values indicating it is eaten proportionally more than expected based on availability. We tested the effects of treatment, site, and season on dik-dik selectivity for the 3 dominant *Acacia* species. We considered glmms with each possible combination of treatment, site, season, and their interactions (e.g., treatment × site, treatment × season, season × site, and treatment × site × season) with block as a random effect. We compared the results of these selectivity analyses based on plant nutritional quality according to each of the 3 response variables: (i) % crude protein, an indicator of higher forage quality; as well as (ii) % neutral detergent fiber; and (iii) protein:fiber ratio, which are indicators of lower forage quality (Barboza et al. 2010). Each of 7 models, including a null model, was structured with Jacobs' *D* as the response variable and the forage quality metric as the main effect. The models also included combinations of treatment, site, and forage quality × treatment or site interaction as main effects and the experimental block as a random effect. We evaluated the models using AICc, as described above.

Because dik-dik are mobile consumers, they may not spend all of their time foraging in 1 plot within their home ranges, as they can choose to allocate time spent under canopy versus in the open cover according to their perceived risk-reward ratio (e.g., balancing perceived resource availability and predation risk; Ford and Goheen 2015). To test whether diet selectivity estimates were sensitive to the possibility that dik-dik move between experimental plots while foraging, we modeled different assumptions about food plant availability. We scaled the assumed daily availability of each plant species based on its abundance in each plot at the mesic and xeric sites. Then, assuming that dik-dik spend different amounts of their daily foraging time in control vs dik-dik-only plots, we plotted selectivity as a function of % time spent in dik-dik-only such that the slope of the line indicates how sensitive our estimate of selectivity for each plant taxon is to different assumptions about the composition of available plants. We plotted a vertical line at 18% of time spent in dik-dik-only plots, based on findings in Ford and Goheen (2015), which showed that dik-dik spent about 18% of their time under canopy cover and 82% of their time in open areas.

Finally, we tested the third hypothesis that dik-dik would suppress saplings of the 3 dominant *Acacia* species, preventing growth to taller heights (Ford et al. 2015; Otieno et al. 2019). We filtered the UHURU tree census data to include only saplings (≤1 m). Using AICc as described above, we compared 5 glmms for each *Acacia* species with sapling abundance as the response variable. The main factors were treatment, site, and treatment × site interaction. Block was nested within the survey as a random effect.

Results

Plant abundance—and hence food availability—differed significantly according to treatment, site, and season. Grass and understory browse abundances increased with large-herbivore and dik-dik exclusion, and they were ~2× more abundant in the mesic site relative to the xeric site (Supplementary Data SD3). The 3 locally dominant *Acacia* species accounted for 43% to 95% of tree stems in mesic plots and 60% to 98% in xeric plots (Fig. 1A-C); among these, the long-spined *A. etbaica* was by far the most abundant, with a mean abundance 3× that of *A. mellifera* or *A. brevispica* across the experiment. The mean abundance of *A. etbaica* did not differ significantly according to either dik-dik or large-herbivore exclusion. However, mean *A. brevispica* abundance was 8× greater in dik-dik-only plots while mean *A. mellifera* abundance was 2× greater in dik-dik-only plots and 5× greater in total-exclusion plots compared to controls (Supplementary Data SD3).

These 3 dominant *Acacia* spp. had higher mean crude protein content and greater digestibility relative to local browse species (23.3% vs. 21.2% and 67.5% vs. 62.3%, respectively). However, they also exhibited relatively high concentrations of neutral detergent fiber (41.3% vs. 31.5%) and a low protein: fiber ratio (0.57 vs. 0.76; Supplementary Data SD4). These dominant *Acacia* spp. also differed substantially from each other in their forage qualities: *A. mellifera* had high digestibility, short spines, and low tannin concentrations (Fig. 1D to F); short-spined *A. brevispica* was significantly less digestible than the other 2; *A. etbaica* had the strongest defenses with significantly longer spines and higher tannin concentrations (Fig. 1D to F). There were no significant differences among the 3 dominant *Acacia* species in foliar crude protein, neutral detergent fiber, or protein: fiber ratio (Fig. 1G to I).

Consistent with our first hypothesis, dik-dik, impala, and elephant diets differed significantly according to species and season, with diet dissimilarity among species increasing during the dry season (perMANOVA; Fig. 2A). Among the 3 dominant herbivore species, dik-dik diets contained the greatest RRA of the 3 dominant *Acacia* spp. (cumulatively 61%), followed by elephant (53%) and impala (44%; Supplementary Data SD5). Overall, dik-dik diets differed widely across sites and seasons (perMANOVA; Fig. 2B). Moreover, there was a significant effect of treatment on the mean RRA of 2 *Acacia* spp. in dik-dik diets out of the 3 locally dominant *Acacia* spp. that we evaluated (glmm; Table 1; Supplementary Data SD6 to 8). Impala diets converged with dik-dik in the dry season, when the diversity of available plants was limited and short-spined *Acacia* spp. dominated their diets (Fig. 2A; Supplementary Data SD6 to 9). Impala diets contained significantly greater *A. brevispica* RRA during the wet season than the dry season (ANOVA: $F_{1,58}$ = 46.7, R^2 = 0.44, P < 0.001) but did not exhibit significant seasonal differences for *A. mellifera* ($F_{1,58}$ = 2.6, R^2 = 0.03, P = 0.110) or *A. etbaica* ($F_{1,57}$ = 1.1, R^2 = 0.00, P = 0.306; Supplementary Data SD6). Elephants maintained the most consistent diet ratios across seasons, as none of the 3 *Acacia* spp. differed significantly in RRA between seasons (*A. brevispica*, $F_{1,39}$ = 3.2, R^2 = 0.05, P = 0.084; *A. mellifera*, $F_{1,39}$ = 3.5, R^2 = 0.06, P = 0.070; *A. etbaica*, $F_{1,39}$ = 2.5, R^2 = 0.04, P = 0.122; Supplementary Data SD9).

Consistent with our second hypothesis, dik-dik activity increased in the absence of larger browsers, and they increased selectivity for the subset of *Acacia* species with poor physical and chemical defenses. Dik-dik dung density was significantly greater (mean 2.3× higher) in dik-dik-only plots compared to controls (Supplementary Data SD10). Dik-dik diet composition switched from predominantly representing short-spined *A. mellifera* during the dry season to long-spined *A. etbaica* during the wet season, especially in the xeric site (Supplementary Data SD8). The RRA of short-spined *A. brevispica* in dik-dik diets was greater in control plots during the dry season and in dik-dik-only plots during the wet season (Supplementary Data SD8). At mesic sites, *A. mellifera* RRA was greater in dik-dik-only sites during the dry season and in control plots during the wet season (Supplementary Data SD8). Finally, there was a significant correlation between dik-dik diet selectivity and 3 measures of resource quality, such that Jacobs' D was strongly and positively correlated with the crude protein and neutral detergent fiber of food species (glmm; Fig. 3; Table 2; Supplementary Data SD11). However, Jacobs' *D* was negatively correlated with

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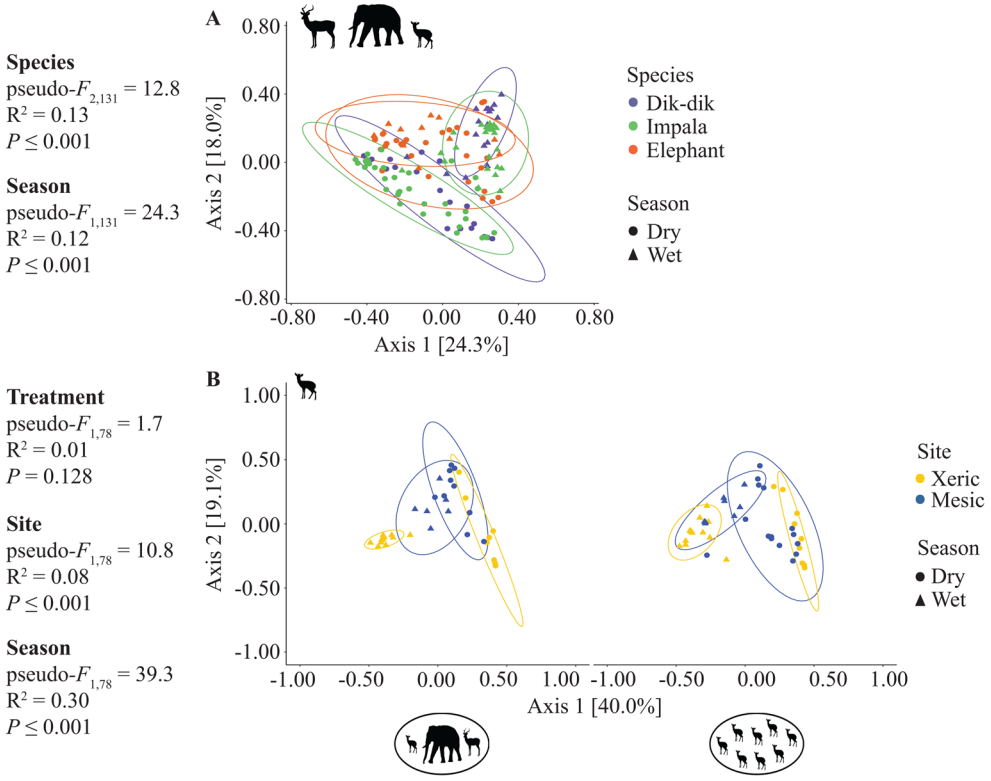

Fig. 2 Spatiotemporal dietary variation (A) among species and (B) among individual dik-dik. Ordinations were generated from principal component analysis using Bray–Curtis dietary dissimilarity and show the percent of variation attributable to each axis; permutational MANOVA results are shown on the left. A) Dik-dik, impala, and elephant diet composition differed significantly despite strong seasonal variation, with dik-dik dietary RRA being most similar to impala in each season. B) Dik-dik exhibited significant intraspecific variation in diet composition across UHURU sites and seasons, but diet composition did not differ significantly according to treatment. To aid visualization of point clouds associated with similar diets in each treatment, we split the ordination presented in panel B according to treatment (left = control; right = large-herbivore exclusion).

protein: fiber ratio and not significantly correlated with digestibility. Supporting the hypothesis that selectivity is relaxed following competitive release, selectivity for plants based on their crude protein content, neutral detergent fiber value, and their protein:fiber ratio was significantly greater in control plots relative to the dik-dik-only plots (Table 2).

Dik-dik selectivity for the 3 dominant *Acacia* spp. differed significantly across sites, treatments, and seasons (glmm: Fig. 4; Table 1; Supplementary Data SD12). Selectivity for short-spined *A. brevispica* was significantly stronger in control plots relative to dik-dik-only plots in the wet season relative to the dry season. There was a significant treatment × site interaction in which selectivity was stronger in mesic control plots relative to mesic dik-dik-only plots (Table 1). Seasonal selectivity shifted as well, with selectivity for short-spined *A. mellifera* increasing significantly in the dry season but selectivity for long-spined *A. etbaica* increasing in the wet season. Selectivity for *A. mellifera* was also greater in dik-dik-only plots. There was a significant site × season interaction in selectivity for both *A. mellifera* and *A. etbaica*—dik-dik selected most strongly for *A. mellifera* in the dry season, and the effect was strongest in the xeric site. Conversely, dik-dik selected most strongly for *A. etbaica* in the wet season, where again the effect was strongest in the xeric site. Finally, since we could not precisely determine the amount of time dik-dik spent in control vs dik-dik-only plots, we modeled the impact of that uncertainty on our results and found that the selectivity estimates were generally robust to this source of uncertainty (Supplementary Data SD13).

Consistent with our third hypothesis, releasing dik-dik from competition with larger herbivores resulted in a significant decrease in the abundance of *Acacia* spp. saplings (glmm: Fig. 5; Table 3; Supplementary Data SD14). This trend was especially strong for short-spined and strongly-selected *A. mellifera*, which were significantly more abundant in total exclusion than in dik-dik-only plots. *Acacia etbaica* saplings were significantly more abundant in both dik-dik-only and total exclusion treatments relative to controls. There was a significant treatment × site interaction in which elephant suppression of *A. mellifera* was stronger in the mesic site relative to the xeric site. In the mesic site, dik-dik had a seemingly facilitative impact on *A. etbaica*, the food species that they typically avoided, given that these saplings were significantly less abundant in total exclusion plots compared to control and dik-dik-only plots.

Discussion

We found strong and significant differences in dik-dik diet composition and apparent selectivity in response to the experimental exclusion of larger herbivores, with important variation across seasons and environments (Fig. 4). These dietary shifts, coupled with increased dik-dik activity following the removal of larger competitors (Supplementary Data SD10), provide strong evidence that dik-dik were released from competition for food resources by larger herbivores. Dik-dik exhibited substantial dietary variation, allowing them to seek and obtain forage on the basis of protein concentrations within their home ranges even as local environmental conditions modulated the abundance and diversity of available foods (Fig. 2; Owen-Smith and Novellie 1982; Potter et al. 2022). They strongly selected for the 2 short-spined *Acacia* species, especially when the availability of these *Acacia* species was limited through competition with larger herbivores (Fig. 4).

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Table 1 Top model(s) for the RRA and Jacobs' D selectivity index for each of the 3 locally dominant *Acacia* species in dik-dik diets.

Species	Model		Coefficients ± SE						
		R^2	Treatment	Site	Season	Treatment × site	Treatment × season	Site × season	Treatment × site × season
Dik-dik diet RRA									
Acacia brevispica	Season	0.14			–0.91 ± 0.24***				
	Treatment × season	0.18	–0.62 ± 0.33		–1.47 ± 0.36***		0.96 ± 0.47*		
	Site + season	0.17		–0.34 ± 0.43	–0.88 ± 0.25**				
Acacia mellifera	Treatment × site × season	0.55	1.15 ± 0.44*	2.07 ± 0.70**	0.09 ± 0.57	–0.61 ± 0.68	–2.23 ± 0.73**	–3.09 ± 0.76***	1.57 ± 1.00
Acacia etbaica	Site × season	0.75		–0.74 ± 0.64	1.90 ± 0.33***			2.99 ± 0.45***	
Dik-dik diet selectivity									
Acacia brevispica	Treatment	0.24	–0.55 ± 0.11***						
	Treatment × site	0.32	–0.24 ± 0.15	0.49 ± 0.29		–0.54 ± 0.21*			
	Treatment + season	0.30	–0.61 ± 0.11***		–0.21 ± 0.10*				
Acacia mellifera	Treatment × site × season	0.44	0.40 ± 0.19*	0.04 ± 0.34	–0.77 ± 0.18***	–0.19 ± 0.27	–0.16 ± 0.24	1.13 ± 0.28***	–0.96 ± 0.36*
Acacia etbaica	Site × season	0.66		0.13 ± 0.13	0.92 ± 0.08***			–0.67 ± 0.11***	

The table shows results from the subset of generalized linear mixed models with a ΔAICc ≤ 2. We show the R^2 and coefficients (± standard error) for each model and predictor variable combination. Treatment coefficients indicate how much the RRA of or selectivity for each *Acacia* species increases or decreases in dik-dik-only plots compared to control plots, with positive values indicating greater RRA or selectivity in dik-dik-only plots. Site coefficients show how selectivity differs in mesic sites compared to xeric sites, with positive values indicating greater RRA or selectivity in the mesic site. Season coefficients show how selectivity differs in the dry season relative to the wet season, with positive values indicating greater RRA or selectivity in the wet season. Asterisks indicate the *P*-value for each predictor based on glmm results (*$P < 0.05$. **$P < 0.01$. ***$P < 0.001$). The table is organized in blocks for RRA and selectivity.

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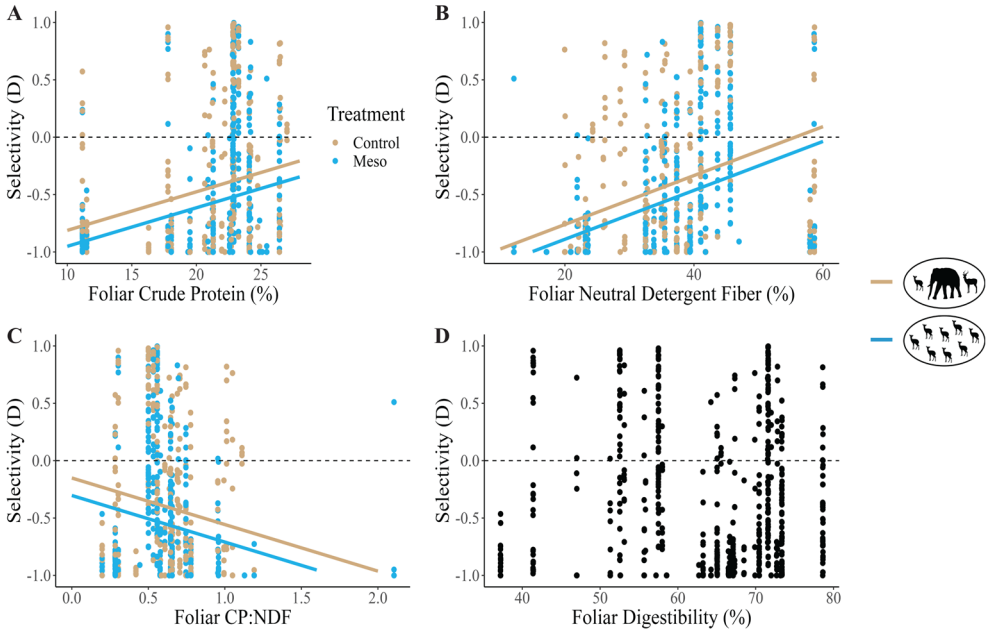

Fig. 3 Jacobs' D selectivity index in relation to 4 metrics of forage quality in dik-dik diets. Selectivity was positively correlated with (A) crude protein and (B) neutral detergent fiber but negatively correlated with (C) protein-to-fiber ratio. The top glmm based on ΔAICc for A-C was forage quality + treatment, and selectivity for/against each quality metric was higher in the control treatment than in large-ungulate exclosures, though selectivity was negative in all cases. D) The top model for digestibility was the null, indicating no strong relationship (Supplementary Data SD11). Each point represents dik-dik selectivity for an individual plant taxon. Each plant taxon has 2 points, 1 for each treatment. The dashed horizontal line indicates no selectivity.

Table 2 Top model(s) for Jacobs' D selectivity index with regards to the forage quality of food species in dik-dik diets.

Forage metric	Model	R^2	Coefficients ± SE	
			Forage metric	Treatment
Crude protein (CP) (%)	CP + treatment	0.06	0.03 ± 0.00***	−0.14 ± 0.04**
Neutral detergent fiber (NDF) (%)	NDF + treatment	0.15	0.02 ± 0.00***	−0.13 ± 0.04**
CP:NDF	CP:NDF + treatment	0.06	−0.41 ± 0.06***	−0.15 ± 0.04***
Digestibility (%)	Null			

*The table shows results from the subset of models with a ΔAICc ≤ 2; only one model per forage metric fit this criterion. We show the R^2 and coefficients (± standard error) for each model and predictor variable combination. Forage metric coefficients indicate how much selectivity increases or decreases with the forage quality metric in that model, while treatment coefficients indicate how much greater or less selectivity is in the total exclusion plots are relative to control plots. Asterisks indicate the *P*-value for each predictor based on glmm results ($P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$).

From prior work, we expected that megaherbivores, especially elephants, would strongly limit *Acacia* spp. growth, survival, and recruitment (Laws 1970; Gordijn et al. 2012) and that excluding them would likely increase *Acacia* spp. abundance. Further excluding dik-dik in addition to large herbivores enhanced the increase in *Acacia* spp. abundance, especially at lower height classes where foraging by short dik-dik is concentrated (Fig. 5). One potential mechanism by which large herbivores (especially elephants) could alter dik-dik selectivity is by breaking branches and creating associational refuges that protect otherwise poorly-defended forbs (Coverdale et al. 2016). Alternatively, elephants knocking down trees may move browse to lower height classes, making them more accessible for small browsers such as dik-dik (Kohl et al. 2011). The degree to which dik-dik suppressed *Acacia* spp. was strongest for their most selected food—the low-tannin, short-spined *A. mellifera*—which was comparatively more prominent in the plant community in the presence of larger herbivores (Fig. 5), consistent with evidence that dik-dik preferentially consume low-tannin forage (Otieno et al. 2019).

The apparent decrease in dik-dik selectivity following large-herbivore exclusion contrasts with predictions from optimal foraging theory, which maintains that animals should be able to select more strongly for their preferred foods when competition is reduced (MacArthur and Pianka 1966). One potential reason that our results may contrast with these predictions is that even though interspecific competition on dik-dik is reduced when large herbivores are excluded, the subsequent increase in dik-dik activity could lead to an increase in intra-specific competition (Svanbäck and Bolnick 2007). Another potential reason that selectivity decreased is that, in addition to changing the availability of food resources, elephants also change the diversity and accessibility of plant species across the habitat (Coverdale et al. 2016). Consequently, dik-dik diet breadth may be constrained when the full suite of herbivores is present because larger herbivores deplete shared resources, especially during dry seasons or in xeric environments.

Plant nutrition and physical defenses such as spines may further shape foraging selectivity. Selection by dik-dik for plants with weak physical defenses increased in the absence of larger herbivores (Fig. 5A and B). Despite the lack of significant differences in crude protein and neutral detergent fiber amongst the 3 acacia species (Fig. 1G to I), relatively high tannin concentrations in *A. etbaica* and *A. brevispica* could render crude protein less accessible than it is in *A. mellifera*, making the latter the most palatable choice (Robbins et al. 1987; Kumar and Vaithiyanathan 1990). Future work could help further resolve the patterns of selectivity that we observed by investigating variation in other classes of defensive compounds, such as volatile organic compounds (VOCs, e.g., monoterpenes; Schmitt et al. 2020).

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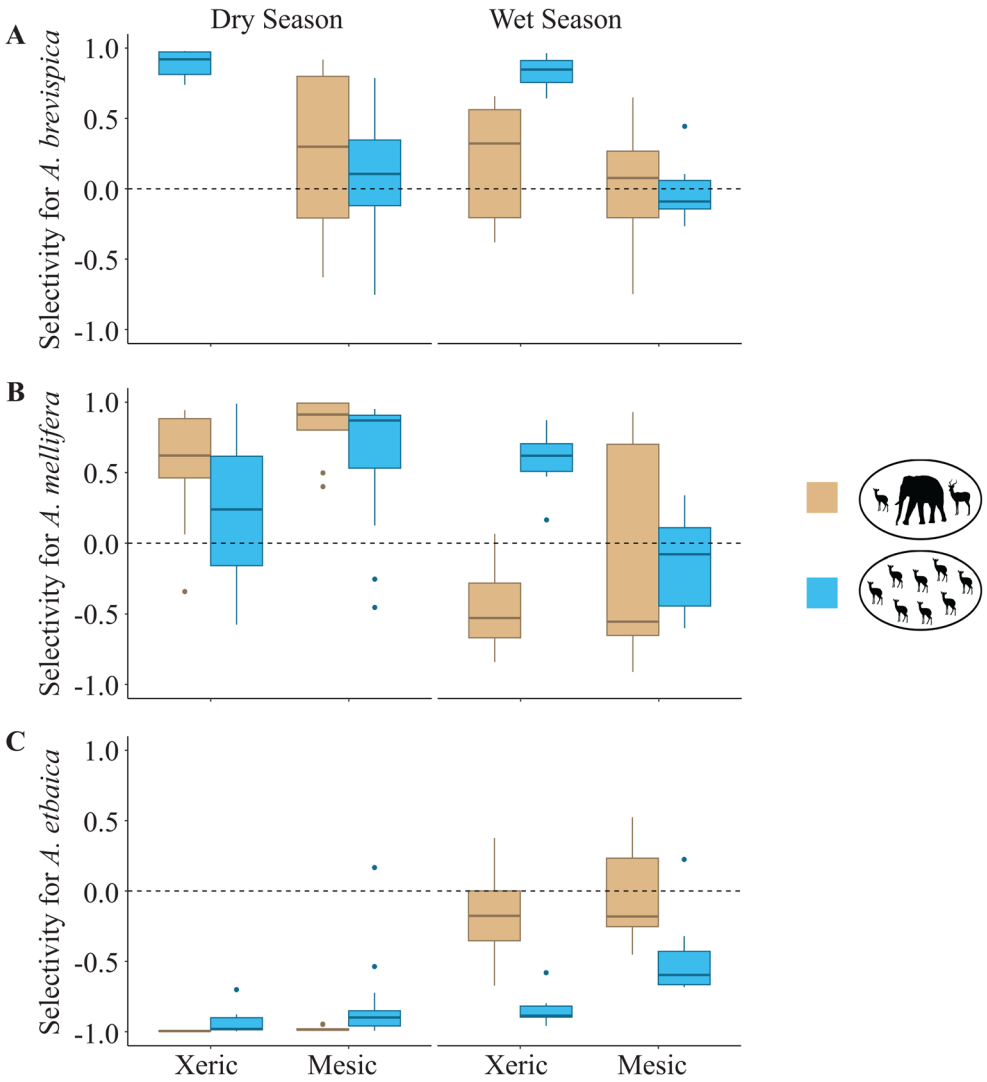

Fig. 4 Diet selectivity for dik-dik populations. Positive values of Jacobs' *D* indicate selection for and negative values indicate avoidance of each of the 3 dominant *Acacia* species (glmm; Supplementary Data SD12). A) Selectivity for short-spined *A. brevispica* was greatest in mesic control plots. Selection for *A. brevispica* is not reported in the xeric control plot due to its exceedingly low abundance in those plots. B) Selectivity for short-spined *A. mellifera* was higher in dik-dik-only sites during the dry season and in the control mesic site during the wet season. C) Dik-dik largely avoided *A. etbaica*, as shown by the negative selectivity values. However, they avoided it less during the wet season, especially in xeric sites. Boxes show the interquartile range, the middle line indicates the median, whiskers extend up to 1.5× the interquartile range, and points are shown for outliers that fall ≥1.5× outside the interquartile range.

Typically, dik-dik and other small browsers are regarded as more selective than larger species and mixed-feeders (e.g., elephant, impala; Fig. 2A). Mixed-feeders are generally expected to have greater diet flexibility across different environmental conditions, as they can switch between grazing on grasses and browsing on other resources as needed (Staver and Hempson 2020). However, many species that are canonically associated with other diet categories may nevertheless exhibit equally profound seasonal dietary changes, given that "grass" and "browse" are 2 plant categories that collectively represent tremendous taxonomic, phylogenetic, and functional diversity (Kartzinel and Pringle 2020; Hoff et al. 2025). Indeed, although dik-dik did not—and were not expected to—follow the diet-switching pattern of increasing grass consumption during the wet season as mixed-feeders do, they were nevertheless attuned to the phenology of the 3 dominant *Acacia* species (and local floras more generally) as the RRA of these dominant resources varied dramatically through time. The extent of diet-switching by dik-dik was more profound at the xeric sites where seasonal variation in food species availability was greatest—corresponding with prior observations of the environmental conditions that promote extensive diet-switching by mixed-feeders (Figs. 3 and 4; Manser and Brotherton 1995; Codron et al. 2011; Owen-Smith and Novellie 1982; Potter et al. 2022). In cases where the effects of wildlife extirpation on local food availability might occur at spatial extents that exceeded dik-dik home ranges, we would expect both foraging behavior and diet composition to change in tandem (Daskin et al. 2023). Further research on plant nutrition and how browsers select for it could help clarify mechanisms by which the diversity of plants and large mammalian herbivores are linked across African savannas.

Although directly documenting competitive interactions between consumer populations ideally entails measuring the effect of a species on the abundance or population growth rate of another (MacArthur and Levins 1967), which we were unable to do in this experiment, the patterns of dietary shifts that we observed are highly consistent with a scenario in which larger browsers competitively limit the foods

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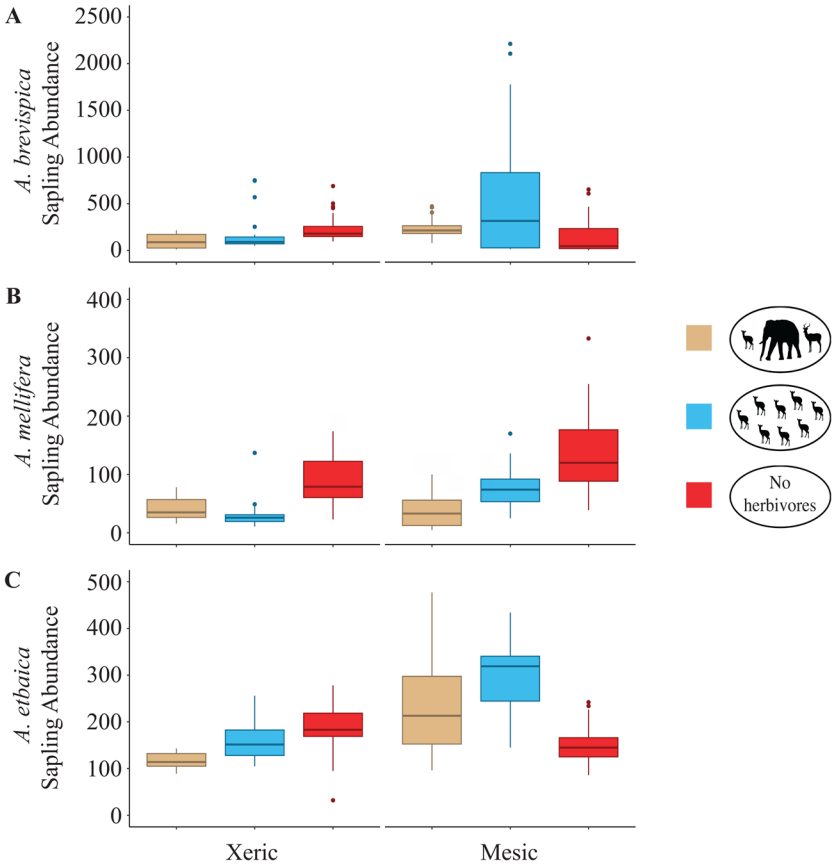

Fig. 5 Abundance of tree saplings (<1 m) across *Acacia* species, sites, and treatments. A) *Acacia brevispica* sapling abundance was overall higher in mesic sites compared to xeric sites, though the opposite was true within total exclusion plots (glmm; Table 3; Supplementary Data SD14). B) *Acacia mellifera* saplings were more abundant in total exclusion plots than dik-dik-only plots, indicating that dik-dik strongly suppressed this preferred food. Elephants suppressed *A. mellifera* saplings as well, but the effect was stronger in mesic sites. C) Long-spined *A. etbaica* were suppressed by elephants and dik-dik in xeric sites. However, in mesic sites, they were more abundant in control and dik-dik-only plots than in total exclusion plots, indicating that large herbivores had a facilitative effect on saplings of this species. Boxes show the interquartile range, the middle line indicates the median, whiskers extend up to 1.5× the interquartile range, and points are shown for outliers that fall ≥1.5× outside the interquartile range. Note that the *y*-axis scales differ depending on the abundance of saplings from each of the 3 species.

Table 3 Top model(s) for effects of experimental dik-dik and large-herbivore exclusions on the abundance of saplings for each *Acacia* species.

			Coefficients ± SE				
***Acacia* species**	**Model**	R^2	**Treatment (dik-dik-only)**	**Treatment (total exclusion)**	**Site**	**Treatment (dik-dik-only) × site**	**Treatment (total exclusion) × site**
Acacia brevispica	Treatment × site	0.23	66.00 ± 77.09	138.89 ± 77.09	141.11 ± 133.73	266.56 ± 109.02*	−232.22 ± 109.02*
Acacia mellifera	Treatment × site	0.46	−10.44 ± 9.89	48.63 ± 9.89***	−4.56 ± 16.40	54.70 ± 14.00***	54.56 ± 14.00***
Acacia etbaica	Treatment × site	0.58	47.05 ± 14.00**	65.96 ± 13.55***	116.04 ± 39.55**	14.25 ± 19.49	−144.96 ± 19.16***

[a]The table shows results from the subset of models with a ΔAICc ≤ 2; only 1 model per *Acacia* species fit this criterion. We show the R^2 and coefficients (± standard error) for each model and predictor variable combination. Treatment coefficients indicate how much acacia sapling abundance increases or decreases in total dik-dik-only and total-exclusion plots compared to control plots. Site coefficients show how sapling abundance differs in mesic sites compared to xeric sites. Asterisks indicate the *P*-value for each predictor based on glmm results ($P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$).

preferred by dik-dik and confine them to suboptimal diets (Fig. 4; Supplementary Data SD9). Further experiments are needed to understand both the direct and indirect mechanisms by which this competition plays out, including differences in predation risk for dik-dik (both real and perceived; Ford et al. 2014; Ford and Goheen 2015; Wells et al. 2021). Yet large herbivore populations are declining across much of Africa (Ripple et al. 2015), and thus our data provide rigorous experimental evidence concerning the potential for competitive release of smaller species to amplify the resulting alteration of ecosystem structure. In this case, the smaller browser created a browse trap (Staver and Bond 2014; Hegland et al. 2021; Palmerlee et al. 2025) with the potential to strongly inhibit future recruitment of a previously dominant overstory species. Our research sheds light on how small browser foraging behavior can amplify the long-term consequences of megaherbivore losses on savannas, potentially leading to long-term decreases in vegetation diversity.

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Author contributions

Courtney Reed (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft, Writing—review & editing), Loren Albert (Data curation, Writing—review & editing), Chrishen Gomez (Formal analysis, Writing—review & editing), Ali Hassan (Data curation), Sam Kurukura (Data curation), Paul M. Musili (Data curation), Maria Stahl (Data curation), David M. Ward (Data curation, Methodology, Writing—review & editing), Truman P. Young (Data curation, Methodology, Writing—review & editing), Todd Palmer (Conceptualization, Writing—review & editing), Jacob R. Goheen (Data curation, Investigation, Resources, Writing—review & editing), Robert Pringle (Conceptualization, Data curation, Investigation, Resources, Writing—review & editing), and Tyler Kartzinel (Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing—original draft, Writing—review & editing)

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1. Text providing additional methodological details on fecal DNA extraction and sequencing methods.

Supplementary Data SD2. Text providing additional methodological details on DNA metabarcode processing and identification.

Supplementary Data SD3. Figure showing grass, understory browse, and *Acacia* spp. abundance across sites and treatments.

Supplementary Data SD4. Figure showing distributions of nutrient concentrations across browse taxa.

Supplementary Data SD5. Figure showing diet composition for dik-dik, impala, and elephants.

Supplementary Data SD6. Table showing model selection for RRA of the three dominant *Acacia* species in elephant and impala diets.

Supplementary Data SD7. Table showing model selection for RRA of the three dominant *Acacia* species in dik-dik diets.

Supplementary Data SD8. Figure showing dik-dik RRA values for three dominant *Acacia* species.

Supplementary Data SD9. Figure showing impala and elephant RRA values for three dominant *Acacia* species.

Supplementary Data SD10. Figure showing dik-dik dung abundance across treatments.

Supplementary Data SD11. Table showing model selection for dik-dik selectivity for forage quality.

Supplementary Data SD12. Table showing model selection for dik-dik selectivity for three dominant *Acacia* species.

Supplementary Data SD13. Figure showing sensitivity of selectivity results based on the amount of time dik-dik are assumed to spend foraging in control vs. dik-dik-only plots.

Supplementary Data SD14. Table showing model selection for effects of dik-diks and large herbivores on saplings of three dominant *Acacia* species.

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Conflict of interest

The authors declare no conflict of interest.

Data availability

UHURU plot coordinates, rainfall, vegetation, and dung data have been previously published in Alston et al. (2022). Raw Illumina sequence reads for impala, elephant, and control dik-dik samples are from Kartzinel et al. (2019) and are available on the Dryad Digital Repository (DOI: 10.5061/dryad.c119gm5). Raw sequence files for dik-dik samples from dik-dik-only plots plus diet composition, plant nutrition, and plant defense data are available on Dryad, as are scripts used for analysis (https://doi.org/10.5061/dryad.2rbnzs832).

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