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KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya

Truman P. Young^{1,2,4}, Bell Okello^{2,3}, David Kinyua², Todd M. Palmer^{2,4}

Abstract. Livestock and wildlife share much of their respective ranges throughout the semi-arid ecosystems of the world. As the profitability of livestock production becomes more marginal and wildlife values increase, there is a need to understand the interactions between livestock and wild large mammalian herbivores (and other indigenous biodiversity). To address this, we have established a long-term multi-species herbivore exclusion experiment in the Laikipia ecosystem in Kenya. Using a series of 'semi-permeable' barriers, we are differentially excluding various combinations of cattle, large wild mammalian herbivores, and 'mega-herbivores' (giraffes and elephants) from a series of replicated four hectare plots. We are monitoring soil characteristics, tree and shrub population structure, herb layer vegetation structure and composition, primary productivity, range use by non-excluded large mammals, physical and chemical plant defense, populations of additional animal taxa (rodents, birds, grasshoppers), and the community of acacia ant symbionts. This multi-disciplinary project is one of the first to include controlled, replicated exclusion of combinations of multiple guilds of rangeland herbivores in the same place at the same time. Established in 1995, the enclosures offer opportunities for collaboration for a wide variety of applied and basic ecologists. We report here 1) details of the experimental design, 2) quantitative vegetation analysis of this important grazing ecosystem, 3) evidence of the effectiveness of the herbivore enclosures, and 4) a summary of some preliminary results.

Key Words: cattle, livestock, enclosure, wildlife, megaherbivore, elephant, giraffe, fencing, Africa

¹Department of Environmental Horticulture, University of California, Davis, CA USA 95616.

²Mpala Research Centre, P.O. Box 555, Nanyuki, KENYA.

³Department of Range and Forage Science, University of Natal, South Africa.

⁴Ecology Graduate Group, University of California, Davis, CA, USA 95616.

Introduction

Rangeland management is undergoing re-evaluation worldwide. There is increasing emphasis on management activities that are both sustainable and more compatible with native biodiversity. As the profitability of livestock production becomes more marginal and wildlife values increase, there is a growing need to understand the interactions between livestock and wild large mammalian herbivores and other indigenous biodiversity.

Semi-arid ecosystems cover the majority of the land area in sub-Saharan Africa, and the majority of these are acacia savannas (Cole 1986, Menault et al. 1985). These ecosystems have been used (and manipulated) by people of traditional cultures for many centuries, and are currently under rapidly increasing pressure for both intensive cattle production and arid-land farming (West 1971, Bernard et al. 1989, Gichohi et al. 1996). These pressures can result in local, regional, and global environmental problems (Gichohi et al. 1996, Herlocker 1996), including soil erosion, threats to endangered species such as elephants and rhinos, and desertification, with its potential effects on global warming. A detailed

understanding of the ecology and dynamics of these ecosystems is critical to long-term development, management and conservation (Bourliere 1983, Tothill and Mott 1985, Hansen et al. 1986, Walker and Menault 1988, Christensen et al. 1996).

Virtually all indigenous large mammal species in Kenya have more individuals on multiple-use lands (mostly on semi-arid range lands) than on land inside parks and reserves (Mbugua 1986, Western 1989). The future of these populations depends on the interaction between enlightened rangeland management and wildlife needs. Interactions between livestock and wildlife in Africa are often negative (reviewed in MacMillan 1986, Prins 1992). There is growing evidence, however, that many wildlife species are not incompatible with moderate livestock production, and can even be beneficial. Because wildlife can provide much needed additional revenue in the form of tourism or game ranching, a mixed strategy of wildlife and cattle may be economically optimal and help maintain biodiversity (Hopcraft 1990). Opinions on the effects of livestock production on biodiversity in the western United States are similarly disparate (Brown and McDonald 1995, Fleischner 1995).

African savannas are among the most intensively studied ecosystems in the world (e.g., Sinclair and Norton-Griffiths 1979, Huntley and Walker 1982, Bourliere 1983, Tohill and Mott 1985, Cole 1986, Proctor 1989, Sinclair and Arcese 1995, Gichohi et al. 1996). Various factors determine the structure and function of savannas, including soil chemistry (Bell 1982, Chapin and McNaughton 1989, Hogberg 1989), small mammals (Belsky 1984, Happold 1983) and invertebrates (Josens 1983). However, rainfall, fire, native herbivores, and livestock are the dominant forces in short-term and long-term savanna community dynamics, and have been the subjects of numerous experimental and descriptive studies (e.g., Kelly and Walker 1976, Lock 1977, Hatton and Smart 1984, O'Connor 1985, Ernst and Tolsma 1989, Moe et al. 1990, Belsky 1992, Stuart-Hill 1992). Considerable literature exists on the effects of various cattle grazing and burning strategies on range quality in Africa (reviewed in O'Connor 1985), and on the effects of indigenous herbivores on the vegetation of protected areas (reviewed in McNaughton 1979, Gordon and Lindsay 1990, McNaughton and Banyikwa 1995, Sinclair 1995, Gichohi et al. 1996).

However, little is known about the interactions among wildlife, domestic livestock, and vegetation in Africa. Understanding these interactions requires controlled experiments that simultaneously manipulate multiple potential causative factors, and long-term monitoring of these experiments. Despite the high densities of native herbivores on many commercially managed rangelands, experimental approaches to the interactions of livestock, wildlife, and vegetation are rare (see Loft et al. 1987, Brown and Heske 1990, Hobbs et al. 1996a,b). There have been no controlled factorial experimental studies on the interactive effects of different domestic and native herbivores on rangeland vegetation in any African ecosystem (Werger 1977, Cumming 1982).

We have initiated the Kenya Long-term Exclusion Experiment (KLEE) in an attempt to address the interactions between livestock and native biodiversity on the rangeland that they share. This experiment is part of the broader Integrated Studies of Behavior and Ecology in the Laikipia Landscape (ISBELL) that includes research by a parallel team of behavioral ecologists.

Methods

Study area

The experiment is located at the Mpala Research Centre in Laikipia District, Kenya. The Centre is a collaborative trust dedicated to conservation in the Laikipia ecosystem and the welfare of its inhabitants. It is administered by a consortium consisting of George Small (the owner of Mpala Farm), the National Museums of Kenya, the Smithsonian Institution, the Kenya Wildlife

Service, and Princeton University. The Centre maintains growing physical plant consisting of a laboratory, administrative offices, and full board accommodation for resident and visiting researchers. It is located on its own 1200ha parcel of land, and researchers have access to the 17,000ha Mpala Farm to the north. Several similar properties nearby also host research, most notably the adjacent Segera Ranch.

These properties are working cattle ranches that encourage native biodiversity. Their stocking rates are moderate (one livestock unit per 5-8ha), and below levels that are detrimental to the range. Year-to-year variation in rainfall is high, and averages 500mm (in the north) to 650mm (in the south), with peaks in April, July, and November. The native biodiversity on Mpala/Segera consists of an estimated 600-800 plant species (>450 collected thus far), more than 300 bird species (current list 280 spp.), and at least 70 mammal species, including 28 species of large herbivorous mammals (20 ungulates) and 19 species of large carnivorous (and insectivorous) mammals (see Appendix 1). Lists of rodents, bats, reptiles, butterflies, and grasshoppers are being compiled.

Two major soil types underlie the Laikipia ecosystem. On the high central plain where the experimental plots are located, level soils of impeded drainage predominate, especially deep clay 'black cotton' vertisols. Similar soils (with similar vegetation) occur at other sites of impeded drainage within Laikipia, and in many sites elsewhere in East Africa (including Nairobi National Park and the western extension of Serengeti National Park). These soils support some of the most productive rangelands in East Africa. Elsewhere in Laikipia, red rocky friable soils predominate on more sloping topographies. More information on the soils and vegetation of the red soil community can be found in Young et al. (1995). Approximately 10% of Mpala and virtually all of Segera are underlain by black cotton soils.

Both soil types are characterized by a landscape mosaic with numerous isolated 'glades'. These features are treeless, have high levels of mineral nutrients, and are preferentially used by wild and domestic herbivores (see Young et al. 1995; see also below). These glades are usually less than one hectare in area, but there are also some extensive areas ('plains') of glade vegetation, most notably on Segera. As in the red soils, glades on black cotton soils are higher in nutrients than are surrounding black cotton soils (Table 1), and are 'hot spots' of herbivore activity.

Compared with those on the red soils, black cotton communities are relatively depauperate in species for some but not all groups. The overstory is dominated by a single tree, *Acacia drepanolobium*, that accounts for

>97% of the overstory cover in the study area (Young et al. 1997, see also below), and is always more than 50% of overstory cover throughout this and similar ecosystems (TPY, pers. obs. BO, unpubl. data). Five grass species and two forbs account for the vast majority of the understory (more than 90% of the relative cover). The fauna of both birds (J. Lynch, pers. comm.) and rodents (Keesing 1997, in press, in review) are also far less rich on the black cotton soils than on the adjacent red soils. However, the species richness of large ungulate herbivores (10-13 species) and carnivores (four species large enough to prey on ungulates) is equally great on both soil types (not including the specialized habitats of rivers, rocky outcrops, and escarpments).

Experimental design

Several conditions make this site ideal for our long-term large-scale experimental study: 1) the Mpala Research Centre (and its partners) are stable and supportive of this research; 2) the baseline ecology of this biome in general, and this ecosystem, are well-studied; 3) the wild and domestic mammalian herbivores are numerous and diverse; 4) the plant community on black cotton soils is both floristically simple; and 5) these widespread soils support some of the most productive East African rangelands.

Extensive preliminary surveys of the study areas within Mpala, carried out between 1992 and 1995, allowed us to identify suitable sites for the establishment of experiments, to maximize homogeneity among potential experimental plots, and to provide a baseline against which to measure long-term change. This background research consisted of the following studies:

1. Baseline surveys of the soils, vegetation, and herbivore use throughout the ecosystem. Some of these baseline data have already been incorporated into published papers (Young et al. 1995, 1997). We are also developing a plant checklist in collaboration with the National Herbarium and the Smithsonian Institution, a local herbarium for the Research Centre with reference collections, and a series of guides and field keys (both reproductive and vegetative) of all the plants found in the study area and in the entire Laikipia ecosystem. In addition, we are collecting daily rainfall and temperature records.
2. An in-depth study of the nutrient-rich glades that occur throughout the study area (Young 1995, Young et al. 1995), and that directed our decisions about the placement and size of the plots.
3. Baseline data on soils and vegetation at the specific sites of the plots before the exclosures were constructed (see below).

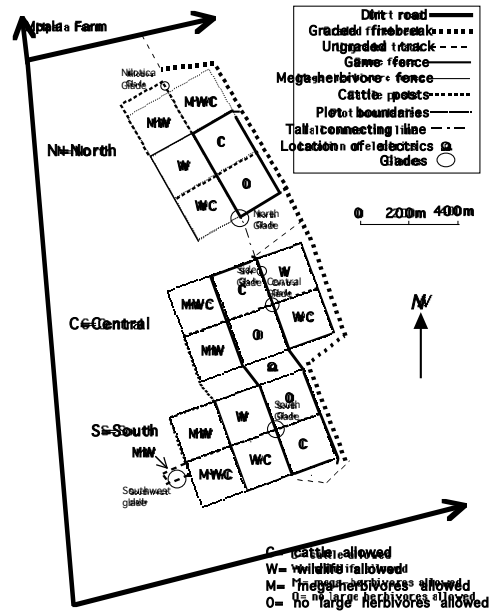


Figure 1. Schematic of experimental plots in Laikipia, Kenya. The letters in each plot indicate which herbivores are allowed: C - cattle, W - wildlife, M - megaherbivores, O - all large herbivores excluded.

Herbivore barriers

We are using a series of 'semi-permeable' barriers to exclude different combinations of large mammalian herbivores. These barriers are similar to those designed by the Kenya Wildlife Services, and have a proven track record in East Africa (Hoare 1992), and in this ecosystem (Thouless and Sakwa 1995). Electric fencing is particularly effective (especially against destructive elephants) when a) the resident herbivores are already familiar with similar fences, avoiding a painful and expensive 'learning curve', and b) when the area enclosed is small, and each stretch of fence is relatively short (our longest linear section is 500m), allowing herbivores to go around rather than through. We use three types of barriers:

1. The 2.3m wildlife fence is eleven strands of bare wire, alternating live and ground. Every second, a burst of 6-7,000 volts is sent through the live wires via a battery charged by a solar panel. The lower nine wires are 16 cm apart, and the spacing for the upper two is 32 cm. The lowermost (ground) wire is at ground level. To minimize shorting of the lowest electric wire, the area along the bottom of the fence is kept free of vegetation by slashing and by regular applications of Round-up® on calm days during the growing seasons using a backpack sprayer. In addition, any higher branches growing into the wires are cut back regularly. In three of the plots enclosed by this fence, there are 1.5m wide gates that can be opened to allow entry by cattle. These gates form a crush to aid in

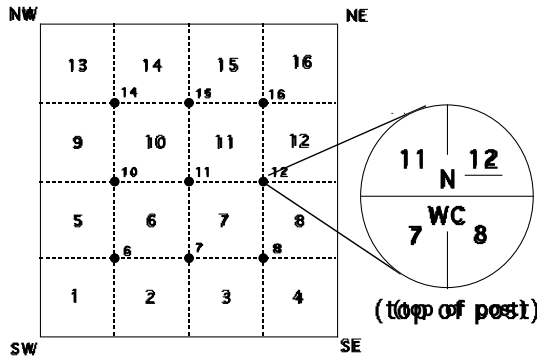


Figure 2. Each four hectare plot is subdivided into sixteen 50m x 50m sub-quadrats. These sub-quadrats are numbered from the southwest (SW) corner in each plot. There are nine small posts located at the internal corners of these sub-quadrats (shown above as small solid circles). Each post is numbered in such a way that a sub-quadrat shares the number of the post at its southwestern corner. This is also the greatest number on each post. On top of each post is a imprinted metal plate showing which four sub-quadrats it corners, with the post number under-lined (see illustration). In the center of the plate are letters showing the block (above: N, C, or S) and plot (below: 0, C, W, WC, MW, or MWC). Locations within each sub-quadrat can be identified with simple x,y coordinates ranging from 0,0 (SW corner) to 50,50 (NE corner).

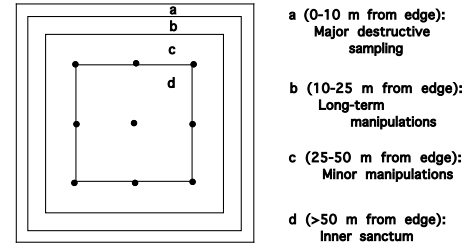


Figure 3. Each plot is a series of nested quadrats, becoming more restrictive as one moves inward. In the innermost one hectare ('d': all area more than 50 m from an edge), only short-visit descriptive studies are allowed. Although flags and tags will be allowed, there will be no manipulative experiments. Short-term student projects will not be allowed. In the second ring ('c'), minor manipulations will be allowed, such as productivity cages and the collection of plant tissues and soil samples. In the next ring ('b'), longer-term manipulations will be allowed, such as rodent enclosures, burning(?) and artificial herbivory experiments. In the outermost ring ('a'), major destructive sampling will be allowed, such as soil profiles, root excavations and bush clearing.

pushing cattle. are hinged on the corner, so that the gate and the fence

2. The mega-herbivore fence (also called a 'dingle-dangle' fence) consists of a single live wire 2m off the ground, and two ground wires. One ground wire is located 32 cm above the live wire. The other runs along the ground, 60cm outside the plot (to increase the chances that an elephant or giraffe will be standing on it when contacting the live wire). Along the live wire, there are single wires ('dingle-dangles') 50 cm long hanging down every 50cm. This fence is not cleared for vegetation, except branches near the upper wires.

3. The cattle barriers are visual. Every 10m, there is a short post (60cm high) painted red on the cattle exclusion side. All cattle on the property travel in discrete herds of ~100 head and are accompanied by individual herders on foot. The cattle herders and the person documenting the cattle run use the painted post markers to ensure that cattle do not enter excluded areas.

The cattle are allowed to graze on a controlled schedule comparable to that generally utilized on Mpala. The number of cattle and the duration of such grazing (in minutes) are quantified for each cattle 'run' inside the plots. Because there are no other large mammals inside the wildlife fences, we can use a physical barrier between areas where cattle are allowed or excluded. This is a single electrified wire 60cm off the ground, attached to short posts. The area below this wire is kept clear of vegetation.

In addition, nine permanent 3m x 7m rodent enclosures (and nine controls) have been placed in the total exclusion plots (Keesing 1997).

A large level tract of acacia wooded grassland of several hundred hectares in the black cotton soils was selected for the study. This site had no evidence of recent burning. Eighteen similar four-hectare plots (200m x 200m) were selected for the following treatments (see Figure 1):

- 1) Full fencing to exclude all large herbivores (three replicates).
- 2) Full fencing, but cattle allowed to graze periodically (three replicates).
- 3) High single-strand electric fencing to exclude elephants and giraffes only (three replicates).
- 4) As in #3, but cattle also excluded (three replicates).
- 5) Unfenced, cattle allowed to graze (three replicates)
- 6) Unfenced, cattle are not allowed to graze (three replicates).

We therefore have a complete 2 x 2 factorial design for the effects of cattle and wildlife (including mega-herbivores), and a complete 2 x 2 design for the effects of cattle and non-mega-herbivore wildlife. (See 'Random stratified design' section, below.)

Our experience in this ecosystem and the experience of other ecologists indicate that three replicates per treatment will be sufficient, particularly since initial site selection was carefully carried out, and baseline data have

been collected (cf. Brown and Heske 1990, Belsky 1992, Heske et al. 1994).

Because of the large size of the plots, each was demarcated into sixteen 50m x 50m subplots (see Figure 2). This allows accurate spatial information to be more easily gathered. For each plot, a variety of activities are allowed, with more manipulative activities being restricted to the edges (and even these are restricted to the minimal), and with no manipulations (only descriptive data collection) being allowed in the central hectare (see Figure 3). For any interventions allowed in the outer parts of each plot (and for the natural glades), edge effects will be quantified to protect against data biases in the innermost sampling hectare.

All eighteen plots have been bordered on their windward sides by fire breaks. Woody and herbaceous vegetation has been cleared from two parallel 5m wide strips, leaving a 2-4m buffer zone of intact vegetable along adjacent plots, and a wider buffer (20-30m) between fire breaks. These fire breaks are maintained by Mpala Farm using a road grader. The plots are large enough to include fire in sub-plot manipulations, and future decisions on experimental burning will be made in the context of ecosystem-wide patterns. Fences are also regularly patrolled to find and repair any breaks in the fence, and to test fence voltage. Any large herbivores (or their signs) seen in the plots during these patrols are recorded, and removed if inside exclosures meant to keep them out..

A stratified random design

The exclosure plots were located and oriented after we conducted extensive preliminary surveys and mapped the entire area for glades, areas of high and low *Acacia drepanolobium* density, and areas of differing typical tree height. These surveys, but not the baseline data (which were collected after plots locations were determined) were the basis of our decision for plot placement. We chose sites to be as homogeneous as possible, avoiding sites of low or high *Acacia* density. We also placed the exclosures as far as possible from graded tracks for security, and to minimize human disturbance and edge effects from the roads. We placed plot boundaries, whenever possible, across existing glades, so that different, randomly assigned treatments would occur within glades and be replicated across different glades. In addition, the six treatments sharing a type of barrier were placed so as to share a side (for cost reduction and maintenance simplicity), and similar 'access' to glades. Finally, individual plots that shared a fence were placed in differing (random) orientation to each other and to other pairs of plots (within each block).

The net result is a random stratified design that minimizes the chances that location and orientation ef-

fects (if any) will bias the results (Figure 1). An additional check against location bias is the baseline data collected before, during, and soon after the construction of the fences. These data indicate that different plots within the blocks (and to a lesser extent, the different blocks) are homogeneous for most edaphic, floristic, and physiognomic traits. Construction began in June 1995, and the exclosures have been fully operational since September 1995.

Caveats on the experimental design

We are using two cattle densities: none and moderate. Although we are considering small within-plot treatments with higher grazing intensities, we are not carrying out full treatment plots of multiple cattle densities, especially the high densities that mimic current densities in 'problem areas' and densities approaching or surpassing the carrying capacity of the land, for several reasons: 1) Many stocking density trials already have been carried out throughout Africa and in rangelands world-wide which attempt to determine which densities are associated with positive and negative environmental and economic outcomes, at least with respect to livestock production (for a review of African research, see O'Connor 1985). It is not our goal to duplicate that research. 2) We are not interested in asking how close we can get to the edge of sustainability without going over, because a) being close to this edge is by definition antithetical to the management goal of coexistence of livestock and a rich indigenous biodiversity, and b) the highly variable climates of these semi-arid and arid ecosystems make the results of such stocking experiments less than reliable for any real management use (Swift et al. 1996). 3) Instead, we are interested in the nature of the relationship between livestock and biodiversity on lands that are managed for both, which by definition are lands on which cattle densities are kept at moderate levels. 4) In addition, the current experimental design involving multiple combinations of three guilds of large herbivores is already fairly complicated (six treatment combinations), and adding even one additional level of cattle density to the two already in the design would increase the size of the project by 50%, and the managerial (and statistical!) problems would increase by even more.

Although the experiment is both large scale and long-term, it is being carried out at specific spatial (four hectare) and temporal (<20 years) scales, and this constrains the ecological issues we can and cannot address: 1) We can examine both functional and numerical responses of plants, invertebrates, rodents, and perhaps some birds to different herbivory treatments. We cannot examine numerical responses of larger (>10 kg) herbivores or mammalian carnivores. 2) We can examine

functional responses of birds, large herbivores, and perhaps mammalian carnivores ('Do they spend more time foraging in certain plots?'), from which we may risk models of numerical responses on a larger spatial scale. 3) We can address how year-to-year variation in climate affects the relationships among the various members of this community, and their short-term sustainability. We probably cannot determine the long-term sustainability of different herbivore combinations, given the tremendous variation in climate on decadal scales. 4) We can ask how different herbivore combinations influence changes in vegetation structure and composition. We cannot fully describe the kinds of (endogenous or climatically driven) cyclical variation in vegetation that have been suggested to occur on the scale of several decades (Caughley 1976, Dublin et al. 1990, Dublin 1995), although we may be able to ask which herbivores are associated with particular states or transitions in a putative ecological cycle.

Baseline data:

To maximize the power of the experimental design and opportunities for future research, we (and our collaborators) have generated several baseline data sets:

1. Soil structure and chemistry (pH and ten elemental nutrients) from both background vegetation and glade sites. Soils were taken from two depths (0-10 cm and 20-30 cm).
2. Frequency of herbaceous species from both background and glade sites, from 100 quadrats per plot.
3. Percent cover of herbaceous vegetation by species, from 100 pin frames (2500 pins) per plot.
4. *Acacia drepanolobium* density, size structure, and defense (thorn length, tannin content, and ant occupancy by species), from both fixed transects ($n > 4000$) and from stratified size sampling ($n = 1800$; see below).
5. Mapping and measurement of individuals of all other woody plant species.
6. Mapping of glade size, shape, and orientation.
7. Complete photographic coverage of the plots, from eight fixed points per plot, revisited every six months.
- (8. Rodent density by species, from 10 x 10 trapping grids- Keesing 1997).

The use of baseline data (as model covariates) and analyses of variance that explicitly incorporate block effects (to control for the remaining variation among blocks) will combine to maximize our statistical power to discern experimental effects. In addition, the replicated experimental design and diligent efforts to control for extraneous factors in the original locating of the plots should give us the power to ask about experimental effects even in the absence of baseline data (and will

therefore be useful for later collaborators whose projects measure effects for which no baseline was collected).

Baseline data methods

Densities of woody species were assessed through a series of nine 5 x 50m transects in each of the 18 plots. Within each transect, each tree and shrub was identified to species, and its height and perpendicular crown diameters measured to the nearest 5cm. Herbivore utilization was assessed on 90 marked trees within each plot, stratified by tree height. On each tree, five branch tips were tagged and regularly surveyed for herbivory. Additional trees and shrubs were similarly tagged and monitored along the edges of glades.

Understory frequency was measured through three 300m line transects. Every 3m, a 0.5 x 0.5m quadrat was placed (alternating left and right), and all species recorded to species, for a total of 100 quadrats per plot. Additional (shorter) frequency transects were run within glades. Understory cover was assessed with nine 30 (or 33) m transects, surveyed every 3m with a ten-pin point frame, for a total of 100 frames (1000 pins) per plot. Plant species are being identified in collaboration with Dr. Christine Kabuye (Chief Botanist) and Mr. Joshua Mwasya of the Herbarium of the National Museums of Kenya, and Robert Faden of the Smithsonian Institution. Duplicate collection sheets are being put into an Mpala Research Centre Herbarium.

Dung densities were measured with six 50 x 2m transects in each plot. Within each transect, each dung pile was identified to species, with ambiguous cases collected and refereed to an experienced tracker. Differences between dung of cattle and cape buffalo, and between Grevy's and Burchell's zebras, could not be distinguished reliably (Stuart and Stuart 1994); therefore all dung typical of these species was classified as 'cattle' or 'zebra' respectively.

Statistical analysis

Total aerial cover, cover by each species, and the densities of *A. drepanolobium* and other woody plants were analyzed with a Model 1 ANOVA (10 error d.f.) for the effects of blocks (2 d.f.) and treatments (5 d.f.). Cluster analysis was done using Ward's Method (JMP).

Results

Soils

The non-glade soils in the study plot are extremely heavy in clay, with values (range 52-64%) that are at the upper end of observed clay content for natural soils. As in the red soils, the glade vegetation is underlain with soils that are richer in most mineral nutrients (Table 1). Glade soils also have less clay than non-glade soils. The

black cotton soils at the study site contain 60% clay on average, with lower values (mean, 45%) in the glades ($F = 29.4$, $p < 0.001$).

Table 1. Mean soil characteristics (\pm one S.E.) of glade and non-glade sites at the experimental plots, on black cotton soils. Soil was collected at 0-30cm in August 1995. Soil nitrogen (note smaller sample sizes) was analyzed at the Range Science Department of the University of Nairobi from samples collected at 10cm in September 1997.

Soil trait	Glades (N=15)	Background (N=6)
<i>Physical</i>		
Clay (%)	45.2 \pm 1.6	59.2 \pm 0.7
Silt (%)	22.2 \pm 0.9	14.8 \pm 0.5
Sand (%)	32.6 \pm 0.9	26.0 \pm 0.4
<i>Chemical (% , unless otherwise noted)</i>		
Total N	0.28 \pm 0.06 (N=2)	0.17 \pm 0.02 (N=5)
C	1.95 \pm 0.11	1.43 \pm 0.13
P (ppm)	269 \pm 21	60 \pm 2
K	3.11 \pm 0.12	1.15 \pm 0.11
Ca	16.9 \pm 1.0	9.7 \pm 0.4
Na	1.99 \pm 0.06	1.50 \pm 0.08
Mn	1.56 \pm 0.12	1.86 \pm 0.06
Mg	4.16 \pm 0.12	3.83 \pm 0.07
pH	6.72 \pm 0.10	6.28 \pm 0.07

Overstory vegetation

Mean density of *A. drepanolobium* trees is 2267/ha, with no block and no herbivore treatment differing in density more than 22% from this mean. Analysis of variance detected no significant block ($p = 0.41$) or treatment ($p = 0.84$) effects in total density. Overall, the size distribution was strongly L-shaped (Figure 4), and was similar among blocks and among treatments. The mean height of *A. drepanolobium* trees in each of the three blocks was within 7% of the grand mean (1.38m).

Several other woody species occur in the plots, but at low densities: *Cadaba farinosa*, *Rhus natalensis*, *Acacia mellifera*, *A. brevispica*, *Balanites* sp., *Boscia* sp., and *Lippia javanica*. These species accounted for 3.2% of the woody plants less than 1.5m tall, and 0.7% of the woody plants more than 1.5m tall (2.3% overall). Many of the smaller plants of these species are represented by apparently old individuals (with stems up to 1.5 cm in diameter) that have been strongly suppressed by herbivory. Treatment (herbivore) classes did not differ in the densities of these other woody species ($F = 0.55$, $p = 0.74$), but the North block had a higher den-

sity of these rarer plants than did the Central and South blocks ($F = 5.48$, $p = 0.025$).

Understory vegetation

Baseline vegetation data demonstrate considerable homogeneity among blocks and among treatment classes. Total aerial cover was within 9% of the overall mean (58.5%) in each of the 18 plots, and there were no significant Block ($p = 0.44$) or Treatment ($p = 0.88$) effects. The five most abundant species, all grasses, accounted for 88% of the relative cover (in order: *Pennisetum stramineum*, *Lintonia nutans*, *Themeda triandra*, *P. mezianum* and *Brachiaria lachnantha*). With the exception of *T. triandra*, these five species had the same rank order in each of the three blocks. The most abundant forb was the semi-woody *Aerva lanata*. In the South block, *T. triandra* and another grass, *Botriochloa insculpta*, were significantly more abundant ($p < 0.001$, $p = 0.04$) than in the two other blocks, at the expense of the two *Pennisetum* spp. ($p = 0.025$, $p < 0.001$). The semi-woody herb *Helichrysum glumaceum* was also more abundant in the South block ($p = 0.04$). No other species differed significantly in cover among blocks. Only *B. lachnantha* differed significantly among treatments, being more abundant in the three control (MWC) plots ($p = 0.02$). In any case, these baseline data will be used as covariates in any future analyses on the effects of the herbivore treatments.

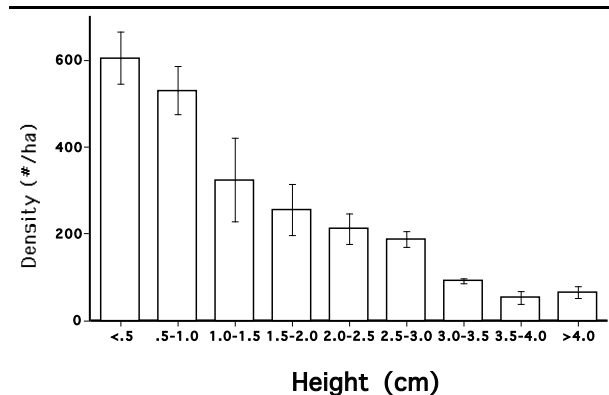


Figure 4. The size distribution of *A. drepanolobium* (total area surveyed: 24,300m²; number of trees surveyed: 5517). Bars represent one S.E., based on three blocks.

Frequency data also indicate considerable homogeneity among blocks. Frequency measures are more sensitive to smaller and less common species, and more useful for multivariate community analysis in this depauperate system. Of the 25 species found in baseline surveys (in 1800 quadrats) only one varied significantly among blocks (*Pennisetum mezianum*). The eight most frequent herbs were the same in all three blocks, with

differences in rank order only among species with very similar mean frequencies (Figure 5).

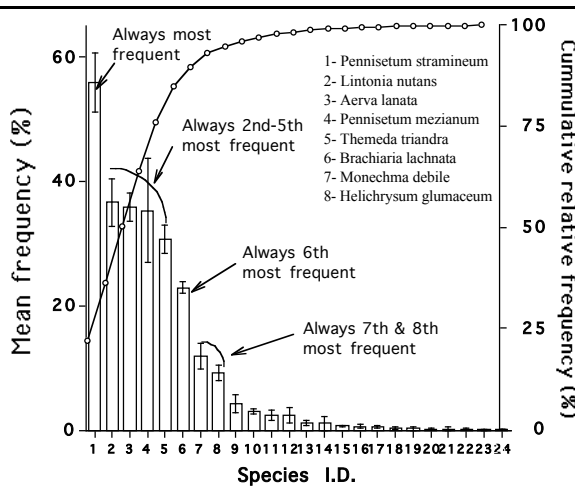


Figure 5. The mean frequencies, across all 18 plots, of the 25 most common herbaceous species (not including tran-sects through glade vegetation). The line is the cumulative relative frequency accounted for. The eight most frequent species account for 93% of the total species frequencies. There was strong homogeneity among blocks. In every block, the rank abundance of the first eight species was essentially the same. Bars are standard errors, based on a sample size of three (blocks).

Cluster analysis based on frequency data demonstrates the similarity of the background vegetation of plots and blocks, compared the vegetation of the glades (Figure 6). The Euclidean distance (9.7) from the average glade to the average non-glade vegetation was more than double the cumulative distance (4.1) among all the branches of the non-glade cluster. There is no strong pattern of similarity in baseline vegetation based either on treatment or on block.

As in the red soils (Young et al. 1997), the glade vegetation of the black cotton soils differs dramatically from background vegetation. The black cotton glades share several floristic traits with the red soil glades. First, they are also treeless (somewhat trivial, since this is our definition of 'glade'). Second, several of the glades have patches of *Cynodon plectostachyus*, virtually absent from other black cotton sites. Third, the dominant grass inside black cotton glades is *Pennisetum stramineum*, the species that characteristically ringed the glades in red soils. This grass accounted for more than three times as much relative frequency as the next most frequent taxon (*Ipomoea* spp.), and was even more dominant in terms of biomass (TPY, pers. obs.). Also common inside the glades are the grasses *Setaria verticil-*

lata and *Sporobolus* sp., and (during rains) the annual forb *Leucas martinicensis*. The shrub *Lyceum europaeum*, virtually absent away from the glades, was commonly found around their peripheries.

Note: Young et al. (1995) reported that *Digitaria milanjiana* was the dominant grass in the glades on red soils, based on vouchers from one glade on deposit at the National Herbarium. We now know that many of the plants later scored in the field as *D. milanjiana* were actually *Cynodon* spp., mainly *C. plectostachyus*.

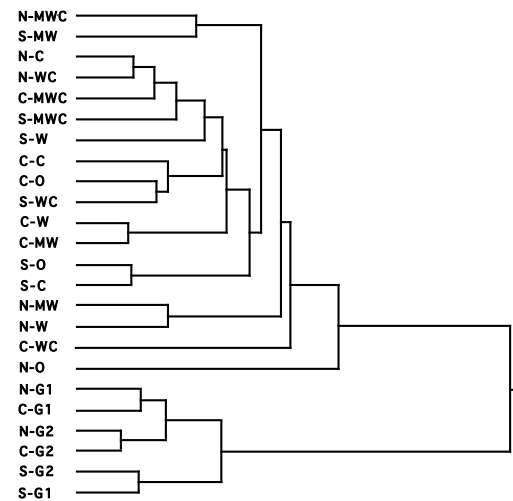


Figure 6. Cluster analysis of glade and non-glade vegetation in the experimental plots, based on frequency data. Note that the vast majority of the variation amongst sites is accounted for by the last step, i.e., the step combining glade and non-glade transects. The labels indicate first the block, and then the treatment (or the glade) where the transects were carried out.

Effectiveness of the herbivore barriers

In the first two years of the experiment, there were breaches of the game fence by single zebras on three occasions, each detected and repaired within a day or two. There have also been three breaches of the mega-herbivore fence by elephants. Each of these lasted only a short time, and in each, the area visited by elephants within the plot was carefully mapped. There was also a single breach of the mega-herbivore fence by a single giraffe.

Our goal is not necessarily the absolute exclusion of target herbivores, but large and well-documented decreases in their abundance. Our acacia utilization data and dung count data indicate that the barriers are achieving this goal. In March 1996, we carried out a preliminary survey of 2300 new shoots of *Acacia drepanol-*

bium in the plots. This survey showed the following patterns (Figure 7): There are no differences in acacia browsing between the plots with and without cattle, confirming the claims of herders that cattle do not eat this species. In the unfenced areas, 4-6% of the shoot tips were browsed at both 1 and 2 m above the ground. Within the mega-herbivore exclusion fence, 5% of the shoots were eaten at 1 m, but less than 1% eaten at 2 m. Within the total game exclusion fence, less than 1% of the shoots tips were eaten at either 1 or 2 m above the ground. An additional survey on shoot herbivory was undertaken in June 1996 showed similar patterns (Young and Okello, in review).

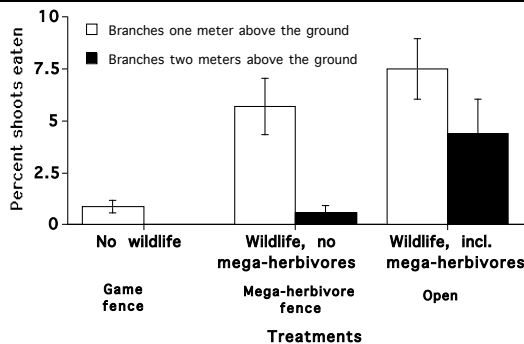


Figure 7. Herbivory of new shoots of *Acacia drepanolobium* in different enclosure plots in March 1996. Plots with and without cattle were lumped, because cattle do not browse this tree. N = 220 trees (~2300 shoots). Treatment categories as in Figure 1. Bars represent one S.E., based on three blocks.

Our dung counts are not meant to be used for comparisons across species. In particular, the cattle are put into the plots only for specific short intervals, and probably defecate less during this period than wildlife species, which have continual access. However, these counts are likely to be appropriate measures of levels of presence within herbivore classes. All three barriers appear to be effective in excluded the target herbivores (Figure 8). The visual barriers used by the herders reduced the abundance of cattle by more than 95% (5.0 ± 1.9 vs. 0.2 ± 0.2 , $n = 3$ blocks). The wildlife fences reduced the abundance of wild large mammalian herbivores by more than 95% (17.9 ± 5.0 vs. 0.5 ± 0.0). The mega-herbivore fences reduced the abundance of elephants and giraffes by 75% (2.0 ± 0.5 vs. 0.5 ± 0.2). Note also that the mega-herbivore fences did not apparently restrict the movement of other wildlife (Figure 8). In addition, elephant tracks were common outside the fences but rare inside, and restricted to the areas in the vicinity of recent breaks (pers. obs.).

There is constancy (homogeneity) of both dung count and herbivory rates within each treatment across all blocks. This strongly suggests that there is not a tendency for the experimental design to 'funnel' animals into any particular plot, nor any strong block or orienta-

tion effects on the animals that this experiment was designed to manipulate.

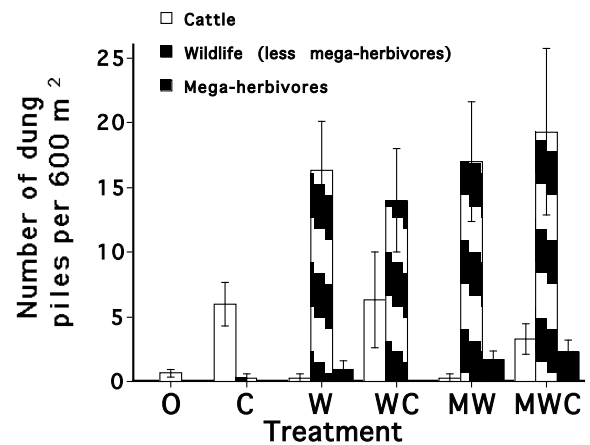


Figure 8. Densities of dung piles found in the enclosure plots in September 1997. Cattle and buffalo dung are not distinguishable (Stuart and Stuart 1994), and are lumped here. Treatment categories as in Figure 1. Bars represent one S.E., based on three blocks.

As an additional measure of effectiveness, in the time since the enclosures were fully operational, there already has been tremendous of growth of several non-acacia woody species inside the game fences. These include *Cadaba farinosa*, *Rhus natalensis*, *Balanites aegyptiaca*, *Lippia javanica*, and *Maerua* sp. The first two species still appear to be somewhat suppressed in the plots within these enclosures accessible to cattle (for *Cadaba*). The increase in all of these shrubs is from old (thick-stemmed) but very small and suppressed individuals already in the plots. This implies that the 'bush encroachment' we are seeing comes not from an increase in the number of individual shrubs, but from the release of a large number of suppressed shrubs previously inconspicuous in the grass (Young and Okello, unpublished data). This realization could have profound effects on how we deal with the problem of bush encroachment in this ecosystem.

Initial responses to different herbivore treatments.

We have already documented significantly different responses to herbivore treatments for several dependent variables. First are the differences in herbivore presence and utilization by browsers mentioned above, which demonstrate the effectiveness of the barriers. However, we have also quantified several non-trivial responses to the experimental treatments: 1) Rodent numbers were significantly higher in treatments with fewer herbivores (Keesing 1997 and in review), suggesting competition (and compensation) between two very different guilds of herbivores. 2) Keesing (1997 and in review) has also demonstrated increased vegetation cover in rodent ex-

sure plots. 3) We have demonstrated a 20% decline in the length of thorns produced by branches protected from herbivory, an effect limited to branch heights accessible to the herbivores allowed (Young and Okello, in review). 4) Preliminary surveys indicate an increase in grasshopper densities in plots from which herbivores are excluded (Palmer, unpublished data). 5) As mentioned above, there has been a release from suppression of several species of woody plants in a form of bush encroachment that does not entail increased recruitment (Young et al., unpublished data).

Current and future collaborations.

KLEE operates in the spirit of collaboration. We encourage research by scientists with a broad variety of interests. We do insist on coordination among research groups, and on the archiving of data gathered in the plots. Large amounts of baseline data are available. Areas currently under-studied include wildlife and cattle foraging behavior, the ecology of invertebrates (especially termites, ticks, Lepidoptera) and (small) carnivores, and manipulations of sub-plots with fire or intense grazing. We are open to other kinds of basic and applied research.

List of project collaborators

Truman P. Young, University of California (Project Director)
 Bell Dedan Okello, University of Natal (biology of *Acacia drepanolobium*)
 David Kinyua, University of Nairobi (herb layer dynamics)
 Maureen Stanton, University of California (acacia ants)
 Felicia Keesing, Siena College and Institute for Ecosystem Studies (rodents)
 Todd Palmer, University of California (acacias and acacia ants)
 Robert Faden, Smithsonian Institution (plants)
 David Ward, Ben Gurion University of the Negev (acacia tannins)
 James Lynch, Smithsonian Institution (birds)
 Randy Dahlgren, University of California (biogeochemistry)
 Michelle Gadd, University of California (elephants)

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Appendix 1. The larger (>2kg) mammals of Mpala/Segera. Species marked with an asterisk have been seen at the study plots or (in similar black cotton soils within 10km). Only the largest six carnivores listed are serious predators of the ungulate herbivores. It is difficult to assess the abundance of the smaller nocturnal carnivores. Nomenclature and weights are taken from Dorst and Dandelot (1972), Estes (1991), and Kingdon (1997). Not included are several smaller 'large' mammals (Bushbaby, Black-tipped Mongoose, Dwarf Mongoose, Genet, Zorilla, Striped Ground Squirrel, Bush Squirrel, Spectacled Elephant Shrew, Hedgehog, Nutria); in addition, Gerenuk occur just across the boundary river. Black Rhinoceros have been protected or are being reintroduced on several nearby properties.

English name	Latin name	Biomass(kg)	Abundance
<i>Herbivorous mammals</i>			
*Elephant	<i>Loxodonta africana</i> Blumenbach	1500-6000	Generally low, but seasonally abundant
Hippopotamus	<i>Hippopotamus amphibius</i> L.	600-3200	Very few
*Giraffe	<i>Giraffa camelopardalis</i> L.	550-2000	Moderate
[Black Rhinoceros	<i>Diceros bicornis</i> L.	900-1400	Locally extinct]
*Cape Buffalo	<i>Syncerus caffer</i> Sparrman	420-870	Low
*Eland	<i>Taurotragus oryx</i> Pallas	340-700(-900)	Moderate
*Grevy's Zebra	<i>Equus grevyi</i> Oustalet	350-450	Low, increasing
*Burchell's Zebra	<i>Equus burchelli</i> Gray	175-325	Abundant
Greater Kudu	<i>Tragelaphus strepsiceros</i> Pallas	120-320	Low
Defassa Waterbuck	<i>Kobus ellipsiprymnus defassa</i> Ruppell	160-260	Moderate
*Beisa Oryx	<i>Oryx beisa</i> Ruppell	130-200	Low, increasing
*Jackson's Hartebeest	<i>Alcelaphus buselaphus jacksoni</i> Pallas	100-170	Abundant
(*)Warthog	<i>Phacochoerus aethiopicus</i> Pallas	45-100	Very few, increasing?
*Grant's Gazelle	<i>Gazella granti</i> Brooke	40-80	Abundant
Impala	<i>Aepyceros melampus</i> Lichtenstein	40-70	Abundant
Bushbuck	<i>Tragelaphus scriptus</i> Pallas	25-80	Low
Mountain? Reedbuck	<i>Redunca sp. (fulvorufula?)</i>	20-35	Very few
Thomson's Gazelle	<i>Gazella (rufifrons) thomsonii</i> Gunther	13-30	Very few (but common on Segera)
Bush Duiker	<i>Sylvicapra grimmia</i> L.	13-25	Low
Klipspringer	<i>Oreotragus oreotragus</i> Zimmerman	11-14	Low
*Steinbuck	<i>Raphicerus campestris</i> Thunberg	9-13	Moderate
Crested Porcupine	<i>Hystrix</i> sp.	up to 20	Low?
*Anubis Baboon	<i>Papio cynocephalus anubis</i> L.	10-25(-50)	Abundant
*Patas Monkey	<i>Erythrocebus patas</i> Schreber	(4-)7-10	Moderate on Segera
Vervet Monkey	<i>Cercopithecus aethiops</i> L.	(2.5-)5-9	Abundant
Kirk's dik-dik	<i>Madoqua kirki</i> Gunther	4-7	Abundant
Rock hyrax	<i>Procavia capensis</i> Pallas	1.8-5.4	Moderate
Bush Hyrax	<i>Heterohyrax brucei</i> Gray	1.5-2.4	Moderate
*Hare	<i>Lepus</i> sp.	1-4	Abundant
<i>Carnivorous mammals (including insectivores)</i>			
*Lion	<i>Panthera leo</i> L.	120-260	Low to moderate
*Spotted Hyaena	<i>Crocuta crocuta</i> Erxleben	50-85	Moderate
Leopard	<i>Panthera pardus</i> L.	30-65	Low to moderate
*Cheetah	<i>Acinonyx jubatus</i> Schreber	35-65	Low
(*)Striped Hyaena	<i>Hyaena hyaena</i> L.	26-45	Low?
Wild Dog	<i>Lycaon pictus</i> Temminck	20-25	Vagrant, virtually extinct
*Aardvark	<i>Orycteropus afer</i> Pallas	up to 70?	Declining?
(*)Serval	<i>Felis serval</i> Schreber	14-18	Low
Cape Clawless Otter	<i>Aonyx capensis</i> Lonnberg	10-18	Low?
Civet	<i>Civettictis civetta</i>	7-20	Low?
*Ratel	<i>Mellivora capensis</i> Schreber	8-15	Low
(*)Caracal	<i>Felis aurata</i> Temminck	8-18	Low
Side-striped Jackal	<i>Canis adustus</i> Sundevall	8	Very few

*Black-backed Jackal	<i>Canis mesomelas</i> Schreber	7-14	Moderate, but fluctuates
Golden Jackal	<i>Canis aureus</i> L.	7-15	Very few, on Segera
(*?)Aardwolf	<i>Proteles cristatus</i> Sparrman	8-12	Low?
(*?)African Wild Cat	<i>Felis (sylvestrus) lybica</i> Forster	3.2-6.5	Low to moderate?
(*?)Bat-eared Fox	<i>Otocyan megalotis</i> Desmarest	3.2-5.4	Moderate, but fluctuates
*White-tailed mongoose	<i>Ichneumia albicauda</i> G.Cuvier	3-4	Moderate
?Marsh Mongoose	<i>Atilax paludinosus</i> G. Cuvier	2.4-3.2	Present?