

# Would East African savanna rodents inhibit woody encroachment? Evidence from stable isotopes and microhistological analysis of feces

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It is well established that massive consumption of plants by the abundant and diverse assemblage of savanna ungulates in East Africa competitively suppresses the native guild of herbivorous to omnivorous small mammals. An important role of woody plant suppression in the Acacia-dominated savannas for this guild of rodents, when released from ungulate competition, has been demonstrated only recently, but without direct evidence of which species are involved. In an effort to establish which of the common species in this guild are most likely to impact growth of trees and forbs, as opposed to grasses or insects, or both, I present data on atomic and isotopic ratios of fecal carbon and nitrogen from 8 commonly occurring muroid rodents from savanna and bush habitats on the Laikipia Plateau of central Kenya: Acomys percivali, Acomys wilsoni, Aethomys hindei, Arvicanthis niloticus, Mastomys natalensis, Mus spp. (thought to be mostly M. minutoides), Saccostomus mearnsi, and Gerbilliscus robustus. In this region where all grasses are  $C_4$  and all trees and other nongrasses are  $C_3$ , different ratios of  $^{13}C$ :  $^{12}C$  ( $\delta^{13}C$ ) in plant tissues give pure grazers, pure browsers, and mixed-feeding herbivores distinctive carbon isotope signatures. Degree of omnivory is revealed by C:N and, arguably, by  $\delta^{15}N$ , but the latter is influenced by dietary protein quality and varies widely by plant species and soil type. Joint consideration of stable-isotope data, total C:N, and microhistological analysis of feces allowed better resolution of dietary niche of each species than any of these data sets could, alone. Grass was either coequal to browse (dicots) or dominated the plant portion of each species' diet, which was somewhat unexpected given rodents' hypothesized role in limiting Acacia recruitment. All species consumed some arthropods. A. niloticus, the only diurnal species, was the most herbivorous, being largely a grazer. S. mearnsi, A. hindei, and M. natalensis were mixed-feeding (grass-browse) herbivores. Mus spp. and Acomys spp. were omnivores whose plant components were largely grass. G. robustus was primarily an insectivore-omnivore whose smaller plant component was grass. Both S. mearnsi and A. niloticus displayed a significant increase in proportion of C<sub>4</sub> grasses in the diet in periods following significant rains, a pattern previously documented from  $\delta^{13}C$  diet studies in large mammalian herbivores. Fecal  $\delta^{15}N$  was significantly higher for rodents that consumed more grass and for rodents released from competition with ungulates, suggesting a partial mechanism for that competitive release. S. mearnsi, followed by A. hindei and M. natalensis, were most likely to feed on woody dicots including Acacia.

Key words: browse, diet, herbivore, insectivore, muroid rodents, omnivore, savanna, stable isotopes

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Studies of trophic and landscape dynamics of the Acaciadominated savannas of East Africa have focused extensively on the diverse and abundant populations of large mammalian herbivores as the dominant consumers of plant productivity (Gwynne and Bell 1968; Wilsey 1996) and shapers of the savanna–bush landscape mosaic (Augustine and McNaughton 2004; Bond et al. 2001). Among many grazers and mixed feeders, this assemblage also includes several pure browsers, such as dik-dik (*Madoqua kirkii*—Augustine and McNaughton 2004), black rhinoceros (*Diceros bicornis*), giraffe (*Giraffa camelopardalis*), gerenuk (*Litocranius walleri*), lesser kudu (*Tragelaphus imberbis*), and eland (*Taurotragus oryx*—Cerling et al. 2003; Kingdon 2004), which along with elephants (*Loxodonta africana*) are known to preserve open savanna habitats by suppressing or reversing woody encroachment (e.g., Bond et al. 2001). Resource limitation and diffuse competition from large mammalian herbivores suppresses populations of small mammals (Sinclair 1972); the latter have

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been shown to increase when large mammalian herbivores are experimentally excluded (Keesing 1998b) and can increase 20-fold in zones outside of protected areas where wild ungulates have been depleted (Caro 2002).

Trophic relations of the smallest mammalian herbivores are comparatively understudied, but they have been implicated variously as seed predators (Holmes 1990), seed dispersers (Midgely and Anderson 2004), or seedling predators (Belsky 1984), especially of woody plants. When and where ungulate populations are depressed (see du Toit and Cumming 1999), small savanna rodents may limit Acacia sp. recruitment by seed or seedling predation, or both (Goheen et al. 2004, 2010; Maclean et al. 2011; Prins and van der Jeugd 1993). However, studies have found that insects played a far greater role than rodents in Acacia seedling predation (Shaw et al. 2002) and that birds and insects, in that order, were more important predators of Acacia seeds than were rodents (Linzey and Washok 2000). Many East African rodents include insects in their diets (Kingdon 2004), suggesting an indirect effect of rodents facilitating woody encroachment. If this is predominantly the case, then encroachment of Acacia spp. and other woody plants may be inevitable following a decline of large herbivores. Also, many rodent species are folivores of savanna grasses, although folivory may be an alternate strategy in some savanna rodents that facilitates coexistence within granivore guilds when seed resources are limiting (Kinahan and Pillay 2008).

However, if certain rodents are important browsers or treeseed predators, increased densities of them may be able to maintain (or slow the loss of—Maclean et al. 2011) the open savanna end of the savanna–bush habitat continuum (but perhaps less so if wild ungulates are replaced by cattle [see Goheen et al. 2010]). The net effect also may be mediated by dietary shifts between wet and dry seasons, if rodents' foraging behavior mirrors that of mixed-feeding ungulates, which increase grass consumption following rains (Augustine and McNaughton 2004).

Numerous studies have examined the natural diets of African ungulates; these have recently included analysis of stable isotope ratios of carbon (e.g., Augustine and McNaughton 2004; Cerling et al. 2003). Carbon isotope analysis allows inference of the proportion of grass relative to browse in the diet when applied to feces, hair, tooth enamel, or other tissues, especially in regions such as the Laikipia Plateau of central Kenya where grasses are all  $C_4$  and non-grasses are  $C_3$ . These 2 CO<sub>2</sub> assimilation pathways result in substantially different ratios of carbon isotopes ( $^{13}C$ : $^{12}C$  or  $\delta^{13}C$ ) in plant tissues (Tieszen et al. 1979), which gives pure grazers, pure browsers, and mixed-feeding herbivores distinctive carbon isotope signatures (Augustine and McNaughton 2004; Kelly 2000). Further, analysis of stable isotope ratios of nitrogen (<sup>15</sup>N:<sup>14</sup>N or  $\delta^{15}$ N) from these same tissues has been used to infer forage nutritional quality and trophic position when analyzing omnivores or carnivores (Post 2002; Sutoh et al. 1987). C:N content of tissues decreases significantly from plant to herbivore, and less so, but still significantly, from herbivore

to predator in arthropods (Fagan et al. 2002), and C:N content of rodent feces should mirror this decrease as their diets shift from mostly plant to mostly insect. In a mammalian herbivoreomnivore (swine [Sus scrofa]) C:N of feces declined with declining fiber content and increasing digestible protein content of a varied, controlled diet (Vu et al. 2009). The amount of enrichment (or "discrimination" or "fractionation" [see Phillips 2012]) of the <sup>15</sup>N isotope by the animal's digestion and metabolism, relative to the  $\delta^{15}N$  of the ingested diet in mammals and birds, was more related to dietary quality (i.e., the degree of match between the amino acid composition of the absorbed dietary protein and the animal's requirements) than it was to quantity of protein ingested (Robbins et al. 2005), suggesting that  $\delta^{15}N$  may not provide as clear a signal of trophic position as previously thought. Further, mean  $\delta^{15}N$  of nonwoody dicots on the Laikipia Plateau of Kenya was 3.5% higher than that of woody dicots, with grasses (monocots) being intermediate, but closer to the latter (all from a single soil type—Fox-Dobbs et al. 2010).

In contrast to the ungulates, relatively few studies have assessed the natural diets of the diverse assemblage of muroid rodents that share savanna and bush habitats with large mammalian herbivores, and none to my knowledge that has employed stable isotope analysis. Such information will reveal which rodent species most likely would play a role in inhibiting woody encroachment following decline or extirpation of browsing ungulates (the latter caused especially by the spread of pastoralism-du Toit and Cumming 1999). The majority of African muroid rodents have been described as omnivores, with the diet often including arthropods, and the plant portion varying from foliage to seeds to other plant parts (Kingdon 2004). I present data on carbon and nitrogen isotope ratios and C:N of fecal pellets, and a small sample of hairs, from Acomys percivali, Acomys wilsoni, Acomys sp. or hybrid, Aethomys hindei, Arvicanthis niloticus, Mastomys natalensis, Mus spp. thought to be largely M. minutoides, Saccostomus mearnsi, and Gerbilliscus robustus from bush and savanna habitats in the Laikipia Plateau of central Kenya. All are in the super family Muroidea (Steppan et al. 2004). For comparison, I include a small sample of feces from the dormouse (Graphiurus sp.; Rodentia: Myoxidae) and the rufous elephant shrew; Macroscelidea: Macroscelididae), both of which are reported to be mostly insectivorous (Kingdon 2004). For an independent assessment of diet of each muroid species, I also performed microhistological analysis of feces.

Oguge (1995) reported these same species of *Mastomys*, *Mus*, and *Gerbilliscus* in Kenya as omnivorous but mainly granivorous. This agrees with studies of sister species of these genera from elsewhere in East Africa and in southern Africa; some *Gerbilliscus* species have been found to be more insectivorous (Monadjem 1997; Odhiambo et al. 2008). Studies of *S. mearnsi* in the Laikipia region of Kenya showed it to feed on dicot foliage and arthropods with a shift toward granivory following the rains (Keesing 1998a). *Arvicanthis* sp., the grass rat, has been described as a grazer (Kingdon 2004) and a mixed-feeding folivore–granivore (Gebresilassie et al. 2004); A. niloticus, the only diurnal species among the muroid rodents I studied, was found to be a specialist grazer in the Serengeti (Sinclair 1972). Arvicanthis testicularis (= niloticus) in northern Nigeria, was found to be more of a generalist omnivore, including browse, seeds, and insects in the diet (Rabiu and Fisher 1989), whereas Arvicanthis dembeensis (= niloticus) in Ethiopia was found to prefer monocot foliage and seeds, with some insects taken (Gebresilassie et al. 2004). Aethomys sp. has been described as an omnivore favoring either foliage or seeds (Monadjem 1997; Perrin and Curtis 1980). Aethomys chrysophilus and M. natalensis have both been described as granivore-herbivores based on stomach contents (Monadjem 1997); M. natalensis had fewer gut adaptations for folivory and showed a stronger preference for seeds than 4 other muroids in South Africa (Kinahan and Pillay 2008). No direct diet studies of African Acomys species are known to me, although Acomys sp. in Israel are known to consume seeds, foliage, snails, and arthropods, with a preference for the latter (Kronfeld-Schor and Dayan 1999). The digestive and dental morphologies of Acomys spinosissimus of southern Africa were among the least adapted to folivory of the 19 muroid species studied by Perrin and Curtis (1980), similar to those of 2 species of Gerbilliscus (= Tatera).

# MATERIALS AND METHODS

Study area and field collection.-Sampling centered on the 19,000-ha Mpala Ranch and Conservancy (MRC), which is located on the Laikipia Plateau of central Kenya, approximately 45 km west of Nanyuki, at 1,600-1,800 m elevation (0°17'N, 36°53'E). Two major habitat types exist in the area: atop the plateau are poorly drained volcanic vertisols ("black-cotton" soil) that support a savanna grassland dominated by Acacia drepanolobium (swollen- or whistlingthorn acacia) and grasses including Themeda triandra, Pennisetum stramineum, P. mezianum, Brachiaria lachnatha, Lintonia nutans, and Agrostis sp., and forbs Aerva lanata, Rhinacanthis ndorensis, Indigofera spp., Dyschoriste radicans, and Commelina spp. (Young et al. 1998); and on the escarpment to the east are red, sandy loam soils that are more densely bushed with a wider variety of woody species, dominated by Acacia mellifera, A. etbaica, A. brevispica, and Grewia tenax, with a discontinuous understory layer dominated by the grasses Digitaria milanjiana, Cynodon dactylon, Pennisetum mezianum, and P. stramineum (Augustine and McNaughton 2004). Rainfall averages 500 mm per annum and is weakly trimodal, with a major peak in April-May and minor peaks in August and October-November.

I livetrapped small mammals using collapsible Sherman traps  $(23 \times 9 \times 8 \text{ cm}; \text{H. B. Sherman Traps, Inc., Tallahassee, Florida) set in grids or transects with 10-m spacing. Traps were baited with cracked maize and wheat kernels. Fecal samples were collected from traps and from animals only upon an animal's 1st capture (all animals were marked with metal ear tags or indelible ink upon 1st capture, and all traps were cleaned after each capture). Samples were collected at various times from August to December 2006 and May to July 2008 at$ 

many localities on both black-cotton and red-soil habitats. A few samples were collected at Ol Pejeta and Segera ranches, to the west and south of MRC, both of which are dominated by *A*. *drepanolobium* savanna on black-cotton soils. Additionally, at least 1 sample each of seeds from 7 of the common grass species and from a few common dicots from the area were prepared as samples, as were stems and leaves from 4 grasses. Trapping and handling procedures accorded with guidelines established by the American Society of Mammalogists (Sikes et al. 2011).

Identification of small mammals followed Meester and Setzer (1971), which indicates that Mus minutoides, M. triton, and M. sorella occur in Kenya. Additionally, M. tenellus and *M. setulosus* have been documented from the Laikipia Plateau, and these 5 species are not reliably distinguished by external characters alone (J. Kerbis, Field Museum of Natural History, pers. comm.), nor is it certain that *M. minutoides* is a single species (Meester and Setzer 1971). Recent studies from MRC reporting field-identified Mus spp. have identified all as M. minutoides (e.g., Maclean et al. 2011), but given the known presence of several cryptic species of Mus in the area, only the genus will be identified for the purposes of this study. Similarly, although A. percivali and A. wilsoni are reliably distinguished by pelage characters (Meester and Setzer 1971), the capture of several apparent hybrids in this study compels me to report most results for Acomys spp. by genus only.

Isotope analysis.-Samples of feces, hairs, foliage, and seeds ranging from 1 to 3 mg each were weighed  $\pm$  0.1 mg and placed into tin capsules, then folded and compressed into a microwell plate. Feces were the more abundant animal tissue type sampled for isotope analysis for 3 reasons: they offered a time- and location-specific snapshot of what the animal had eaten (within 24 h-Tieszen et al. 1983), which could then be used to test for within-species differences between habitats (soil types) and seasons (wet versus dry); C:N ratios of nonruminant mammalian feces show strong direct correlation with dietary fiber and indirect correlation with digestible organic matter intake (Vu et al. 2009; also see Jenkins 2005), thus revealing trophic position along the herbivore-omnivore continuum; and fecal isotope-ratio results could be compared to microhistological analysis of diet using fecal samples collected from the same animal at the same time (see Painter et al. 2009). Isotope analysis of a smaller sample of hairs allowed longer time-averaged assessment of diet. Each hair sample consisted of 2 or more hairs from a field sample taken the same day as the fecal sample and that had been clipped from the distal one-half to two-thirds of the hairs. This meant 5- to 10-mm lengths were included for each hair strand, which represents anywhere from 5 to 25 days of hair growth (Priestly 1966). I avoided including large pieces of arthropod carapace in a fecal sample, although smaller fragments likely were included as they presented.

Samples were analyzed for <sup>13</sup>C and <sup>15</sup>N isotopes at the University of California–Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, United Kingdom). Stable isotope values are

expressed in delta notation ( $\delta^{13}$ C,  $\delta^{15}$ N), comparing  $^{13}$ C: $^{12}$ C or  $^{15}$ N: $^{14}$ N of the samples to that of the standard, and are calculated as follows; for instance,

$$\delta^{13}(\%) = (\mathbf{R}_{\text{sample}} / \mathbf{R}_{\text{standard}} - 1) \times 1,000,$$

where  $R_{sample}$  and  $R_{standard}$  are the  ${}^{13}C{}:{}^{12}C$  ratios of the sample and standard, respectively.  $\delta^{15}N$  is calculated in similar fashion. The standard for carbon is Vienna-Pee Dee Belemnite, and nitrogen is expressed with respect to atmospheric nitrogen.

Digestion and metabolism of ingested food changes its  $\delta^{13}C$ and  $\delta^{15}N$  in predictable ways and differentially for different animal tissues, so I used average values for diet-to-fecal fractionation, or enrichment ( $\epsilon$ ), for  $\delta^{13}C$  and  $\delta^{15}N$  (-3.77%) and 2.11‰, respectively) from a controlled feeding study of 6 species of wild-caught small rodents (Hwang et al. 2007) to calibrate the delta values. In other words, the above  $\varepsilon$ -values were added to the  $\delta^{13}C$  and  $\delta^{15}N$  values from feces to arrive at estimated dietary values of  $\delta^{13}C$  and  $\delta^{15}N$  for the rodent species in this study. These fecal-calibrated estimates for dietary  $\delta^{13}C$  were then converted to percentage  $C_4$  in the rodents' diets using IsoError "Case A" for a single isotope with 2 food sources (Phillips and Gregg 2001) for which Source A (equaling a 100% C<sub>4</sub> diet) mean ( $\pm$  SD)  $\delta^{13}$ C = -13 ( $\pm$  0.5) and Source B (equaling a 100% C<sub>3</sub> diet, or 0% C<sub>4</sub> diet)  $\delta^{13}$ C =  $-27.5 (\pm 1.3)$ . Source delta values represented the aggregate mean and standard deviation of a combined sample of grasses and dicots at MRC from this study, Fox-Dobbs et al. (2010), and Cerling et al. (2003).

Because the diet-hair fractionation of carbon isotopes is different than the diet-feces fractionation, and because Hwang et al. (2007) did not give diet-hair enrichment factors, I used composite average diet-hair  $\epsilon$ -values (3.0% for <sup>13</sup>C; 2.9% for <sup>15</sup>N) from 3 controlled-feeding studies, of cricetid rodents (DeMots et al. 2010; Sare et al. 2005) and rabbits (which are cecal digesters of cellulose, as are rodents—Sponheimer et al. 2003), to estimate dietary isotope ratios.

Microhistological examination of feces.--Fecal samples from 5 individuals (4, in the case of *M. natalensis*) of each of the 7 muroid genera were selected and 3 slides were prepared for each individual. For each slide, 1 fecal pellet was entirely ground with mortar and pestle as finely as possible and until it was homogeneous in texture and color. Then, approximately 0.5 ml of this ground fecal material was suspended in 2 drops of 70% ethanol and covered with a cover slip. Five fields per slide were observed under  $100 \times$ magnification, and presence-absence was recorded for each of the following categories: monocot epidermal tissue, dicot epidermal tissue, unclassified plant material (nonepidermal or nonfoliage-Sass 1958), and arthropod exoskeleton. The 15 fields for each sampled animal allowed from 0 to 15 (0% to 100%) possible occurrences for each of the 5 categories, which was independent of the percentage occurrence scores for all other categories.

Statistical analysis.—Mean differences in the variables  $\delta^{15}$ N,  $\delta^{13}$ C, and total C:N between seeds and foliage from plant samples, between soil types for fecal samples, and between wet

and dry seasons for fecal samples were assessed for significance using 1-way analysis of variance (ANOVA; *F*-test—Minitab, Inc. 1996) when group sample sizes were roughly equal, because this test is robust to deviations from normality or homoscedasticity in such cases (Glass et al. 1972). When sample sizes among groups varied widely, as in comparisons among the rodent species, the nonparametric equivalent tests Kruskal–Wallis (*H*) and Mann–Whitney (*U*), which make no assumptions about underlying distributions, were instead used (Minitab, Inc. 1996).

## RESULTS

Stable isotope ratios from plant tissues.--No significant differences in  $\delta^{15}$ N,  $\delta^{13}$ C, or total C:N were found between grass seeds (n = 12) and grass leaves (n = 9), as groups  $(F_{1,19} =$  $0.05, P = 0.82; F_{1,19} = 1.17, P = 0.29; F_{1,19} = 1.34, P = 0.26;$ respectively). Collectively, grass seeds and leaves (n = 21)from this study had the following means ( $\pm$  SE):  $\delta^{15}N = 3.4\%$  $(0.59\%), \delta^{13}C = -13.6\%$  (0.22%), C:N = 32.03 (4.22). The  $\delta^{13}$ C values were in the range of the larger samples from MRC reported by Cerling et al. (2003) and Fox-Dobbs et al. (2010). and I used aggregate mean ( $\pm SD$ )  $\delta^{13}C$  values from the 3 studies of -13.0% for graminoids and -27.5% for dicots as source deltas in the IsoError mixing model (Phillips and Gregg 2001; see "Materials and Methods"), which allowed me to estimate percentage of C<sub>4</sub> grasses in the short-term diet of each species. It should be noted that both mean (-28.4‰) and minimum (-29.0‰)  $\delta^{13}$ C of leaves of A. drepanolobium leaves from Fox-Dobbs et al. (2010) were more negative (less enriched in <sup>13</sup>C) than the -25.2% and -25.8%  $\delta^{13}$ C values for 2 seeds of A. drepanolobium from this study, and also higher than values reported for "dicots" by Cerling et al. (2003), who did not specify which plant parts were analyzed. However, further reference to  $\delta^{13}C$  for nongraminoid vegetation will not differentiate shrub from forb nor seed from leaf or stem, because the pooled average mentioned above is intermediate within these extreme  $\delta^{13}$ C values.

Pooling data on vegetation sampled at MRC by this study and Fox-Dobbs et al. (2010), mean ( $\pm SE$ ; *n*)  $\delta^{15}$ N was 2.4‰ (0.19‰; 58) for grasses, 4.9‰ (0.29‰; 40) for forbs, and 1.3‰ (0.16‰; 40) for shrubs (mostly leaves of *A. drepanolobium*).

Stable isotope ratios from feces.—Mean estimated dietary  $\delta^{15}$ N was highest (5.8‰) in *A. niloticus*, lowest (2.3‰) in *S. mearnsi*, and intermediate in the other 5 rodent taxa (Table 1; Fig. 1). There was significant variation in  $\delta^{15}$ N among the 7 taxa ( $H_6 = 33.85$ , P < 0.001), with *A. niloticus* being significantly higher and *S. mearnsi* significantly lower than all other taxa in pairwise comparisons, and no significant differences between all other pairs of taxa (Table 1). For comparison, 2 elephant shrews (*E. rufescens*), which are reported to be insectivores (Kingdon 2004), had estimated dietary  $\delta^{15}$ N of 3.8‰ and 2.7‰, and a single insectivorous dormouse (*Graphiurus* sp.) had an estimated dietary  $\delta^{15}$ N of 6.2‰.

**TABLE 1.**—Mean and standard deviation of nitrogen isotope ratios ( $\delta^{15}$ N, in ‰), estimated mean dietary  $\delta^{15}$ N (subtracting diet-to-feces enrichment factor of 2.11‰—Hwang et al. 2007), and mean and standard deviation of C:N ratios from feces of 7 taxa of muroid rodents from Laikipia, Kenya. Note: the same superscripted letters following mean  $\delta^{15}$ N and C:N indicate species not significantly different from each other ( $U, P \ge 0.05$ ); different superscripted letters indicate significant pairwise differences (U, P < 0.05).

| Species               | n  | $\delta^{15}N$   | SD   | Estimated dietary $\delta^{15}N$ | C:N ratio            | SD   |
|-----------------------|----|------------------|------|----------------------------------|----------------------|------|
| Saccostomus mearnsi   | 46 | 4.4 <sup>A</sup> | 1.78 | 2.3                              | 10.24 <sup>B</sup>   | 3.47 |
| Acomys spp.           | 14 | $6.0^{B}$        | 1.66 | 3.9                              | 11.06 <sup>B,C</sup> | 5.87 |
| Arvicanthis niloticus | 12 | 7.9 <sup>C</sup> | 3.00 | 5.8                              | 21.10 <sup>A</sup>   | 9.59 |
| Mus spp.              | 13 | 6.4 <sup>B</sup> | 1.05 | 4.3                              | 10.86 <sup>B</sup>   | 1.72 |
| Gerbilliscus robustus | 9  | $6.6^{B}$        | 1.27 | 4.5                              | 6.82 <sup>C</sup>    | 2.19 |
| Aethomys hindei       | 5  | 6.9 <sup>B</sup> | 2.40 | 4.8                              | 8.99 <sup>B,C</sup>  | 4.34 |
| Mastomys natalensis   | 4  | 5.5 <sup>B</sup> | 0.61 | 3.4                              | 11.22 <sup>B</sup>   | 3.58 |

Significant variation in fecal C:N ratio was found among the 7 muroid taxa ( $H_6 = 29.43$ , P < 0.001), with *A. niloticus* having the highest and *G. robustus* the lowest ratio. In pairwise comparisons, *A. niloticus* had significantly higher C:N than each of the other 6 rodent taxa; *G. robustus* had significantly lower C:N than each other rodent taxon except *A. hindei* and *Acomys* spp.; and there were no other significant pairwise comparisons (Table 1; Fig. 1). The small sample of nonmuroid insectivores had somewhat lower C:N ratios: the 2 elephant shrews (*E. rufescens*) had average C:N of 6.68, and the single dormouse (*Graphiurus* sp.) had a C:N of 5.19.

Significant variation in  $\delta^{13}$ C existed among the 7 muroid taxa ( $H_6 = 63.74$ , P < 0.001), with *A. niloticus* and *Mus* spp. having the highest (least negative)  $\delta^{13}$ C values; *A. hindei*, *M. natalensis*, and *S. mearnsi* having the lowest  $\delta^{13}$ C; and *Acomys* (species pooled) and *G. robustus* having intermediate  $\delta^{13}$ C values (Table 2). Converting these fecal isotope ratios to estimates of actual dietary  $\delta^{13}$ C and then to percentage C<sub>4</sub> in the diet, *A. niloticus* and *Mus* spp. had approximately 100% estimated C<sub>4</sub> plant component to their diets (which could include grazing [i.e., grass folivory] or grass granivory, or some combination; Table 2). *G. robustus* and *Acomys* spp. had around 80% C<sub>4</sub> in the diet, and *A. hindei*, *M. natalensis*, and *S. mearnsi* had a roughly equal mixture (40–60%) of C<sub>4</sub> and C<sub>3</sub> in the diet (Table 2).

For fecal samples from all individuals (all taxa pooled), there was a significant positive correlation between  $\delta^{13}$ C and  $\delta^{15}$ N (r = 0.302, P = 0.002, d.f. = 101), indicating that increased C<sub>4</sub> component of diet was associated with increased enrichment of <sup>15</sup>N. Using just the means for the 7 taxa, this relationship showed a similar, but nonsignificant, trend (r = 0.361, P = 0.153, d.f. = 6).

Effect of season and habitat on fecal isotope ratios.— Rainfall gauges at MRC indicated dry periods from 1 September to 15 October 2006, and the month of June 2008 (<10 mm per month, prorated for partial months), and wet periods including November–December of 2006 and May and July of 2008 (55–106 mm per month). Sample sizes for 3 rodent taxa were sufficient to test for diet differences between

**TABLE 2.**—Mean and standard deviation of carbon isotope ratios  $(\delta^{13}\text{C in }\%)$  from feces of 7 taxa of muroid rodents from Laikipia; estimated dietary  $\delta^{13}\text{C}$  (adding diet-to-feces enrichment factor of 3.77—Hwang et al. 2007); and estimated percentages of C<sub>4</sub> in the diet (relative to C<sub>3</sub>,  $\pm$  *SE*) as estimated by IsoError (using mean— $\pm$  *SD* Phillips and Gregg 2001) isotopic signature  $\delta^{13}\text{C} = -13.0 (\pm 0.5)$  for 100% C<sub>4</sub>, and  $-27.5 (\pm 1.3)$  for 0% C<sub>4</sub> (i.e., 100% C<sub>3</sub>; see "Materials and Methods"). Note: the same superscripted letters following mean  $\delta^{13}\text{C}$  indicate species not significantly different from each other (*U*, *P* > 0.1); different superscripted letters indicate significant pairwise differences (*U*, *P* < 0.01).

|                       |    | $\delta^{13}C$  |      | Estimated                    | Estimated                   |        |  |
|-----------------------|----|-----------------|------|------------------------------|-----------------------------|--------|--|
| Species               | п  | $\bar{X}$       | SD   | dietary<br>δ <sup>13</sup> C | % C <sub>4</sub><br>in diet | SE (%) |  |
| Saccostomus mearnsi   | 46 | $-23.3^{A}$     | 2.51 | -19.5                        | 55                          | 2.6    |  |
| Acomys spp.           | 14 | $-19.2^{B}$     | 1.98 | -15.5                        | 83                          | 3.7    |  |
| Arvicanthis niloticus | 12 | $-16.8^{\circ}$ | 2.30 | -13.0                        | 100                         | 4.6    |  |
| Mus spp.              | 13 | $-16.3^{\circ}$ | 2.24 | -12.6                        | 103                         | 4.3    |  |
| Gerbilliscus robustus | 9  | $-19.9^{B}$     | 1.62 | -16.2                        | 78                          | 3.7    |  |
| Aethomys hindei       | 5  | $-23.7^{A}$     | 1.65 | -19.9                        | 52                          | 5.1    |  |
| Mastomys natalensis   | 4  | $-25.4^{A}$     | 1.49 | -21.6                        | 41                          | 5.2    |  |

red and black-cotton soils, or between dry and wet seasons, or both. Feces of S. mearnsi were significantly enriched in <sup>15</sup>N (i.e., higher  $\delta^{15}$ N;  $F_{1.44} = 15.02$ , P < 0.001) on red soil ( $\bar{X} =$ 5.9‰  $\pm$  1.96‰, n = 12) compared to black-cotton soil ( $\bar{X} =$  $3.9\% \pm 1.4\%$ , n = 34). Feces of Mus spp. also were significantly enriched in <sup>15</sup>N ( $F_{1,11} = 6.0, P = 0.032$ ) on red soil  $(\bar{X} = 7.2\% \pm 0.58\%, n = 5)$  compared to black-cotton soil  $(\bar{X} = 7.2\% \pm 0.58\%, n = 5)$  $= 5.9\% \pm 1.02\%$ , n = 8). For these same 2 rodent taxa, there were no significant differences in  $\delta^{13}$ C ( $F_{1,44} = 1.94, P = 0.17$ for S. mearnsi;  $F_{1,11} = 0.33$ , P = 0.58 for Mus spp.) or C:N ratios ( $F_{1,44} = 0.63$ , P = 0.43 for S. mearnsi;  $F_{1,11} = 0.02$ , P =0.88 for Mus spp.) between red soil and black-cotton soil. Feces of S. mearnsi had significantly higher C:N ratios ( $F_{1,29} =$ 9.70, P = 0.004) during wet seasons ( $\bar{X} = 11.6 \pm 3.65$ , n = 12) than during dry seasons ( $\bar{X} = 8.7 \pm 1.34$ , n = 19), and significantly more negative ( $F_{1,29} = 5.28$ , P = 0.029)  $\delta^{13}$ C in dry seasons ( $\bar{X} = -23.8\% \pm 1.42\%$ , n = 19) than in wet ( $\bar{X} =$  $-21.9\% \pm 3.01\%$ , n = 12). The latter translates to an estimated diet of 52%  $C_4$  in the dry season and 64%  $C_4$  in the wet season for S. mearnsi. Soil and season differences for the C and N variables were similarly examined for feces of A. niloticus, and the only comparison that was significant was a more negative ( $F_{1,11} = 5.53$ , P = 0.038)  $\delta^{13}$ C during the dry season ( $\bar{X} = -18.0\% \pm 2.40\%$ , n = 7) than during the wet season ( $\bar{X} = -15.5\% \pm 0.90\%$ , n = 6). This translates to an estimated diet of 92% C<sub>4</sub> in the dry season and 109% C<sub>4</sub> in the wet season for A. niloticus.

Comparison with hair samples.—There appears to be no systematic bias in differences between hair and fecal  $\delta^{13}$ C-estimated percentage dietary C<sub>4</sub> for 13 individual rodents (Table 3). Four of the individuals showed <10% difference in either direction in estimated percentage dietary C<sub>4</sub> from hair compared to feces; 4 had 11–20% higher estimated dietary C<sub>4</sub> from hair than from feces; 3 had 11–20% higher estimated dietary C<sub>4</sub> from feces than from hair; and 2 had 25–35% higher

| $\delta^{15}N_{diet-hair}$ enrichment factors, $\epsilon$ , of 3.0‰ and 2.9‰, respectively (see "Materials and Methods"; for feces, see Tables 1 and 2). |  |  |   |                                |                                |   |             |              |
|--|--|--|---|--------------------------------|--------------------------------|---|-------------|--------------|
| Species  | Estimated dietary $\delta^{13}$ C hair (% C <sub>4</sub> ) | Estimated dietary $\delta^{13}C$ feces (% C <sub>4</sub> ) | $\begin{array}{c} \text{Difference} \\ \delta^{13}\text{C} \end{array}$ | Estimated $\delta^{15}$ N hair | Estimated $\delta^{15}N$ feces | $\begin{array}{c} \text{Difference} \\ \delta^{15} N \end{array}$ | Hair<br>C:N | Feces<br>C:N |
| Acomys percivali   | -16.8 (74)   | -12.7 (102)  | -4.09   | 4.3                            | 2.3                            | 2.08  | 3.0         | 25.7         |
| Acomys hybrid  | -18.7 (61)   | -18.7 (60)   | 0.07  | 3.7                            | 3.3                            | 0.44  | 3.0         | 8.7          |
| Acomys wilsoni   | -18.1 (65)   | -13.1 (100)  | -5.01   | 3.0                            | 4.4                            | -1.45   | 3.0         | 10.8         |
| Acomys wilsoni   | -17.3 (70)   | -15.0 (86)   | -2.32   | 5.0                            | 2.0                            | 3.01  | 3.4         | 15.9         |
| Aethomys hindei  | -18.5 (62)   | -18.3 (64)   | -0.27   | 6.0                            | 3.3                            | 2.75  | 3.0         | 12.1         |
| Aethomys hindei  | -20.6 (48)   | -22.5 (35)   | 1.91  | 5.2                            | 3.5                            | 1.65  | 3.1         | 10.6         |
| Mastomys natalensis  | -19.1 (58)   | -20.7 (47)   | 1.55  | 4.8                            | 3.4                            | 1.45  | 3.1         | 8.5          |
| Gerbilliscus robustus  | -13.5 (97)   | -13.1 (99)   | -0.38   | 5.2                            | 2.4                            | 2.79  | 3.0         | 11.9         |
| Saccostomus mearnsi  | -20.5 (48)   | -21.9 (38)   | 1.35  | -0.1                           | -1.1                           | 0.92  | 3.1         | 9.5          |
| Saccostomus mearnsi  | -21.3 (43)   | -19.8 (54)   | -1.51   | 3.1                            | 1.5                            | 1.64  | 3.2         | 10.0         |
| Saccostomus mearnsi  | -20.1 (51)   | -21.7 (40)   | 1.62  | 2.2                            | 0.4                            | 1.82  | 3.1         | 9.3          |
| Saccostomus mearnsi  | -18.8 (60)   | -15.9 (80)   | -2.88   | 4.9                            | 2.9                            | 1.99  | 3.2         | 11.7         |
| Saccostomus mearnsi  | -21.4 (42)   | -18.5 (63)   | -2.91   | 5.0                            | 2.0                            | 1.96  | 3.2         | 7.0          |

**TABLE 3.**—Carbon and nitrogen isotope-ratio values (estimated dietary, ‰) and C:N for hairs and feces collected simultaneously from 13 individual rodents from Laikipia, Kenya, and differences between the 2. Raw isotope ratios for hairs were adjusted using  $\delta^{13}C_{diet-hair}$  and  $\delta^{15}N_{diet-hair}$  enrichment factors,  $\epsilon$ , of 3.0‰ and 2.9‰, respectively (see "Materials and Methods"; for feces, see Tables 1 and 2).

estimated dietary C<sub>4</sub> from feces than from hair (Table 3). These last 2 were both *Acomys* spp. whose fecal  $\delta^{13}$ C indicated pure grass and whose hair  $\delta^{13}$ C indicated a more mixed grass– browse diet. Fecal and hair  $\delta^{13}$ C for the 1 individual of *G*. *robustus* both indicated pure grass, and for all other individuals both values indicated mostly mixed feeding with either small differences between fecal and hair  $\delta^{13}$ C or an equal number of higher percentage C<sub>4</sub> from hair to lower percentage C<sub>4</sub> from hair. A hair sample from 1 individual of *A. niloticus* (without corresponding fecal sample, and so not displayed in Table 3) had an estimated dietary C<sub>4</sub> of 93%.  $\delta^{13}$ C values from hair and feces were significantly positively correlated (r = 0.772, P <



FIG. 1.—Fecal  $\delta^{15}$ N values ( $\bar{X}$  unadjusted ‰, *SE*) displayed against C:N values ( $\bar{X}$ , *SE*) for 7 genera of Laikipia rodents. See Table 1 for significance tests of species-pairs comparisons for both variables. Asterisks (\*) mark 4 species that were determined to be "grass specialists" based on fecal  $\delta^{13}$ C values (cf. Fig. 2).

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**TABLE 4.**—Average percentage occurrences by field (range among individual animals, if any, in parentheses) of monocot, dicot, unidentified plant, and arthropod in feces of muroid rodents from Laikipia, Kenya, from microhistological analysis; 15 fields per individual (n) at 100× magnification.

| Species n             |   | Monocot     | Dicot      | Unidentified plant | Arthropod   |  |
|-----------------------|---|-------------|------------|--------------------|-------------|--|
| Saccostomus mearnsi   | 5 | 67 (47-80)  | 53 (27-67) | 100                | 35 (20-53)  |  |
| Acomys spp.           | 5 | 68 (28–93)  | 27 (7–53)  | 100                | 73 (47–100) |  |
| Arvicanthis niloticus | 5 | 96 (87-100) | 25 (0-40)  | 100                | 17 (7-27)   |  |
| Mus spp.              | 5 | 76 (47–93)  | 35 (20-53) | 83 (13–100)        | 61 (13-100) |  |
| Gerbilliscus robustus | 5 | 45 (20–93)  | 7 (0-20)   | 35 (0-100)         | 99 (93-100) |  |
| Aethomys hindei       | 5 | 76 (47–87)  | 39 (0-53)  | 100                | 39 (0-73)   |  |
| Mastomys natalensis   | 4 | 47 (73–100) | 30 (20-67) | 100                | 18 (7–53)   |  |

0.002, d.f. = 12). Values of  $\delta^{15}$ N for hair were greater than for feces in 12 of 13 cases, averaging 1.66‰ higher.  $\delta^{15}$ N values from hair and feces were significantly positively correlated (r =0.715, P < 0.005, d.f. = 12). C:N ratios of the 13 hairs were highly consistently (coefficient of variation [CV] = 3.85%) around 3:1 (Table 3), as expected, which indicates that samples were not significantly contaminated by nonhair substances.

Microhistological analysis of feces.-Upon cursory inspection before sample preparation, all feces of G. robustus were dark and packed with chitinous exoskeletons, and all feces of A. niloticus were pale and resembled hay (i.e., grass). Feces of the other taxa appeared intermediate in color and texture. Identification of plant and animal epidermal features under 100× magnification confirmed this, in that virtually all fields from G. robustus had arthropod exoskeletons while also having the lowest occurrence of plant material of any of the 7 taxa (and the only species to average <50% for all plant categories; Table 4). Acomys spp. and Mus spp. were the only other rodents that had >50% occurrence of arthropods, but all species had some. Feces of A. niloticus had 96% occurrence of monocots (the highest of any species) and 17% of arthropods (the lowest; Table 4). M. natalensis had similarly low occurrence of arthropods, whereas S. mearnsi had the highest occurrence of dicots. A composite representation of grass versus browse and degree of insectivory for the 7 taxa, as revealed by both carbon isotope ratios and microhistological analysis, is given in Fig. 2.

#### DISCUSSION

*Could these cryptic consumers fill in for missing large herbivores and halt woody encroachment?*—Among these 7 most common muroid rodents of the Laikipia savannas, there does not appear to be a counterpart to the several browse specialists among the sympatric megaherbivores (see Augustine and McNaughton 2004). Four of these rodents specialize on grasses for the plant component of their diet, and the other 3 have roughly coequal contributions of grass and browse. In the former group, *A. niloticus*, with a fecal C:N ratio of 21 and the lowest occurrence of arthropods, is the most herbivorous of the rodents in this study (horse manure has C:N of 25–30, swine 14, and human 5–10—Jenkins 2005, and references therein). *G. robustus*, with a C:N ratio of around 7 (close to the C:N ratio of chitin, which is 6.9—Schimmelmann

and DeNiro 1986) and nearly 100% occurrence of arthropods from microhistological analysis, is the most insectivorous.

Fecal C:N ratios (Fig. 1) suggest that all taxa other than *A.* niloticus are fairly omnivorous (i.e., consuming significant amounts of insects, with *G. robustus* toward the insectivorous end of the omnivore spectrum). Because the  $\delta^{13}$ C, as well as total C:N, did not differ significantly between grass seeds and grass leaves in this study (this agrees with prior studies of C<sub>4</sub> plants—Cernusak et al. 2009), I cannot say from the isotope results, alone, that *A. niloticus* is a "grazer," as opposed to a granivore that specializes in grass seeds, or some mixture of granivore and folivore. However, the haylike appearance of all feces of *A. niloticus* I collected and the nearly 100% occurrence of monocot epidermal tissues from microhistological analysis suggest it is a true grazer (i.e. grass folivore).

*Mus* spp. has an equally " $C_4$ "  $\delta^{13}C$  signature, but its percentage occurrence of monocot epidermis from microhistological analysis is lower and, in fact, nearly identical to that of *A. hindei*, which has a "mixed  $C_3/C_4$ "  $\delta^{13}C$  signature. This may suggest that *Mus* spp. acquires an important part of its " $C_4$ " signature from grass seeds. These particularly tiny mice (adult body mass 5–8 g—B. J. Bergstrom, pers. obs.) would be more likely to forage economically on small grass seeds than would much larger granivorous rodents; all of the other taxa in this study aside from *Acomys* spp. are an order of magnitude larger than *Mus* spp. (see Bergstrom [1986] and Pulliam [1985] for allometric relationships in seed-size preference in granivorous mammals and birds). Monadjem (1997) found an 82% occurrence for seeds (not further identified) in stomachs of this species.

Microhistological analysis of feces of *S. mearnsi*, *A. hindei*, and *M. natalensis* largely confirms the conclusions from carbon isotopes that these species are mixed feeders on grass and browse (*Mus* spp. had a similar percentage occurrence of dicot epidermis, but microhistological analysis does not account for volume). It has been suggested that the fecal isotope signal may be influenced by differential digestibility of food types (see Hwang et al. 2007), although controlled-diet studies (Codron et al. 2005; Sponheimer et al. 2003) have not found either monocot or dicot to be overrepresented in feces. A feeding preference study of *S. mearnsi* on black-cotton soils at MRC found a strong preference for dicot foliage, especially of the forb *Commelina africana* (Metz and Keesing 2001). A small sample (n = 10) of stomach contents suggested that *S. mearnsi* 



FIG. 2.—Fecal  $\delta^{13}$ C values ( $\bar{X}$  unadjusted ‰, *SE*) displayed against mean percentage occurrence of arthropod exoskeleton from microhistological analysis for 7 genera of Laikipia rodents, along with threshold percentages of estimated C<sub>4</sub> in diets (dashed lines; see text for full explanation). Note on diet characterizations (labeled arrows): all species are "omnivores," defined as incorporating some arthropods and some plants in the diet, but the 3 taxa with >60% occurrence of arthropods cluster as more insectivorous than the 4 taxa with <40% occurrence, which are comparatively more herbivorous. The former 3 also cluster with *Arvicanthis niloticus* in having a C<sub>4</sub> signal >75% (grass specialists), distinct from the remaining 3 species with a 40–55% C<sub>4</sub> signal (mixed-feeding grass–browse generalists).

at MRC preferred forbs (dicots) and insects during the dry season and switched largely to seeds in the wet season, with grass foliage comprising <10% in any season (Keesing 1998a). In contrast, clippings of S. mearnsi found in the habitat during one wet season were about 42% grasses, although grasses constituted 88% of available foliage (Metz and Keesing 2001). Neither of these studies revealed any direct evidence of consumption of foliage or seeds of A. drepanolobium by S. mearnsi (Maclean et al. [2011] erroneously reported that Metz and Keesing [2001] had done just that), although it is possible that some of the seeds (unidentified in Keesing 1998a) could have been of this dominant savanna tree. Keesing (2000) cites unpublished data that 70% of seeds of A. drepanolobium placed on the ground by experimenters were removed (presumably consumed) by rodents, again without confirmation of which species removed them.

Carbon isotope results from the sample of 46 individuals of *S. mearnsi* from this study indicated 55% dietary C<sub>4</sub>, and it is possible that a significant portion of this C<sub>4</sub> component was grass seed. However, microhistological analysis of feces indicated a two-thirds occurrence of monocot foliage and one-half occurrence of dicot foliage in this species' diet. Both *S. mearnsi* and *A. niloticus* in this study displayed a significant increase in proportion of C<sub>4</sub> grasses in the diet in periods following significant rains; this same pattern was confirmed for

mixed-feeding impala (*Aepyceros melampus*) in Laikipia (Augustine and McNaughton 2004). The switch from browsing to grazing following rains is a common pattern in many species of mixed-feeding wild ungulates in Africa (Kingdon 2004). Protein content increases and fiber content decreases as grass growth is renewed following rains (McNaughton 1987). Feces of *S. mearnsi* also had significantly higher C:N ratio in wet seasons, which would suggest more strict herbivory and less intake of insects; this agrees with previous observations of seasonal diet shifts for *S. mearnsi* (Keesing 1998a).

Saccostomus mearnsi was by far the most abundant small mammal—and showed the greatest compensatory increase in adundance on the large-herbivore exclusion plots—in the black-cotton soils at MRC, and *A. niloticus* was the 2nd most abundant (Keesing 1998b). *A. niloticus* was by far the most abundant rodent on red-soil glades and large-mammal exclosures at MRC (B. J. Bergstrom, pers. obs.). The lack of direct evidence of *S. mearnsi* feeding on seedlings or seeds of *A. drepanolobium*, and the evidence from this study that *A. niloticus* does not consume C<sub>3</sub> plant tissues to a significant degree—plus the fact that both rodent species specialize more strongly on grass during wet periods—suggest that increased seedling mortality of *A. drepanolobium* in those same exclusion plots during a wet period (Goheen et al. 2004) may not have been primarily the result of browsing by the 2

most common rodent species as opposed to other factors (e.g., large invertebrates, which were excluded from caged seedlings just the same as rodents; and rodents were not identified to species in Goheen et al. [2004] or in Maclean et al. [2011]). The diet of *M. natalensis*, a species that increased in density after large-herbivore exclusion (Keesing 1998b), was the most mixed (highest proportion of dicots) of the rodents in my study, so it also might have the potential to suppress Acacia recruitment. It is important to note that seed or seedling predation by rodents need only occur sporadically, when the trees actually reproduce, and that a fraction of a rodent's diet composed of Acacia seedlings during a short period of time may have a significant negative effect on recruitment (Baldock et al. 2011; Maclean et al. 2011). Under this scenario, results of this study indicate that S. mearnsi and M. natalensis, and possibly A. hindei (which was never common in the blackcotton exclosures-Keesing 1998b) would be the most likely of the small mammalian herbivores to replace a missing browser component of the native megafauna and have potential to preserve the savanna landscape structure.

Possible confounding factors in interpreting percentage  $C_4$ in the diet.-Although this study found no significant difference in  $\delta^{13}$ C between leaves and seeds of grasses, other studies have found that seeds, fruits, stems, and roots of C<sub>3</sub> plants (dicots) tend to be enriched (i.e., less negative  $\delta^{13}$ C) in <sup>13</sup>C by 1–3‰ over leaves (Cernusak et al. 2009, and references therein). The mean source  $\delta^{13}C$  I used for pure C<sub>3</sub> in the mixing model was taken from large samples of foliage at MRC (present study; Cerling et al. 2003; Fox-Dobbs et al. 2010), and if nonphotosynthesizing dicot plant parts, such as seeds, were indeed 1-3‰ enriched and rodents included 50% of the latter in their diets, the estimated percentage  $C_4$  (Table 2; Fig. 2) would be overestimated by 3.5-10% (correspondingly lesser or greater error for lesser or greater proportional amounts of dicot nonleaves in the actual diet). This would not substantially change the general characterizations of the diets of the 7 rodent taxa (Fig. 2). If we assumed a full 3‰ enrichment of dicot seeds over leaves, a rodent that ate exclusively dicot plants, half seeds and half leaves, would have an estimated 36% dietary C<sub>4</sub>; but that same rodent would not show monocot epidermal tissue in its feces, as 45-96%, on average, of samples from the 7 taxa in this study did.

Finally, it is possible that the fecal "C<sub>4</sub>" signatures of *G. robustus*, *Mus* spp., and *Acomys* spp. were influenced by the >50% occurrence of arthropods, given that whole bodies from 11 orders of insects (phytophagous to carnivorous) and 7 families of spiders from the Serengeti all had "C<sub>4</sub>" isotope signatures ( $\delta^{13}$ C averages ranging from -10% to -16% deVisser et al. 2008). No controlled feeding studies have been done to assess <sup>13</sup>C fractionation of arthropod tissues in the guts of omnivores. But considering that each of these 3 rodent taxa showed >65% occurrence of monocot foliage in the feces, and less than half as much dicot as monocot, and that the 2 more omnivorous rodents had intermediate C:N, compared to the very low C:N of *G. robustus*, this also would not substantially alter characterization of these species' diets.

What do N isotope results tell us about these small omnivores' foraging?-Counter to expectations, A. niloticus-the most herbivorous species—had the highest  $\delta^{15}N$  of any of the muroid rodents in this study, and S. mearnsi the lowest. G. robustus, the most insectivorous, was intermediate in  $\delta^{15}N$ , and in fact had a dietary  $\delta^{15}$ N lower than whole-body samples of insects from 9 of 11 orders, including Orthoptera (grasshoppers), in a study on black-cotton soils on the Serengeti Plain of Tanzania (deVisser et al. 2008). The insectivorous dormouse had only slightly higher  $\delta^{15}$ N than the grazer A. *niloticus*, and the 2 insectivorous elephant shrews had  $\delta^{15}N$  within the intermediate range of the group of herbivore-omnivore muroids. This seems counterintuitive. Higher  $\delta^{15}N$  has often been used as an indicator of feeding at higher trophic levels in isotope studies (Kelly 2000-although this has mostly come from whole-body samples), including those of aquatic consumers (Post 2002), mammalian carnivores (Ambrose and DeNiro 1986), and terrestrial insects (Davidson et al. 2003; deVisser et al. 2008), but the dearth of N isotope studies on omnivorous small mammals in the wild (Kelly 2000) makes it unclear how strong an influence trophic position has on  $\delta^{15}$ N relative to many other factors. For instance, Robbins et al. (2005) suggest that protein quality (or biological value, the match between amino acid composition in the diet and each species' dietary requirements) affects nitrogen isotope discrimination in mammals and birds to a greater degree than does trophic position.

In the present study,  $\delta^{15}N$  of foliage varied by 3.6‰ between forbs and shrubs from a single soil type (black cotton), and insects eaten by omnivorous rodents could be specialist feeders on 1 or more of these vegetation types but also could occupy secondary or even tertiary consumer trophic levels. Furthermore, some studies indicate that soil chemistry has a more significant influence on plant  $\delta^{15}N$  values than protein content of the plant (Handley and Raven 1992; Kelly 2000). Likewise, I found that feces of S. mearnsi and Mus spp. were significantly enriched in <sup>15</sup>N on red soil compared to blackcotton soil. It is not clear how this can be reconciled with the finding of greater primary productivity on black-cotton soil than on red soil (Young et al. 1998-although Pringle et al. 2007 found it highly variable across red soils). Possible confounding factors were the capture of some animals on glades (nutrient-enriched sites of former pastoralist bomassee Augustine and McNaughton 2004) and recent burn sites, but 7 and 11, respectively, of the 34 black-cotton-soil S. mearnsi came from glades and burn sites, whereas only 3 of the 12 red-soil S. mearnsi came from glade sites.

Contrary to predictions, a review of stable isotope studies in terrestrial ecosystems found that omnivores had the lowest  $\delta^{15}$ N of any trophic group (Kelly 2000). In my study, the 2 species with lowest mean  $\delta^{15}$ N (*S. mearnsi* and *M. natalensis*; Fig. 1) indeed had intermediate C:N ratios. Considering only strict herbivores, and especially folivores, as digesta become enriched in  $\delta^{15}$ N within the gut of a small mammal, the greatest amount of enrichment occurs in the cecum (Hwang et al. 2007; Sutoh et al. 1987); given that *A. niloticus* appears to be the 1 species in this study that is a specialist grazer, I would expect it

to have the most developed cecum (see Kinahan and Pillay [2008], and Perrin and Curtis [1980], although neither study included Arvicanthis spp.). The most specialized grazer-Microtus pennsylvanicus-among the 6 rodent species in the study by Hwang et al. (2007) also had the highest diet-to-feces  $\delta^{15}$ N enrichment factor. The significant positive correlation between fecal  $\delta^{15}N$  and  $\delta^{13}C$  for all animals in my study suggests that grasses have higher biological value for cecaldigesting rodents (and that diet-tissue enrichment of <sup>13</sup>C for C<sub>4</sub> diets is actually much greater than the *\varepsilon*-values used in my study), or that rodents forage for grasses more selectively, choosing newer, more protein-rich growth, or both. But this correlation also suggests that likely more of the dicots consumed by S. mearnsi (which had significantly lower  $\delta^{15}N$ than the other 2 mixed feeders Fig. 1) were Acacia ( $\delta^{15}$ N  $\bar{X}$  = 1.4‰) than nonwoody dicots or forbs ( $\delta^{15}$ N  $\bar{X} = 4.9$ ‰—Fox-Dobbs et al. 2010).

Does competitive release from ungulates involve increased forage nutrition for rodents?—As an a posteriori test of the effect of competition with large mammalian herbivores on C and N isotope ratios of rodent feces, 12 S. mearnsi trapped inside of exclosures that kept wild ungulates and cattle out (Young et al. 1998) had significantly higher  $\delta^{15}N$  ( $\bar{X} = 5.38\%$ ) than 34 S. mearnsi trapped outside of exclosures ( $\bar{X} = 3.695\%$ ; H = 7.92, P = 0.005). However, there were no differences in  $\delta^{13}$ C (*H* = 1.82, *P* = 0.177) or C:N (*H* = 0.30, *P* = 0.582) between these 2 groups. This suggests that the protein quality of available forage may have been better (Robbins et al. 2005) inside the plots where large herbivores were excluded. Of the entire group of 104 rodents, the 28 that were caught inside exclosures had significantly higher  $\delta^{15}N$  ( $\bar{X} = 6.41$ ) than the 76 caught outside ( $\bar{X} = 4.965$ ; H = 7.16, P = 0.007). Because 11 of 12 A. niloticus were caught inside exclosures (note that sample sizes among species and exclosure categories were too unbalanced to perform a 2-way ANOVA), this also may partly explain the significantly higher  $\delta^{15}N$  for that species (Table 1).

Among the 7 genera of most common rodents at MRC, results of microhistological analysis parallel those of C:N and  $\delta^{13}$ C, pointing to 1 specialist insectivore (with limited grass consumption), 1 specialist grazer, 2 insectivore-omnivores whose plant component is grass, and 3 mixed-feeding herbivores with equal grass and browse intake and low to moderate consumption of insects. In this last group, S. mearnsi, also the most abundant rodent in the A. drepanolobium savannas, may be the most likely consumer of Acacia seeds given that its  $\delta^{15}$ N was significantly lower than that of the other rodents and that Acacia has the lowest  $\delta^{15}N$  of any plant so far reported from MRC. Further research must still demonstrate this directly, as well as disprove the counteracting indirect effect of insectivory by S. mearnsi reducing insect seed and seedling predation, which some studies have shown to be the strongest effect of competitive release from ungulates on woodland regeneration (e.g., Shaw et al. 2002). M. natalensis also is a mixed feeder with a relatively low  $\delta^{15}$ N, and the fact that it is prone to periodic population explosions throughout Africa (Stenseth et al. 2001) could magnify its potential effect on shrub regeneration. The significant positive correlation between  $\delta^{15}N$  and  $\delta^{13}C$  suggests that the grasses consumed by these rodents had higher biological value than the dicots.  $\delta^{15}N$ results further suggest that biological value of forage for rodents is higher on red soils, and where large mammalian herbivores have been excluded long-term. The latter may be a partial explanation for rodents' increased population growth on ungulate exclusion plots, that is, competitive release resulting not just from an increase in quantity of available resources but also from an increase in quality of those resources.

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