

Searching for cover: soil enrichment and herbivore exclusion, not fire, enhance African savanna small-mammal abundance

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Abstract. Large mammalian herbivores (LMH) are known to suppress populations of small mammals in African savanna ecosystems; whether this suppression is driven by depletion of nutrients and food resources, or of cover, is poorly understood. Cattle management creates scattered, persistent, nutrient-enriched areas (glades). Similarly, prescribed fire may enhance forage nutrition of burned patches. Both enriched microhabitats attract wild and domestic LMH and are fertilized by their wastes, but removal of vegetative cover by LMH or fire may negate the benefits of enhanced nutrition to risk-averse small-mammal species or individuals. We used replicated LMH exclusion experiments on red sandy loam and black-cotton clay soils, and a multi-scale burn experiment on black cotton to examine abundance, diversity, and biomass of small mammals across sites varying in vegetation cover and enrichment. Small-mammal species composition varied dramatically among habitats. Species diversity and density on red sands were roughly double that of black cotton soils. Small-mammal densities and diversity were dramatically greater inside LMH exclosures; maximal densities occurred inside fenced, nutrient-rich, tall-grass glades. Small-mammal density was similar between black-cotton burn sites and unburned matrix habitat but was significantly greater on unburned than burned patches within the burn sites. Burned patches contained less grassy cover up to 50 months post-burn, although vegetation differences diminished following significant rains. Mice captured on burned patches traveled farther but were not heavier than mice captured on unburned patches. Small mammals were nearly 20-fold more abundant on totally fenced glades than matrix habitat on both soils and ninefold more abundant on fenced bushland (non-glades) on red sands. Unfenced glades supported intermediate densities in black cotton but lower densities in red sands because of close cropping by LMH. Total small-mammal biomass tended to be greater on red sands (though mean body mass was greater on black cotton for two common species), within exclosures, and on glades. Both the grass rat and pouched mouse reached maximal densities within glade LMH exclosures on both soils. This and the positive association of small-mammal densities with grass height and dead-stem density suggest loss of cover is a primary driver of large-herbivore suppression of certain savanna small mammals.

Key words: cover; diffuse competition; East African savanna; grazing; habitat selection; large-herbivore exclusion; prescribed fire; small-mammal community.

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INTRODUCTION

Climate, soils, fire, and herbivory—with direct and indirect human intervention in the latter three—are widely recognized as key drivers of complex spatiotemporal variation in species composition and structure of vegetation in African savannas (Bond 2005, Yarnell et al. 2007, Sankaran et al. 2008), which in turn profoundly affect herbivores of all sizes, from insects to rodents to elephants. Many savanna native woody shrubs and grasses are adapted to periodic fire (Okello et al. 2001, Higgins et al. 2012). Humans have manipulated savanna fires for millennia; both native and domestic large mammalian herbivores (LMH) respond by altering their foraging, usually by increased use of post-burn sites (Archibald et al. 2005, Sensenig et al. 2010). In some areas of Africa, anthropogenic burning has subsided since the 1960s (Roques et al. 2001) but is beginning to return locally for experimentation and management in savanna systems with significant fuel loads (Sensenig et al. 2010, Archibald et al. 2012, Eby et al. 2014, Kimuyu et al. 2014, Archibald 2016).

Livestock directly affect savanna vegetation structure by consuming biomass and altering plant species composition, and continuing traditional pastoralist use of nocturnal livestock corals (bomas) indirectly affects the distribution of soil nutrients. After large quantities of dung and urine concentrate in bomas, they are abandoned and colonized by unique plant communities, thereby generating nutrient-enriched vegetation patches, called glades, typically 0.5–1.0 ha in size, within the surrounding nutrient-poor matrix across many sub-Saharan savannas of Africa (Stelfox 1986, Blackmore et al. 1990, Reid and Ellis 1995, Augustine 2003, Veblen 2012).

Two distinct types of savanna predominate on the Laikipia Plateau of central Kenya. The first, occurring on relatively flat, black-cotton clay soils, is characterized by a continuous grass layer with a scattered overstory dominated by *Acacia drepanolobium*. The second savanna type, occurring on red, sandy loam soils, is rockier, hillier, and characterized by a patchy, discontinuous grass layer and a more diverse assemblage of trees and shrubs (*Study Area*; Augustine et al. 2011, Appendix S1: Figs. S1, S2).

It is increasingly evident that grazing, fire, and soil variability interact in complex ways to alter

grass quality and quantity (Sensenig et al. 2010, Eby et al. 2014, Donaldson et al. 2018), yet little is known about the cascading consequences for small-mammal communities. For example, the cause of increased abundance and diversity of savanna rodents following LMH exclusion (Keesing 1998b, Keesing and Young 2014) could be either release from exploitative competition for food or increased cover, which is a limiting resource for rodents in these systems. Fire and glades may enhance LMH herbivory, which could both increase competition and suppress cover locally for small mammals.

Large mammalian herbivory

Combined biomass density of domestic and wild LMH can reach 75 kg/ha in African grasslands (Augustine 2010). Native LMH are undergoing population declines and range fragmentation and contraction globally, including in East Africa (Ripple et al. 2015), where the decline is coincident with increased densities of livestock. Cattle are primarily grazers, whereas the native assemblage of ungulates represents a mix of grazers, browsers, and mixed feeders; their combined effect on the landscape dynamics of the *Acacia* savanna-grassland interacts with precipitation and fire to yield a complex spatiotemporal pattern (Okello et al. 2001, Young et al. 2005, Veblen et al. 2016). The LMH assemblage differs substantially between the two ecosystems (soil types), with native browsers and mixed feeders dominating on red sands, and native grazers dominating on black cotton soils (Augustine et al. 2011). Small-mammal densities increase after either wild or domestic LMH are excluded (Keesing and Young 2014, Young et al. 2015) and can increase as much as 20-fold in zones outside of protected areas where wild ungulates have been depleted (Caro 2001). This may have implications for transmission of certain human diseases in Africa. The widespread savanna rat, *Mastomys natalensis*, is a natural host of Lassa fever virus and also of the fleas that carry plague (*Yersinia pestis*) and is prone to dramatic population irruptions (Lecompte et al. 2006, Makundi et al. 2007). Increases in the dominant small rodent of black cotton vertisols in Kenya, *Saccostomus mearnsi*, after LMH removal led to a proportional increase in density of fleas and the human pathogen *Bartonella* spp. (McCaughey et al. 2008, Young et al. 2014).

Glades

Both ecosystems contain enriched, grass-dominated glades, which lack woody vegetation. Repeated close cropping of some glades (especially in the red soils) by LMH, in particular cattle (*Bos taurus*), zebra (*Equus burchellii* and *Equus grevyi*), and impala (*Aepyceros melampus*), and also by elephants (*Loxodonta africana*; McNaughton 1984), and in South Africa by white rhinos (*Ceratotherium simum*; Hempson et al. 2015) converts them to lawns, thereby removing cover necessary for most rodents (Appendix S1: Figs. S4–S6). Persistence of glades may range from decades to perhaps millennia (Young et al. 1995, Marshall et al. 2018) and depends on both grazer density and soil type. Impala, which primarily occupy the red-sands ecosystem, show the strongest preference for glades (Augustine et al. 2011). For this and other reasons, short-grass glades persist much longer in the cropped, grazing-lawn stage in red sands (Augustine 2003), whereas they transition more quickly to a tall-grass (but still shrub-free) stage in black cotton (Veblen and Young 2010, Veblen 2012). Glades can also have long-term effects on the patchiness of burns in savanna grasslands, because cropped glades do not sustain fire (Bond et al. 2001).

Fire

We are only beginning to understand how spatial heterogeneity and scale of fire affect species diversity and community composition of savanna plants and their herbivores (Turner et al. 1994, Sensenig et al. 2010). Fires temporarily enhance grass quality and attract both small mammals (Yarnell et al. 2007) and LMH (Sensenig et al. 2010, Eby et al. 2014); the latter in turn reduce standing biomass and may limit cover for small mammals. It is unclear whether increases in plant quality benefit small-mammal foraging (Kern 1981). Arthropod abundance and seed production may also be greater in burned plots (N. Gregory, *personal communication*). Additionally, post-burn patchiness can enhance overall biodiversity due to successional niche differences among species (Fox 1982, Schweiger et al. 2000, Plavsic 2014). Patchy burns produce a mosaic of successional stages of vegetation, which results in a similar landscape of small-mammal succession (the habitat accommodation model; Fox 1982, 1995).

Persistence of plant structural changes: rainfall, soil, and herbivory

Flushes of new shoot growth as well as the openness of both glades and burns attract medium-to-large herbivores (Tomor and Owen-Smith 2002, Sensenig et al. 2010, Augustine et al. 2011, Riginos 2015). How long these patch types are perpetuated by grazer-induced positive feedback cycles will determine whether their enrichment enhances small-mammal foraging (Rowe-Rowe and Lowry 1981, Monadjem and Perrin 1998) or their continued cropping inhibits it, due to the lack of cover (Grant et al. 1982). Rainfall can accelerate the return of full cover, especially on burn sites (Sensenig et al. 2010), and this post-rain regrowth can affect small mammal species differently (Yarnell et al. 2007, Plavsic 2014). Over the longer term, biomass of large insects, including some (but not all) grasshoppers, may respond significantly to post-burn grass regrowth (Whelan and Main 1979, Anderson et al. 1989, Bieringer 2002), affecting the omnivorous–insectivorous small mammals in this system as well (Bergstrom 2013).

Hypotheses

We examined the effects of three replicated, long-term experimental manipulations on the abundance, diversity, and biomass of small mammals at Mpala Research Centre and Conservancy (MRC) and adjacent properties in Laikipia: (1) partial to complete exclusion of LMH on glades in black cotton soil (the Kenya Long-term Exclusion Experiment or KLEE; Young et al. 1998), (2) complete exclusion of LMH on both glade and non-glade (matrix savanna) plots in red sands (Augustine and McNaughton 2004, 2006), and (3) prescribed fires of varying size (1, 9, 81 ha) and patchiness on black-cotton matrix habitat (Sensenig et al. 2010). These sites represent a broader range of grassland habitat structure and forage quality than has been studied previously, including the full range of habitats found under traditional pastoralist conditions (glades, fire, cattle, and wildlife) to present-day fire-exclusion conditions (with cattle and wildlife) to future scenarios of fire-exclusion plus loss of cattle and/or native LMH.

If cover is the most important factor limiting rodent abundance and diversity, then rodents should respond most strongly to variation in understory vegetative structure as measured by

grass height and dead-stem density (more so than live-stem density). We predicted that increased cover over time inside LMH exclosures (Young et al. 2005, Augustine and McNaughton 2006) would increase rodent abundance and that the exclosure response on glades would be stronger on red sands than black cotton given the greater persistence of short-grass lawns in the former habitat.

If food resources are the strongest limiting factor, then rodent abundance, biomass, and condition (mean body mass per individual) should increase more in LMH exclosures in glades than non-glades and should be greater in or near burned savanna than unburned areas. Further, we hypothesized that rodents would benefit more from burns of smaller areal coverage and greater patchiness as well as in areas that had been burned long enough ago to show reduced cropping effect by large grazers.

STUDY AREA

The 19,870-ha Mpala Research Centre and Conservancy (MRC), which is also a working cattle ranch, is located on the Laikipia Plateau of central Kenya, ~45 km northwest of Nanyuki, at 1600–1800 m elevation (0°17' N, 36°53' E). Additional trapping of prescribed burn sites on black cotton soils occurred at Ol Pejeta Ranch (~30 km SSW of MRC) and Segera Ranch (immediately W of MRC) in Laikipia County (see Appendix S1: Figs. S1, S2 for habitat map and sample site locations). Two major habitats and soil types exist in the area: (1) atop the escarpment are level, poorly drained volcanic vertisols (black-cotton clays) that support a savanna grassland dominated by *A. drepanolobium* (swollen- or whistling-thorn acacia) and grasses including *Themeda triandra*, *Pennisetum stramineum*, *Pennisetum mezianum*, and *Brachiaria lachnantha* (Supplement 1 in Porensky et al. 2013); and (2) a red sandy loam (hereafter “red sands”) of metamorphic origin on the more dissected escarpment and lower plateau, with occasional rock outcrops, dominated by *Acacia mellifera*, *Acacia etbaica*, and *Acacia brevispica*, with a discontinuous understory layer dominated by the grasses *Digitaria milaniana*, *Cynodon dactylon*, *P. mezianum*, and *P. stramineum* (Augustine 2003). Black-cotton savanna has greater primary productivity (Pringle et al. 2007) and produces a greater

fuel load for fire (Sensenig et al. 2010) than red sands. The native, large-grazer assemblage differs somewhat between the two soil types. Impala (*A. melampus*), dik-dik (*Madoqua kirkiti*), and elephant (*L. africana*) dominate on the red sands, while plains zebra (*E. burchelli*), Grant’s gazelle (*Nanger granti*), hartebeest (*Alcelaphus buselaphus*), giraffe (*Giraffa camelopardalis*) and elephant dominate on the black cotton soils (Augustine et al. 2011). Rainfall averages ~500–700 mm annually across the study sites and is weakly trimodal, with a major peak in April–May and minor peaks in August and October–November.

METHODS

Live trapping of small mammals

From August to December 2006 and May to July 2008, one of us (BJB) live-trapped small mammals using collapsible Sherman traps (23 × 9 × 8 cm; H.B. Sherman Trap, Tallahassee, Florida, USA) set in grids or transects with 10-m spacing. To enhance the validity of presence/absence sampling on a small spatial scale, traps were baited with the relatively low-odor bait of cracked maize and wheat kernels, opened in late afternoon, then checked, and closed in the morning. The only diurnal species commonly caught during this study (*Arvicornis niloticus* and *Elephantulus rufescens*) were caught almost exclusively in exclosures; traps were left open 24 h and checked periodically throughout the late morning and afternoon in exclosures only (see Appendix S1 for further taxonomic information on small mammals). Most grids or transects were trapped for five consecutive nights, or in a few cases for five nights within a 10-night period, due to weather delays. If >20% of captures on day 5 were new captures, trapping was extended to a 6th night; conversely, trapping was suspended after four nights if 100% of captures on day 4 were recaptures. Trapping grids were employed to sample treatment and control plots within the exclosures, plus control glade sites, and linear trapping transects were employed to sample the larger scale burn treatments and the matrix habitat controls; each trap station was uniquely mapped. Upon first capture, each animal was fitted with a numbered Monel metal ear tag (National Band and Tag, Newport, Kentucky, USA) or given a distinguishing mark with permanent ink. Each animal was weighed (± 1 g) with a Pesola spring scale and

measured (± 1 mm) for total length, tail length, right hind foot length, and ear length. Sex and reproductive condition were noted as possible from external examination. Recaptured animals were weighed, and their tag/mark numbers were recorded along with trap-station number. All animal trapping and handling procedures adhered to guidelines adopted by the American Society of Mammalogists (Sikes et al. 2016). After 5 nights (or 4 or 6, as previously described) of trapping, a minimum number alive (MNA) was calculated for each mammal species captured.

We used direct enumeration or MNA (calculated after sufficient trapping effort, as described above) rather than a mark-recapture index because most individuals of the common *Mus* spp. and individuals of several less common species were rarely or never recaptured; some relatively common species were not sufficiently recaptured in the 6-d sampling periods on some sites; and we wanted empirical values (not estimates) of total small-mammal biomass per plot and treatment.

Experimental manipulation I: Large herbivore exclosures—glade and non-glade

We trapped small mammals at three glades on black cotton soils which are part of the KLEE experiment. Two glades were subdivided into four large-mammal treatments consisting of (1) all large herbivores excluded (Zero; Appendix S1: Fig. S3), (2) all herbivores except cattle excluded (C), (3) cattle and megaherbivores (elephant and giraffe) excluded, but wild mesoherbivores present (W), and (4) megaherbivores excluded but cattle and wild mesoherbivores present (WC). A rectangular grid consisting of five rows of five traps each, with 10-m spacing, was established in each of the four adjacent treatment areas, with 20 m separating closest traps between treatments (across electric fence wire). The third glade was divided into a Zero treatment and an adjacent unfenced area (MWC), which we sampled using a grid of 50 traps placed in each treatment. Thus, we sampled three replicates of the Zero treatment, two replicates each of C, W, and WC, and one replicate of MWC. Note that MWC constituted a control, open to all herbivores, which was replicated in other black cotton sites separate from the KLEE experiment (see *Other control plots*). We used a trap-detection distance of half

the trap interval (5 m) to determine the rectangular area sampled, which was 0.25 ha for the 25-trap grids and 0.5 ha for the 50-trap grids. Thus, total area sampled per Zero plot was 1.0 ha and per C, W, WC, and MWC plots 0.5 ha.

A separate LMH exclusion experiment established in 1999 on the red sandy loam soils consisted of three replicate pairs of 0.5-ha exclosures, with one in each pair located on a portion of a glade and the other located in adjacent red-sands matrix savanna (or bushland; Augustine and McNaughton 2004, mapped locations in Appendix S1: Fig. S2a). The exclosures prevented access by all herbivores the size of hares (*Lepus* sp.) and larger. Each of these six exclosures, plus each of six equal-area controls outside but adjacent to each exclosure, was trapped for five nights in August–October 2006 using seven rows of six traps each with 10-m spacing (sampled area of 0.42 ha per plot), calculated in the same manner as the KLEE exclosures.

Experimental manipulation II: Prescribed burns

In 2004 and 2005, prescribed burns were implemented on unfenced areas in the black cotton soils dispersed across three adjacent ranches (Sensenig et al. 2010; see Appendix S1: Fig. S2a, b). Burns were implemented at three different extents (area burned equal to 1, 9, or 81 ha) and two different spatial configurations (continuous [C] vs. patchy [P] within the above plot sizes; Appendix S1: Fig. S2c). We sampled small mammals at nine sites that included two replicates of 1C, one replicate of 1P, three replicates of 9C, two replicates of 9P, and one replicate of the 81P burns (Appendix S1: Fig. S2c). All nine sites were sampled during a dry season that occurred 20–50 months after the burn. In addition, one set each of 9C and 9P burns and paired controls were sampled twice more during wet seasons occurring 3–20 months after the first dry-season sampling.

We used diagonal trap transects oriented on a southeast-to-northwest axis, with 10-m spacing between traps to sample the black-cotton burn plots, to cover a mixture of burned and unburned patches (subplots) across the extent of the plot (patchy plots) or to cover the extent of the central burn plus a number of unburned stations to the southeast and northwest of the central burned area (continuous plots). For each of the two

smaller patchy burns, 1P and 9P, because the main transect primarily crossed the larger (0.188 and 3.0 ha, respectively) of the two burn patches, an additional line of 7 or 15 traps, respectively, was placed perpendicular to the main transect so as to project into one of the smaller burn patches (0.062 and 1.0 ha, respectively). The transect on the 81P plot was oriented to cover a roughly equal extent of burned and unburned patches. Total numbers of traps per plot were 37 for 1C, 41 for 1P, 100 for 9C, 115 for 9P, and 120 for 81P.

For the dominant species, the nocturnal, burrow-dwelling *S. mearnsi*, each individual first captured on a transect was observed (through 8 × binoculars, observer remaining stationary as long as possible) upon its daytime release from the trap site until it entered a burrow, and this linear travel distance (± 1 m) was recorded. The average travel distance of these mice was applied as a perimeter around the transect line to determine the rectangular area that was sampled by the trapping transect. Then, for consistency, we applied the same perimeter to red-sands transects (see *Other control plots*) in the calculation of area sampled.

Other control plots

Both to increase our baseline sampling of small mammals in matrix savanna and because of the potential for a proximity effect in control plots established adjacent to exclosures and burns, we also censused sites in areas of matrix savanna on black cotton and red sands soils far from the exclosures and burn plots. We sampled three 1000-m transects in matrix black-cotton savanna, and a black-cotton glade far removed from exclosures (using a grid designed to fit the contours of the latter). On the heterogeneous red-sands matrix savanna habitats, we sampled seven sites ranging from shrubby, seasonal stream banks to rocky cliffside areas to grassy patches to bare-soil patches. The latter two patch types were sampled with a single grid each, whereas the remaining five sites were sampled with 1000-m transects. Area sampled was calculated in the same manner, for grids and transects, respectively, as previously described.

In our analysis of abundance and diversity, we include captures only of nine genera of small mammals readily capable of being sampled by our traps, which were primarily members of seven

genera of rodents of the family Muridae (*Mus*, spp., *Acomys* spp., *Gerbilliscus* spp., *S. mearnsi*, *A. niloticus*, *M. natalensis*, *Aethomys hindiei*), shrews of the genus *Crocidura* (Soricomorpha: Soricidae), and the elephant shrew *E. rufescens* (Macroscelidea: Macroscelididae). Due to infrequency of capture, we did not include *Crocidura* spp. in any of the species-specific statistical analyses of treatment effects. See Appendix S1 for other details about mammal species.

Vegetation measurements

Along each grid or transect, vegetation measurements were taken at alternate trap stations (i.e., every 20 m). A 10-pin frame was placed and the pins were dropped vertically, and total numbers of contacts were recorded for dead grass, live grass, and bare soil. Both at the trap station and 1 m at each cardinal direction, maximum grass height (± 1 cm) was recorded as the tallest grass stem or blade within a 5-cm horizontal radius of each of the 5 points and averaged. For the burn plots on Mpala and Segera ranches in 2008, an estimate of live tree density was made at each vegetative sampling station by a point-quarter method. Distance to the nearest live tree (nearly always *A. drepanolobium*) ≥ 1 m in height was recorded within each quadrant (NE, NW, SW, SE, centered on the station marker). Tree density per station was calculated as $12/\pi \sum_{x=1}^4 d_x^2$, where d_x = distance to nearest tree in each quadrant x .

Data analysis

Total density of small mammals (MNA/ha), biomass density (kg/ha) of small mammals, species richness of small mammals, and Shannon–Wiener diversity (H' ; Krebs 1999) of small mammals, per treatment per site, were the primary dependent variables. Body mass, sex, and reproductive condition were also examined for species caught in large numbers and in multiple treatments. Treatment effects (burned vs. unburned; LMH exclusion vs. control; glade vs. non-glade), as well as soil-type effects (black cotton vs. red sands), on these dependent variables, and also on the primary vegetation variables, were examined with linear (or polynomial) regression, t tests, and one-way and two-factor ANOVA (F test, or general linear model—Minitab 2016) 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, the nonparametric equivalent tests Kruskal–Wallis (H) or Mann–Whitney (W), which make no assumption about underlying distributions, instead were used (Minitab, Inc. 2016). When ANOVA was not possible due to one or more zeros in the dependent variable (i.e., no captures for a site), a chi-square goodness-of-fit test was used. ANCOVA was used to test for preference of small mammals for burns of varying size and patchiness.

To examine prescribed burn effects on small mammals and their habitat, we fit generalized linear mixed models (GLMM) for grass height and small-mammal density in which we evaluated the timing of sampling (months since burn) and season (dry or wet) as covariates to assess whether these factors influenced small-mammal density in addition to the burn treatment. We fit models that accounted for the repeated-measures design of sampling (repeated measures at two of nine sites), and the pairing of burned vs. control plots at all nine sites. For small-mammal density, we logarithmically transformed the response variable due to heteroscedasticity in residuals for the non-transformed results, and we report back-transformed least-square means and standard errors (SEs) from the GLMM (SAS v9.4; SAS Institute, Cary, North Carolina, USA). We used GLMMs similarly to examine the effects of grazing (LMH exclusion vs. control) on both levels of enrichment (glades vs. matrix bushland), plus interactions, in the red-sands grazing experiment.

We examined multiple linear regression models with potential predictor variables including the four vegetation variables (dead grass hits, live grass hits, bare soil hits, grass height), Exclude (an index of the degree of LMH exclusion scored at 0 for no exclusion [control, or MWC], 1 for partial exclusion [W, C, or WC], and 2 for total exclusion [as in Zero exclusions]), and Glade (a binary index for glade sites vs. all others), soil type (black cotton vs. red sands for the combined data set). Response variables for separate runs of model selection were total small-mammal density, species richness (S), and small-mammal H' . Model selection employed the Mallows' C_p minimization procedure, which is a form of parsimonious model selection equivalent to Akaike's information criterion in the case of Gaussian

linear regression (Boisbunon et al. 2014), where $C_p = (SSE_p/MSE_m) - (n - 2p)$; n = sample size; p = number of parameters in the model; SSE_p = sum of squares error for the best model with p predictors; and MSE_m = mean square error for the model with all m predictors. In cases of ties for minimum C_p , the model with the highest coefficient of determination, or adjusted R^2 —equivalent to the smallest MSE_m —was chosen as the best (most parsimonious; Minitab 2016). Best models were examined for red and black soils both separately and combined.

RESULTS

Trapping effort and capture summary for red sands vs. black cotton

For 2006 and 2008 combined, a total of 14,431 trap nights yielded 1004 total captures of 619 small mammals of 12 genera and at least 14 species (Appendix S1: Table S1b). Trapping success (captures per 100 trap nights) in red sands sites was generally twice that of black cotton sites for matrix habitat and about 50% higher for LMH exclusions (Appendix S1: Table S1a). Small-mammal densities were always greater in the red-sands vs. the black-cotton savanna when grazing, nutrient inputs, and fire were held constant (Table 1). However, the latter three processes substantially influenced small-mammal densities (noting that there were no burned sites on red sands). Small-mammal density was greatest on red sands that were enriched in nutrients from cattle manure inputs (i.e., in red-sands glades), but only when grazers were excluded. In grazed glades, small-mammal density approached 10 individuals/ha on both soil types, and total biomass density was 0.7–0.8 kg/ha. Both measures increased fourfold or fivefold with total exclusion of LMH on black cotton, and ninefold or 10-fold with LMH exclusion on red sands (Table 1). Partial exclusion of LMH on black cotton resulted in intermediate small-mammal densities and biomass. Grazed matrix habitats also had less than half the small-mammal densities and biomass as grazed glades on both soil types (Table 1).

On the black cotton soil, the small-mammal community was less diverse, with *S. mearnsi* dominant and *Mus* spp. subdominant, in the areas distant from the LMH exclusions (KLEE), whether on glade or non-glade sites (Appendix S1:

Table 1. Per-treatment mean individual densities (MNA/ha \pm SE) and total biomass densities (kg/ha \pm SE) of small mammals in savannas of central Laikipia, Kenya.

Treatment	Density (Individuals/ha)		Biomass density (kg/ha)	
	Red sands	Black cotton	Red sands	Black cotton
Glades: Ungrazed	99.2 \pm 19.3	52.0 \pm 8.3	6.1 \pm 1.7	4.0 \pm 1.1
Glades: Partially Grazed	n/a	34.0 \pm 4.7	n/a	2.3 \pm 0.4
Glades: Grazed	8.7 \pm 2.9	12.4 \pm 0.4	0.7 \pm 0.3	0.8 \pm 0.1
Matrix savanna: Ungrazed	45.2 \pm 7.3	n/a	3.1 \pm 0.5	n/a
Matrix savanna: Grazed	5.3 \pm 1.2	2.7 \pm 0.8	0.2 \pm 0.1	0.3 \pm 0.1
Matrix savanna: Grazed + Burned	n/a	1.8 \pm 0.4	n/a	0.2 \pm 0.1

Notes: MNA, minimum number alive; SE, standard error. Variables include relation to soil types (red sands is red sandy loam; black cotton is clay vertisol); local nutrient enrichment (glades are nutrient-enriched grass patches lacking trees; matrix is background, nutrient-poor savanna containing grass and tree layer); presence of large mammalian herbivores manipulated by electrically fenced exclosures (ungrazed is all large herbivores excluded; partial is pooled results of three subsets of large herbivores excluded, on black cotton only; see *Methods*; grazed is all large herbivores present); and presence vs. absence of fire (black cotton only).

Table S1b). *Arvicanthis niloticus* occurred in black cotton only within exclosures, where it was a sub-dominant species (Appendix S1: Table S1b), but none of the six other genera of murid rodents commonly caught on red sands (several of those also within KLEE exclosures) was caught beyond the immediate vicinity of the KLEE exclosures on black cotton soils.

Mean trap-to-burrow distances were obtained for 80% of *S. mearnsi* individuals first captured at non-exclosure sites and averaged 14.7 m (standard deviation [SD] = 17.4; $n = 104$, range 0.5–150 m). In 99 of these 104 cases, the burrow entered was in a termite mound, which in the black cotton are slightly elevated mounds from 1 to 3 m in diameter with patches of bare soil (if active). Based on this estimate, a trap detection distance of 15 m was added around the perimeter of each transect to estimate the area sampled (e.g., for a 1000-m transect, the area sampled was 30,900 m², or 3.09 ha).

Total sampling of red-sands replicate exclosures and adjacent controls in 2006 revealed mean richness of 4 and 5, respectively, in glade and matrix savanna (bush), with *A. niloticus* and *S. mearnsi* the most frequently captured, respectively, in glade and bush, and *Gerbilliscus* sp. the second most in both (Appendix S1: Table S2; relative abundance followed roughly the same pattern; Appendix S1: Fig. S8). A partial resample of one each glade and bush exclosure (inside only) in 2008 found the same richnesses but *Gerbilliscus* sp. and *A. hindei*, the top two species captured in each (Appendix S1: Table S2).

On the diverse and widely dispersed red-sands matrix sites, species richness averaged 4.17 (range 3–6) and was 10 in the aggregate (Appendix S1: Tables S1b, S2; as noted in *Methods*, this subsumes the two *Acomys* spp. and the likely two *Gerbilliscus* spp. and thus may underestimate richness by 2). *Acomys* spp. (including *A. wilsoni*, *A. percivali*, and hybrids) accounted for 33% of total captures, *A. hindei* for 23%, *Gerbilliscus* spp. for 20%, *Mus* spp. for 14%, *M. natalensis* for 4%, *S. mearnsi* for 2%, *Crocidura* spp. for 2%, and *A. niloticus*, *E. rufescens*, the pygmy squirrel *Paraxerus ochraceus*, and the dormouse *Graphiurus* sp. each accounting for a single capture. One of the red sands sites was a shrubby hillside with rock outcrops; here, *Acomys* spp. (including both *A. percivali* and *A. wilsoni*) constituted 57% of captures, and the lone *Graphiurus* sp. was captured. A site with extensive bare-soil patches yielded only *Gerbilliscus* spp., *Acomys* spp., and *E. rufescens*. Two sites along dry seasonal streambeds together yielded at least seven species, including both *Acomys* spp., which collectively comprised 32%, and *A. hindei* at 24%. The red-sands matrix site with the greatest herbaceous cover was a grassy floodplain (not recently grazed by cattle) next to the Ewaso N'giro River; it yielded, among five species, *A. niloticus* and *S. mearnsi* and was the only red sands site away from exclosures where either of these two species was caught. The transitional soil site's small-mammal fauna was characteristic of a red sands site, with 60% of individuals being *Acomys*, of both species, but also including one *S. mearnsi*.

Effects of burns on habitat and small-mammal densities, condition, and movement

On black cotton soils, burns significantly reduced small-mammal density relative to unburned patches ($t = 2.25$, $P = 0.04$, $df = 15$, see Fig. 1). Burns reduced grass height independent of months since burning (months post-burn \times treatment interaction; $F_{1,3,1} = 0.001$, $P = 0.97$). Grass height increased over time both on and off burns ($F_{1,2,3} = 62.2$, $P = 0.011$). The dramatic dry-season difference in grass height between unburned and burned patches (Appendix S1: Fig. S7) nearly disappeared at the two sites resampled twice in subsequent wet seasons (Appendix S1: Fig. S9), yet there was no parallel trend of converging small-mammal abundance. The overall treatment \times season interaction was not significant ($F_{1,4} = 2.56$, $P = 0.18$; treatment main effect, $F_{1,4} = 112$, $P < 0.001$), and grass height increased strongly in the wet season ($F_{1,3} = 241$, $P < 0.001$; Fig. 1).

Burns dramatically reduced small-mammal density across dry-season measurements occurring 20–50 months post-burn (months post-burn \times treatment interaction, $F_{1,16} = 0.71$, $P = 0.41$; treatment: $F_{1,16} = 5.94$, $P = 0.03$). Small-mammal density did not vary as a function of months post-burn ($F_{1,21} = 0.02$, $P = 0.89$). All nine sites in this experiment were first measured during a post-burn dry season. Burn effects were contingent on

the season of sampling (season \times treatment interaction, $F_{1,13,6} = 4.89$, $P = 0.04$), because burns reduced small-mammal density even more in the wet season than in the dry season (Fig. 1).

Live tree densities for all five burn plots on Mpala and Segera ranches were on average 89% (± 56.9) greater for unburned vs. burned patches; these differences were highly significant ($P \leq 0.004$) for the three continuous burns (the combined 1 ha and two 9 ha) and marginal ($P \approx 0.1$) for the two patchy burn replicates (9- and 81-ha). No ANCOVA model testing for relationship between total small-mammal density and area burned (total per plot, or minimum patch size), with either burned/unburned or patchy/continuous as covariate, was significant.

On all burn sites, male *S. mearnsi* ($n = 54$) were 19% heavier than females ($n = 66$; $F_{1,116} = 9.61$, $P = 0.002$). Two-factor ANOVA with body mass as the response found a significant sex effect ($F_{1,115} = 7.50$, $P = 0.01$) but non-significant burn effect and burn-by-sex interaction; that is, mice had similar mass on burned ($n = 35$) and unburned ($n = 86$) patches. Females comprised 49% of 35 individual *S. mearnsi* on burned patches and 57% of 86 individuals on unburned patches.

A two-factor ANOVA of foraging distance (travel-to-burrow following release at capture site) for

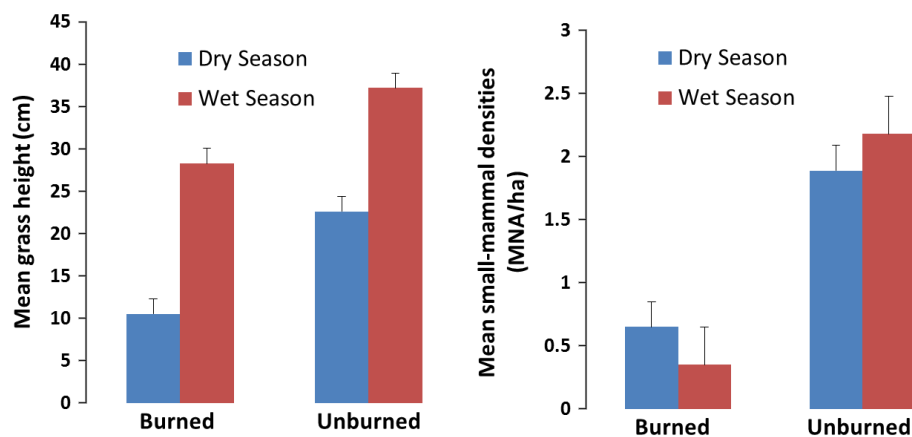


Fig. 1. Effects of burning and season on mean grass height and total small-mammal density in burned vs. adjacent unburned plots within the black-cotton burn experiment. Back-transformed least-square means are shown (Methods); error bars represent +1 standard error. Both treatments significantly affected grass height and small-mammal density, with a significant interaction effect on density (density was more suppressed on burn sites during the wet season than the dry).

S. mearnsi on black-cotton burn-site transects found significant main effects for sex ($F_{1, 103} = 5.79$, $P = 0.02$) and burn status ($F_{1, 103} = 6.68$, $P = 0.01$) but no significant interaction ($F_{1, 103} = 1.42$, $P = 0.24$; $df = 45$); that is, both mice released in burned patches, and male mice, traveled significantly farther. Mice captured in burned patches ($n = 12$, median = 24.5 m) traveled significantly farther than mice captured in unburned patches ($n = 37$, median = 11.0 m; Kruskal–Wallis $H = 4.48$, $P = 0.03$, $df = 1$). For all captures on black-cotton transects (including controls), males ($n = 29$, median = 20.0 m) traveled significantly farther than females ($n = 29$, median = 9.0 m; $H = 8.05$, $P = 0.005$, $df = 1$). Females on black-cotton transects that were pregnant and/or lactating ($n = 16$) did not travel farther than non-reproductive females ($n = 14$; $H = 0.14$, $P = 0.71$, $df = 1$).

Effects of LMH exclusion on small-mammal abundance, biomass, and diversity, and on habitat, on glade and on bush (non-glade matrix) sites in red sands

On red sands soils, total small-mammal densities were significantly affected by community (glade vs. bushland; $F_{1,6} = 8.35$, $P = 0.03$), LMH exclusion ($F_{1,6} = 43.99$, $P < 0.001$), and their interaction ($F_{1,6} = 7.0$, $P = 0.04$; Fig. 2). Small

mammals were 12 times more abundant inside glade LMH exclosures compared to adjacent glades with LMH present, and eightfold more abundant inside matrix savanna LMH exclosures compared to adjacent savanna with LMH present (Fig. 2). Total small-mammal densities inside red-sands glade exclosures in 2006 were generally twice that of matrix exclosures (Fig. 2; Appendix S1: Fig. S9). Richness and diversity were greater in matrix savanna compared to glades on the red sands. *Saccostomus mearnsi* and *Gerbilliscus* spp. occurred inside all red-sands LMH exclosures. Of the 20 total captures in grazed red-sands control plots (glade and bushland), 15 were *Gerbilliscus* spp., two were *E. rufescens*, two *A. niloticus*, and one *S. mearnsi*.

Compared to the red-sands exclosures, the distant red-sands matrix sites had comparably diverse but lower density small-mammal communities, but with much different species composition, dominated by *Acomys* spp., followed by *Mus* spp. (these two species were rarely found in LMH exclosures), *A. hindei*, and *Gerbilliscus* spp. (Fig. 3). *Mastomys natalensis* was infrequently captured in LMH exclosures and somewhat more frequently captured in red-sands matrix. *Gerbilliscus* spp. occurred with equal frequency in red-sands exclosures, controls, and matrix (Appendix S1:

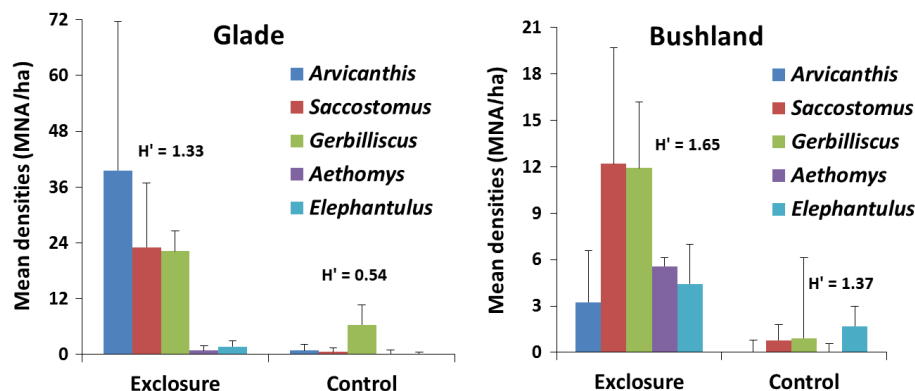


Fig. 2. Back-transformed least-square mean densities (minimum number alive/ha) +1 standard error of small mammals by genus across three replicates of red-sands large mammalian herbivores (LMH) exclosures in both glade (open, nutrient enriched) and bushland (unenriched, scrub matrix) habitats, comparing experimental plots (total LMH exclusion) with adjacent grazed controls. Total small-mammal densities were significantly greater in glade than bushland (note different scales on Y axes) and highly significantly greater inside LMH exclosures in both habitats, with a significant interaction effect (Results); however, species diversity was somewhat greater in bushland. (2006 results only; does not include 2008 partial resampling of one experimental replicate in which three *Mastomys* spp. were caught in a glade exclosure and one *Acomys* sp. was caught in a bushland exclosure).

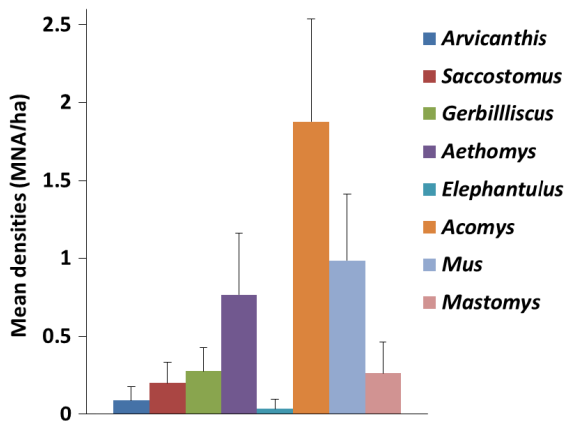


Fig. 3. Mean densities (minimum number alive/ha) +1 standard error of small mammals by genus across seven replicates of red-sands matrix (bushland) sites dispersed across MRC and distant from the large mammalian herbivores exclosures (cf. Fig. 3). Includes 2008 sampling only. See text for further information about red-sands matrix sites.

Table S1b; although their density was far greater inside red-sands exclosures; $20.0 \text{ ha}^{-1} \pm 11.1 \text{ SD}$ inside, $n = 10$; $1.5 \text{ ha}^{-1} \pm 1.7$ elsewhere in red sands, $n = 18$; $t = 5.26$, $P = 0.001$).

Estimated mean small-mammal biomass density (kg/ha) was 6.1 and 3.1 inside red-sands glade and matrix savanna LMH exclosures, respectively, but these differences were not significant ($t = 1.71$, $P = 0.18$, $df = 3$). However, each was far greater than the grazed red-sands matrix sites (0.2 kg/ha; compared to matrix, $t = 6.26$, $P = 0.01$, $df = 3$; compared to glade, $t = 3.54$, $P = 0.04$, $df = 3$). Mean biomass densities were 0.7 and 0.2 kg/ha for glades and matrix savanna controls adjacent to LMH exclosures, respectively (Table 1; also see Appendix S1: Fig. S11).

On the red sands, exclusion of grazers dramatically affected vegetation cover in both glades and matrix savanna. All three glade control plots were closely cropped lawns frequently seen being grazed by cattle, elephants, impala, zebra, eland, and waterbuck (Appendix S1: Fig. S5). Grazer removal significantly increased grass height ($P < 0.001$) and marginally increased dead-stem density in both glades and matrix savanna (Appendix S1: Fig. S13), and marginally reduced bare soil coverage in glades.

Effects of LMH exclusion on small-mammal abundance and diversity, and on habitat on black cotton (KLEE) glades

On black cotton soil, the grass rat *A. niloticus* was found exclusively in ungrazed (Zero) glades (21 of 27 individuals from KLEE; Appendix S1: Fig. S10) and partially grazed glades (W, C, and WC plots; Fig. 4). For 76 recaptures (out of 188 total captures of 112 individuals of all species), there was not a single instance of movement between KLEE treatment plots. Total small-mammal density was significantly greater in Zero than in MWC ($\chi^2 = 6.26$, $df = 1$, $P < 0.02$). *Saccostomys mearnsi* was more evenly distributed among the four treatments (Fig. 4), although a two-factor ANOVA of wildlife and cattle effects on total captures of *S. mearnsi* was significant for cattle effect ($F_{5,8} = 7.70$, $P = 0.04$) but not for wildlife, or cattle \times wildlife interaction effect ($P > 0.7$). Specifically, the density of *A. niloticus* was significantly greater in Zero plots than all others ($\chi^2 = 50.9$, $df = 4$, $P \ll 0.001$) and 2–3 times greater than the partial LMH exclusion treatments (Fig. 4), whereas density of *S. mearnsi* was not significantly different among the five treatments ($\chi^2 = 8.52$, $df = 4$, $P > 0.07$). The two treatments with combined cattle and wildlife grazing (WC, MWC) had distinctly lower species richness and diversity (Fig. 4) and had low overall total small-mammal densities (with Zero plots having higher densities; $\chi^2 = 33.0$, $df = 4$, $P \ll 0.001$). For all KLEE replicates, total small-mammal biomass density (mean per treatment kg/ha) for Zero, C, W, WC, and MWC treatments, respectively, was 4.0, 2.8, 2.5, 1.5, and 0.8 (also see Appendix S1: Fig. S12).

Exclusion of grazers from black-cotton glades generated the tallest grass and highest density of dead stems found anywhere in the landscape. Black-cotton glades lacking grazers (Zero) or grazed only by wildlife (W) contained substantially taller grass than those grazed by cattle, either alone or in combination with wildlife (C, WC, and MWC: $F_{4, 191} = 7.54$, $P < 0.001$; Appendix S1: Fig. S14). Still, grazed glades in black cotton had mean maximum grass height of 39.9 cm (33.0 cm for the MWC plot), compared to 12.5 cm on grazed red-sands glades and 15.0 cm on grazed red-sands matrix plots.

Each of the three black-cotton glades (treatments pooled) supported greater small-mammal

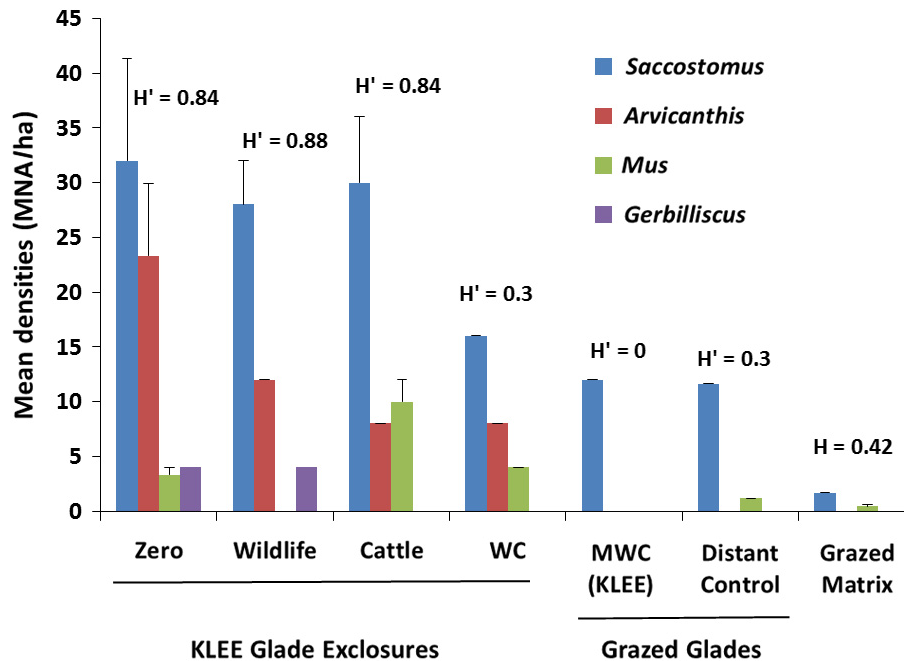


Fig. 4. Mean densities (minimum number alive/ha) +1 standard error of small mammals by genus across four treatments of the Kenya Long-term Exclusion Experiment (KLEE) grazing experiment on black-cotton glades (three replicated large mammalian herbivores treatments and one adjacent control), plus a grazed glade distant from KLEE, and three transects through grazed matrix savanna distant from KLEE. Above the bars are mean Shannon–Wiener diversity indices (H') of small mammals captured within each treatment. See text for further explanation.

densities and diversity than did a black-cotton glade far from the KLEE enclosures, which in turn had greater density and diversity of small mammals than the grazed black-cotton matrix site (Fig. 5). Across all surveys conducted on black cotton sites (burns, enclosures, and matrix sites), a single vegetative variable—mean grass height—was significantly and positively related to small-mammal density (Fig. 6), with ungrazed and partially grazed glades containing the tallest grass and greatest small-mammal abundance. Both variables reached their maxima with complete LMH exclusion. Burn plots (including burned and unburned patches) and matrix habitat generally had low small-mammal abundance and burned patches (20–50 months post-burn) had the shortest grass of all sites (Fig. 6).

Across all black cotton sites and both sampling years, 58% of *S. mearnsi* in ungrazed plots ($n = 64$) were female, whereas 44% in grazed plots ($n = 127$) were female. Males, overall, were heavier ($F_{1, 188} = 8.4$, $P = 0.004$) than females (73.3 ± 23.7 g vs. 64.75 ± 16.6 g, respectively),

which was also true for grazed sites ($F_{1, 125} = 6.3$, $P = 0.01$) and ungrazed sites ($F_{1, 62} = 8.4$, $P = 0.04$) separately. Individual *S. mearnsi* on glades or in enclosures were not heavier than those away from glades or enclosures in black cotton for either males (Mann–Whitney $W = 3077$, $P = 0.1$) or females ($W = 2235$, $P = 0.2$).

However, comparing *S. mearnsi* caught inside glade enclosures only, we found a significant soil effect, with individuals heavier in black cotton ($n = 62$; $\bar{X} = 71.4$ g) than in red sands ($n = 50$; $\bar{X} = 63.4$; $F_{1, 110} = 4.91$; $P = 0.01$) with no significant sex effect or sex–soil interaction. Mean weights of *A. niloticus* captured inside glade enclosures (26 in black cotton, 62 in red sands) did not differ by soil type ($F_{1, 86} = 1.5$, $P = 0.22$), sex, nor sex-by-soil interaction.

Multivariate models predicting abundance and diversity of small mammals

Large mammalian herbivores exclusion and presence of glades enhanced small-mammal density across both soil types and separately by soil

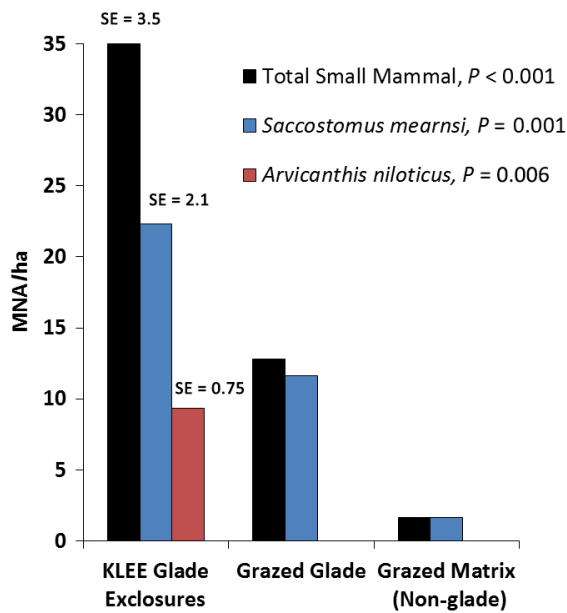


Fig. 5. Aggregate densities (minimum number alive/ha) of *Saccostomus mearnsi*, *Arvicanthis niloticus*, and total small mammals on all replicates of the five treatments of large-mammalian herbivore exclusion at three black cotton (Kenya Long-term Exclusion Experiment, KLEE) plots sampled at their 0.25-ha glade sites (Appendix S1: Fig. S3), plus a non-adjacent glade site and a non-adjacent matrix (non-glade) site. (These two species constituted $\approx 93\%$ of the individual small mammals captured on KLEE glade plots.) P -values from chi-square goodness-of-fit tests.

type (Table 2). For the combined data set, the positive partial regression coefficient for soil type indicates increased densities on red sands. Additionally, grass height was an important positive predictor within black cotton sites (see also Appendix S1: Fig. S14), and dead-stem density was the most important and positive predictor within red sands sites. Live-stem density was a positive variable for both soils combined but not for either separately. These three vegetative variables were positively correlated with Exclude for the combined data set, though not quite significantly so for live-stem density (Table 2; vs. grass height $r = 0.57$; $P < 0.001$; vs. live stem $r = 0.24$; $P = 0.08$; vs. dead stem $r = 0.41$; $P = 0.002$).

In the best multivariate models predicting species diversity, both greater H' and greater S were most strongly associated with taller grass for all sites, as well as for each soil type separately

(Table 2B, C). Exclude was included, and loaded positively, in all three data sets predicting S but only in the black-cotton data set predicting H' . Greater richness and Shannon–Wiener diversity were both associated with red sands in the combined data set (Table 2B, C). Dead-stem density loaded negatively in five of six runs predicting diversity, even though it was positively correlated with exclude in black cotton and overall (Table 2). Although loading last, the partial regression coefficient for Glade in the model predicting S for both soils was negative (Table 2C; cf. Fig. 2: bush exclusions had greater species richness than glade exclusions in the generally more species-rich red sands).

Treatment effects on small-mammal biomass density and body mass of *Saccostomus mearnsi* and *Arvicanthis niloticus*

Small-mammal biomass was greater on red sands, within exclusions, and on enriched sites (glades; two-factor ANOVA, Soil and Exclude as main effects, plus interactions, Glade as covariate; all P s > 0.05 ; see Appendix S1: Fig. S2a, b). The two most abundant species in this study, overall, the diurnal grazer *A. niloticus* and the nocturnal omnivore *S. mearnsi*, each reached greatest abundance within glade total exclusions on both soils. Excluding individuals weighing < 30 g (juveniles and subadults; no animal of this weight was found to be reproductively mature), *A. niloticus* within black-cotton glade total exclusions (KLEE Zero) were 20% heavier (median 85.5 g, mean 84.4 ± 29.2 g, $n = 16$) than on red-sands glade exclusions (median 71.0 g, mean 67.8 ± 22.2 g, $n = 52$; $H = 3.81$, $P = 0.05$, $df = 1$). Only 31% of 16 animals from black-cotton exclusions were females, whereas 52% of the 52 animals from red-sands exclusions were females. There was no significant sex difference in body mass (30 females: 70.7 ± 24.2 g; 38 males: 72.5 ± 25.7 g; $t = 0.30$, $P = 0.77$, $df = 63$). Adult *S. mearnsi* (≥ 30 g) were non-significantly heavier on black-cotton glade total exclusions (median 72.5 g, mean 72.9 ± 19.2 g, $n = 66$; 58.5% females) than on red-sands glade exclusions (median 67.0 g, mean 66.6 ± 18.8 g, $n = 31$; 35.5% females; $H = 2.31$, $P = 0.13$, $df = 1$). Male *S. mearnsi* (74.3 ± 21.7 g, $n = 47$) in this sample were 10% heavier than females (67.2 ± 15.8 g, $n = 49$), though not quite significantly so ($t = -1.81$, $P = 0.07$, $df = 83$).

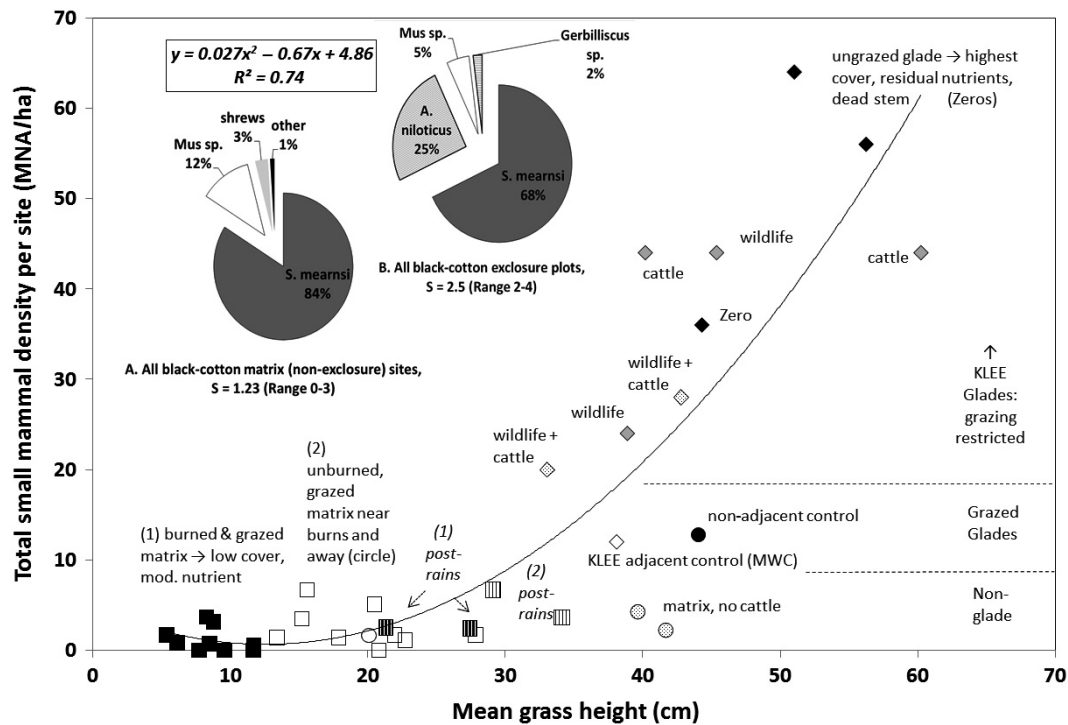


Fig. 6. Relationship between small-mammal density and mean grass height at all black-cotton study sites sampled in both 2006 and 2008. Quadratic regression is significant ($F_{2,33} = 30.4$, $P < 0.001$). Diamonds = Kenya Long-term Exclusion Experiment (KLEE) glade enclosure plots: solid black (complete [Zero] exclusions); gray (partial exclusions, lower grazing, either W or C); stippled (partial exclusions, higher grazing, WC); open (grazed KLEE controls, MWC). Circles indicate black cotton matrix sites non-adjacent to burns or KLEE: solid (control glade); open (control non-glade); stippled (non-glade matrix sites where native ungulates grazed but cattle did not). Squares indicate prescribed burn sites: open (unburned patches); solid (burned patches); nested within these, mostly sampled during dry periods in 2006, are four re-samples during wet period in 2008—black with white vertical stripes (two burned patches) and white with black vertical stripes (two unburned patches). See *Methods* for further site description.

Similarly, *S. mearnsi* had significant or marginally significant differences in mass, based on soil type ($F_{1, 111} = 6.3$, $P = 0.01$) and sex ($F_{1, 111} = 3.3$, $P = 0.07$), with no soil \times sex interaction ($F_{1, 111} = 2.1$, $P = 0.15$); heavier mice tended to be male and on black-cotton glade exclusions. For the 126 *S. mearnsi* caught on all black cotton sites, grouped by habitat/treatment—glade total exclusions, glade partial exclusions, glade controls, and matrix controls—mean weight was similar across the four treatments ($F_{3, 122} = 0.45$, $P = 0.71$).

DISCUSSION

Our measures of small-mammal density in the presence of LMH on both soil types were low for

a productive equatorial tropical savanna ecosystem (range of $0\text{--}6.7\text{ ha}^{-1}$ for black cotton and $1.8\text{--}8.5\text{ ha}^{-1}$ for red sands). Estimates in similar, but largely ungrazed, ecosystems in Africa are uniformly higher (Kenya grassland near Nairobi: $7\text{--}52\text{ ha}^{-1}$, Martin 1985, fallow farm fields in Tanzania, up to 230 ha^{-1} ; wetter ungrazed subtropical grassland in Swaziland, $>100\text{ ha}^{-1}$; Monadjem 1999), as they are in subtropical grasslands of Kruger National Park (lacking cattle; $20\text{--}60\text{ ha}^{-1}$; MacFayden et al. 2012). Maximal small-mammal densities in LMH exclusions in this study (64 ha^{-1} in black-cotton plots, 131 ha^{-1} in red-sands plots; Appendix S1: Figs. S9, S10; and roughly a doubling of species richness and diversity compared to controls; Figs. 2, 4; and

Table 2. Results of model selection analyses to determine the best model for predicting total small-mammal density and diversity.

Response variable and data set	Sampling sites	Best model	aR ² (%)	Mallows' C _p	P
(A) Small mammal density (MNA/ha)					
Both soils	54	+Exclosure, +Glade, +Live, +Soil	77.3	3.3	<0.001
Red	18	+Dead, +Exclosure, +Glade	76.7	1.8	<0.001
Black	36	+Exclosure, +Glade, +GrassHt	84.4	1.1	<0.001
(B) Small mammal diversity (H')					
Both soils	54	+GrassHt, +Soil, -Dead	67	2.7	<0.001
Red	18	+GrassHt, -Dead	47.6	0.1	0.003
Black	36	+GrassHt, +Exclosure, -Dead	50.4	1.9	<0.001
(C) Small mammal species richness (S)					
Both soils	54	+GrassHt, +Soil, +Exclosure	70.9	3.2	<0.001
Red	18	+GrassHt, +Exclosure	45.3	2.3	0.004
Black	36	+GrassHt, +Exclosure, +Live, -Dead	66.4	5.1	<0.001

Notes: aR², adjusted R²; MNA, minimum number alive. (A) Small-mammal species diversity (B), and small-mammal species richness (C) on two different soil types in central Laikipia, Kenya. Results show best-subsets, multiple regression model selection by Mallows' C_p minimization procedure for small-mammal surveys conducted in 2006 and 2008. The most parsimonious subsets were chosen from 6 to 7 predictor variables: (1) mean grass height, (2) live-stem hits (Live), (3) dead-stem hits (Dead), (4) bare soil hits, (5) glade, (6) exclosure (0–2), and where applicable (7) soil type (black = 1; red = 2). Predictor variables are listed in the order in which they entered the model in stepwise selection; + or – indicates the sign of the partial regression coefficient for that predictor on the response variable. See *Methods* for further descriptions of variables and model-selection procedure.

Appendix S1: Fig. S8) are more comparable to abundance and diversity reported by the aforementioned studies in other African grasslands lacking large grazers or in otherwise disturbed systems. Similarly, in North American Chihuahuan Desert grassland without large grazers, rodent densities were 15–25 ha⁻¹ during peaks and 0–10 ha⁻¹ during low periods (Lightfoot et al. 2012).

One difference between our study and the aforementioned African studies is that *Mastomys* spp. comprised 44–70% of small mammals in the latter but were never abundant in ours, nor in a previous study at MRC (Keesing 1998b). High relative abundance of *Mastomys* spp. has been suggested as an indicator of disturbance in tropical and subtropical African grassland ecosystems (Avenant 2000). Although there was an additive effect of wildlife and cattle suppressing abundance and diversity of small mammals in our study, consistent with other recent studies in this habitat (Goheen et al. 2010, Keesing and Young 2014), on a hectare scale, cattle-created glades enhance small-mammal abundance (Young et al. 2015).

The only diurnal rodent in this study, a specialist grass folivore (Bergstrom 2013), *A. niloticus*, was captured almost exclusively inside exclosures (Figs. 2–4), at densities in black-cotton glades four to six times higher than a study on

non-glade portions of KLEE Zero exclosures (Keesing 1998b), and up to 20 times higher on red-sands glade exclosures. This species was also highly sedentary within exclosures, not even moving between adjacent experimental treatments. While these exclosures may exclude predators (large carnivores, at least, are partially excluded; D. Kimuyu, unpublished data), *A. niloticus*, more than the nocturnal small mammals, would demonstrate risk-averse behavior with respect to diurnal visual predators, and raptors still had access to these plots (Appendix A in Ogada et al. 2008), as did snakes, which occur at higher densities inside LMH exclosures (McCaughey et al. 2006). Because live-stem density was not greater inside exclosures on either soil type, but dead-stem density and vegetation height were greater inside exclosures on the black-cotton glades, and vegetation height was greater and bare-soil percentage lower inside red-sands exclosures, the very strong preference for exclosures by this small diurnal grazer probably reflects its need for enhanced visual cover (see also Long et al. 2012).

Given that *S. mearnsi* is a generalist, with greater arthropod, forb, and tree-seed intake than *A. niloticus* (Bergstrom 2013), its greater density inside exclosures than outside, particularly on red sands where it is otherwise rare, may possibly be explained by enhanced availability of insects

(Pringle et al. 2007, Jonsson et al. 2010) or browse or seeds from forbs and shrubs such as *Acacia* spp. (Goheen et al. 2004, Sankaran et al. 2013, Long et al. 2017). Similarly, enhanced insect availability and enhanced visual cover may explain why 14 of 15 captures of the diurnal insectivore *E. rufescens* were inside or adjacent to exclosures in red sands.

Feces of *S. mearnsi* individuals captured inside exclosures were significantly more enriched in N (higher $\delta^{15}\text{N}$) than those caught outside exclosures, which may indicate higher forage quality inside, whereas the two groups did not differ in C:N ratios (Bergstrom 2013), indicating a similar degree of omnivory. *Saccostomus mearnsi* were no heavier inside exclosures on either soil type than they were on grazed sites, but they were sharing the former habitat with much greater densities of conspecifics and small mammals in total. The female-biased sex ratio inside black-cotton exclosures, compared to male-biased sex ratio outside exclosures, may also reflect greater availability of food resources, which would be a strong attractant for the greater metabolic needs related to reproduction in the female. Doubling of coleopteran abundance within KLEE exclosures was attributed to indirect effects of enhanced herbaceous cover in the absence of LMH grazing (Pringle et al. 2007). Enhanced arthropod food resources might explain why insectivorous (Bergstrom 2013) and non-cover dependent *Gerbilliscus* spp. in black cotton were found only inside exclosures.

Red-sands matrix habitats of MRC are inherently more diverse topographically and floristically (Augustine et al. 2011), and more heterogeneous in terms of habitat for small mammals (e.g., incised seasonal stream channels; rock outcrops [to which *Acomys* spp. were strongly tied]; patches of tall grass at the bases of denser shrub growth—out of reach of large grazers—offering forms of cover not available in black cotton; Augustine 2003), and this is reason enough for their much greater diversity of small mammals. Conversely, vegetation on black cotton soils is relatively homogeneous, except for the glades and low termite mounds (Pringle et al. 2010). Our results suggest that the dominant *S. mearnsi* has adapted to this waterlog-prone soil by exclusively inhabiting termite burrows, whose properties include less heavy-clay and thus reduced, potentially destructive

shrink–swell dynamics in rainy periods (Keesing 1998a). In contrast, all species captured in red-sands exclosures were also found in red-sands matrix, and at least one found in the latter was not found in the exclosures (Figs. 3, 4; Appendix S1: Table S1b). One reason for the dramatic difference in small-mammal densities inside and immediately outside red-sands glade exclosures was the removal of cover by close cropping of control (unfenced) glades by LMH. Cross-fence differences in grass height and small-mammal abundance were less dramatic on black-cotton glades because this heavy cropping did not happen to the same extent. Such greater exclosure-effect sizes on red sands than black cotton were also found for densities of lizards, trees, coleopterans, and total arthropods and were attributed to the lesser primary productivity of the red sands soil (Pringle et al. 2007).

Even though male pouched mice were heavier than females on black-cotton burn sites, similar mass of mice caught on burned and unburned patches argues against a nutritional advantage to foraging in areas with potentially better quality forage, at least not one that outweighs the cost of having larger home ranges in potentially more stressful habitats (which *S. mearnsi*, particularly males, did). Indeed, on these same and other nearby burn plots, crude protein in grass was significantly higher and acid detergent fiber significantly lower on burned patches than on unburned patches, at least through 35 months post-burn (Sensenig et al. 2010). Also, arthropod biomass was greater on burned patches in the 9-ha burn sites (Gregory et al. 2010, although this effect may be limited by drought and increasing time elapsed since burning), which would benefit the omnivorous *S. mearnsi* (Bergstrom 2013).

Taken together, these patterns suggest that mice were choosing better cover over higher quality forage. As an a posteriori test, stable C and N isotope data on *S. mearnsi* feces (collected for Bergstrom 2013) showed that $\delta^{15}\text{N}$ values—a possible indicator of forage quality—did not significantly differ in mice captured on burned vs. unburned patches ($H = 0.87$, $P = 0.35$) but that C:N ratios were higher on burned patches ($H = 4.12$, $P = 0.04$), indicating a greater proportion of plant material consumed there, or conversely, a greater proportion of arthropods consumed on unburned patches. The preference of even pregnant and lactating females for unburned patches (although

slightly weaker than for non-reproductive females) may suggest enhanced food resources, possibly arthropods, on unburned patches (female small mammals may substantially increase their exposure to predation risk while lactating; Larimer et al. 2011).

Although we found no effects of burn size or patchiness on small-mammal occurrence, it was surprising that greater use of unburned than burned patches was still apparent four years post-burn. Springtime densities of small mammals in Kansas tallgrass prairie increased following fire where large grazers were absent but decreased in plots with either bison or cattle present (Matlack et al. 2001), probably because cropping by large grazers removed cover for small mammals. One would expect this suppression of cover to end after a few rainy seasons (or even one; Yarnell et al. 2007, Plavsic 2014); the fact that it continued for so long on black-cotton burns may be because, as ambitious as the experimental burns were, they were still too few and covered too small an area not to be effectively saturated by the great biomass of wild and domestic grazers in an otherwise unburned landscape, at least for several years. Previously, when in widespread use by pastoralists and European range managers, frequent fires would have covered much larger overall area (Heady 1972) and not have resulted in the local concentration of large grazers seen here. It is also possible that *S. mearnsi* could be drawn to the greater availability of seeds of forbs and particularly *Acacia* spp., living trees of which were denser on the unburned plots a few years after the fire (Long et al. 2017), although body mass was the same for this species on burned as unburned patches.

Even maximal per-plot total biomass density of small mammals in exclosures in this study was only approximately one-tenth that of the large herbivore guild in Laikipia (Augustine 2010), suggesting their suppression by the latter. However, the higher metabolic and turnover rates of small mammals than metabolically slower LMH (Rebollo et al. 2013) would magnify their bioenergetic and trophic effects beyond that represented by their standing biomass.

This study and others from the same sites (Keesing 1998a, b, Bergstrom 2013) have documented at least 11 species of small rodents and several insectivores (not including several likely

cryptic species; J. Kerbis, *personal communication*) whose abundances can fluctuate dramatically over time and space. At least one of these—*A. niloticus*—occurred at very high densities inside exclosures that were many kilometers apart yet virtually never was encountered in the intervening habitats. *Saccostomus mearnsi* was abundant in some red-sands exclosures many kilometers removed from its typical black-cotton habitat. Conversely, insectivorous *Gerbilliscus robustus*, generally common in red sands and absent from black cotton, dispersed several kilometers to inhabit a black-cotton glade exclosure. This suggests some small mammals in this system are capable of occasional long-distance dispersal between widely spaced patches of suitable habitat (with heavily grazed and recently burned habitats intervening; see Letnic 2002), and these patches serve as scattered source populations to maintain regional metapopulations in the face of strong habitat and trophic effects from large grazing and browsing herbivores.

Extreme responses in this study of *A. niloticus* to LMH exclusion—reaching densities of 80 ha⁻¹ in single red-sands exclosures—rival densities reached by *Mastomys* spp. in disturbed systems elsewhere in Africa. This may be a concern if loss of native large grazers continues, because this rodent is known as not only an agricultural pest but also a carrier of intestinal schistosomiasis (Duplantier and Sene 2000) and was implicated in the origins of bubonic plague in Egypt (Panagiotakopulu 2004). In the shrinking landscapes still dominated by the full assemblage of native LMH along with traditionally managed cattle, such as in Laikipia, this and other species of small mammals persist at low densities and to a greater degree segregate into their preferred habitats, with red sands harboring the greater diversity.

CONCLUSIONS

The 10-fold positive effect of LMH exclusion on density of both MNA and biomass of the relatively species-rich small-mammal community on red-sands glades—plus the similar exclosure effect size for red-sands matrix savanna—and the fourfold to fivefold LMH exclusion effect on the relatively species-poor small-mammal community of black-cotton glades supports the

cover-limitation hypothesis. *Saccostomus mearnsi* and *A. niloticus* accounted for most of the increased abundance and biomass within glade exclosures on both soils, with *A. niloticus* clearly responding to increased cover. Preference of *S. mearnsi* for unburned patches in black-cotton matrix suggests it, too, prefers dense cover. The possibility of greater insect availability in both unburned savanna and within LMH exclosures could also explain this omnivore's preferences, but there were no differences in mean body mass among the various black-cotton treatments and controls in this species, which might have resulted from greater food availability in the habitats it chose. *Gerbilliscus* spp. was common in all red-sands sites, including those with little vegetative cover, but its increased density inside exclosures suggests increased food resources for this insectivorous but non-cover-dependent rodent (Bergstrom 2013). Because we found *Acomys* spp. to be highly petrophilic, the lack of exclosure placement, or glade occurrence, in rocky microhabitats precluded tests of enrichment or LMH exclusion effects.

Small-mammal densities or biomass were not significantly greater on burn sites (though they were greater in unburned than burned patches) than black-cotton matrix sites, again suggesting that cover (and not fire-enhanced forage quality) drives small-mammal habitat selection. Throughout this study, LMH were effectively usurping the enhanced nutrients of burned patches while simultaneously removing cover. One experiment that remains to be done—to determine whether small-mammal populations are limited by forage quantity and quality, independent of large grazers—is LMH exclusion from burn sites.

Although total small-mammal biomass tended to be greater inside exclosures and in red sands habitats, mean body mass of individual *S. mearnsi* and *A. niloticus* was greater in black-cotton glade exclosures than in red-sands glade exclosures. This could reflect a tradeoff of lesser small-mammal diversity and abundance in the relatively featureless and less plant species-rich environment (black cotton) that nevertheless has greater primary productivity and promotes greater growth rates in primary consumers. The importance of grass height as a predictor of small-mammal richness and diversity on both soil types suggests that this vegetative structural attribute provides a refuge

for many small mammal species, with a comparable per capita provisioning of food resources as grazed matrix, but with enhanced protection from predators. Grass height in black cotton reached its maximum in total LMH exclusion plots on glades (Fig. 6), which, although they possess residual enrichment as former bomas, have not had additional LMH fecal enrichment for many years (unlike partially or totally grazed glades, or burned patches, which receive continuing nutrient subsidies from LMH and have shorter, and much shorter, grass, respectively). This reinforces that it is cover quantity, not forage quality, that drives the highest densities of small mammals seen in this study, the components of which are primarily *S. mearnsi* and *A. niloticus*.

In the context of complex interactions among fire, LMH grazing, and soil nutrients in grassland systems, our findings suggest these processes exert cascading effects on diversity and abundance of small mammals. This may have important consequences for savanna community composition, and even human health, when large grazers and fire are removed from the landscape. Preserving both of these natural processes keeps small mammals patchily distributed in their specialized niches and generally at low densities.

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DATA AVAILABILITY

Data associated with this paper are available at: <https://www.researchgate.net/project/Response-of-African-savanna-small-mammal-communities-to-fire-and-large-grazers>

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2519/full>