Cryptic Consumers and the Ecology of an African Savanna

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East African savannas have fascinated generations of explorers, scientists, and the public. Nowhere else is there such a concentration and diversity of large, charismatic animals, and nowhere else is ecology portrayed so dramatically. Spectacular migrations of a million wildebeest tracking the rains dominate the Serengeti–Mara ecosystem of Tanzania and Kenya (McNaughton 1976, Sinclair and Norton-Griffiths 1979, Sinclair and Arcese 1995). Lions and hyenas pursue gazelle, zebra, and buffalo in a conspicuous contest between predator and prey (Kruuk 1972, Schaller 1972, Sinclair 1977). And giraffe and elephants shape the landscape by browsing and trampling savanna trees (Cumming 1992, Dublin 1995).

The abundance of so many large mammals in East Africa has led to the assumption that interactions among these prominent animals dominate the ecological dynamics of savanna communities. Recent research, however, has shown that there is also a cryptic web of interactions hidden in the tall savanna grasses. This web is centered around a group of herbivorous mammals that share both habitat and forage with their much larger hooved counterparts. These are the small mammals, and until recently almost nothing was known about their importance in savannas of East Africa.

The small mammals

The small mammals of East Africa include a diverse assortment of rodents, insectivores, elephant shrews, and rabbits. Aspects of the natural history of many of these inconspicuous mammals have been known for decades, including information about their diets, reproductive biology, and habitat preferences (Delany 1972, 1986, Kingdon 1974, 1997, Packer 1983, Leirs 1995). The most widely reported observation about their biology is that several rodent species periodically undergo dramatic population outbreaks. For example, a report from the Serengeti National Park in Tanzania described an outbreak of grass rats (*Arvicanthis*) in which the rats were so abundant that "one could hardly avoid stepping on them and many were killed by passing trucks. Survivors were feeding on the dead" (Hubbard 1972, p. 425). In agricultural areas, the multimammate mouse (*Mastomys natalensis*) reaches population peaks during which it destroys as much as 80–100% of crops throughout its range in sub-Saharan Africa (Taylor 1968, Fiedler 1988, Leirs 1995). Destruction of crops and stores caused by hordes of rodents has repeatedly inflicted heavy costs on humans.

THE CASCADING EFFECTS OF UNGULATES ON SMALL MAMMALS MAY HAVE PROFOUND IMPLICATIONS FOR ECOLOGICAL DYNAMICS IN EAST AFRICAN SAVANNAS

Population outbreaks of *Arvicanthis* and *M. natalensis* around human settlements have been considered particularly problematic because these species are reservoirs for a number of diseases, including Lassa fever, plague, spotted fever, relapsing fever, leptospirosis, leishmaniasis, and Crimean–Congo hemorrhagic fever (Fiedler 1988, Gratz 1997, Mills et al. 1997, Oguge et al. 1997). Although the ecology of diseases in Africa is poorly understood, studies in other areas have linked increases in disease transmission to increases in population densities of reservoirs for the disease (Mills et al. 1992, Ostfeld 1997). Moreover, in Africa there are reports of disease outbreaks being linked to high population densities of rodents (Monath et al. 1974a, 1974b).

This dual pest status for East African rodents as both destroyers of crops and carriers of disease has led to great interest in the population dynamics of particular species (Neal 1977, 1981, Delany 1986, Leirs 1995). Understanding the triggers for rapid population growth could suggest effective ways of predicting, preventing, or mitigating population outbreaks, thus potentially decreasing their impacts on humans (Fiedler 1988, Leirs 1995). Since the 1930s, outbreaks of both *Arvicanthis* and *Mastomys* have

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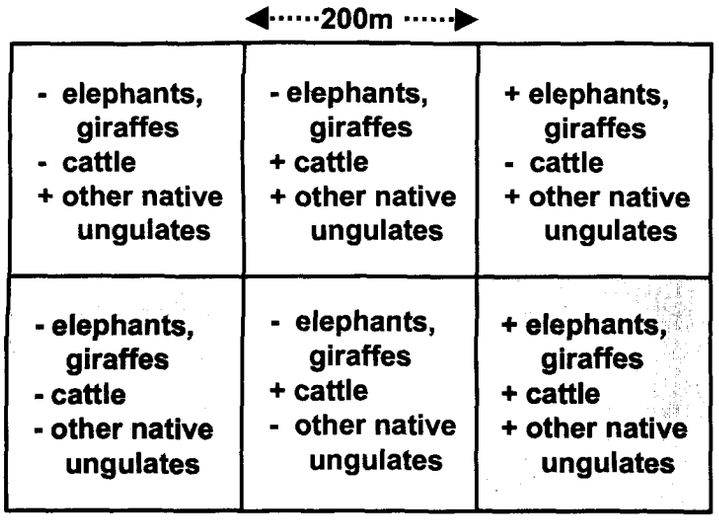


Figure 1. Schematic diagram of the Kenya Long-Term Exclusion Experiment large-mammal exclusion design. Each treatment area is 4 ha (200 m × 200 m), and there are three replicates of this block design. The focal treatments for the study of small mammals (i.e., all ungulates allowed access or no ungulates allowed access) are shaded.

been linked to heavy rainfall (Taylor 1968, Taylor and Green 1976, Leirs et al. 1994, Leirs 1995), and recent studies suggest that this connection could prove useful in establishing effective rodent control measures around human settlements (Leirs et al. 1996). In North and South America, Europe, and Japan, however, population dynamics of rodents in natural and semi-natural areas are known to be influenced by biotic interactions, especially by predators and competitors (Korpimäki and Norrdahl 1991, 1998, Heske et al. 1994, Meserve et al. 1996, Saitoh et al. 1998).

These findings raise the question of whether African rodents are regulated primarily by rains, or whether they are also members of webs of interacting species. Such interactions could affect the abundance of both the rodents and the species with which they interact. These ecological relationships could have important implications for areas of human settlement as well as natural areas with comparatively little human impact. Until recently, however, ecological interactions involving small mammals in East Africa had not been seriously considered. Do herbivorous small mammals compete with large mammals for food? Are small mammals abundant enough to influence the dynamics of other species within savanna communities? Answers to such questions could provide important insights, both for scientists concerned with small mammals as pests of humans and for those concerned with preserving and protecting natural savanna habitats.

A savanna setting

The Mpala Research Centre (MRC) in central Kenya, where I have been investigating ecological interactions involving small mammals, is located on the equator at an altitude of 1800 m. Rains at MRC, as elsewhere in tropical areas, are highly seasonal. Heavy rains typically fall between April and July and then taper off until a period of lighter rains occurs in October through November. From January through March there is typically no rain at all, although the onset, intensity, and duration of both rainy and dry periods vary considerably from year to year (Keesing 1998a).

The vegetation at MRC is dominated by the whistling thorn tree (*Acacia drepanolobium*), five species of grasses (*Themeda triandra, Pennisetum mezianum, Pennisetum stramineum, Brachiaria lachnatha, Lintonia nutans*), and several forbs (*Aerva lanata, Helichrysum glumaceum*; Young et al. 1998). This habitat harbors a rich diversity of ungulates, including elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), Grevy's and Burchell's zebra (*Equus greveyi* and *Equus burchelli*), hartebeests (*Alcelaphus buselaphus*), buffalos (*Syncerus caffer*), elands (*Taurotragus oryx*), steenbucks (*Raphicerus campestris*), oryx (*Oryx beisa*), and Grant's gazelles (*Gazella granti*). Carnivores are also common, including lions (*Panthera leo*) and an assortment of smaller predators, such as mongooses (*Ichneumia albicauda, Herpestes sanguineus*) and black-backed jackals (*Canis mesomelas*). Patas monkeys (*Erythrocebus patas*) and vervet monkeys (*Cercopithecus aethiops*) are being studied in the area (Isbell et al. 1998), and a classic study of sexual selection in long-tailed widowbirds (*Euplectes progne*) was conducted nearby (Andersson 1982). A current study is investigating interactions among several species of ants and the whistling thorn tree (Young et al. 1997, Stanton et al. 1999).

MRC is more representative of most of East Africa than are the famous game parks, such as the Serengeti of Tanzania and the Maasai Mara of southern Kenya. Ungulate densities are lower at MRC than in the parks, and because the land is outside park protection native grazers share much of the area with livestock (LWF 1996). The importance of conserving wildlife in areas outside of reserves and national parks is currently the subject of intense debate in East Africa (McRae 1998). Of particular concern is how to resolve the apparent conflicts between humans and their livestock, on the one hand, and populations of native ungulates, on the other, given that some scientists and pastoralists believe that native grazers compete with cattle for food (Prins 1992, Happold 1995, Swift et al. 1996).

Because livestock and native ungulates coexist at MRC, this site is an ideal location for studies of the interactions among these two groups of grazers. In August 1995, the Kenya Long-Term Exclusion Experiment (KLEE) was

Figure 2. One of the Kenya Long-Term Exclusion Experiment fences at the height of the dry season. This treatment allows access only by livestock, which enter and exit through the gate. The trees in the background are whistling thorn trees, **Acacia drepanolobium.**

Figure 3. The pouched mouse, **Saccostomus mearnsi,** *is the most common small mammal at the study site. Photo: Steve Takata.*

established at MRC to investigate such interactions and to consider the separate and combined effects of domestic and wild ungulates on vegetation (Young et al. 1998). The experimental removal of native large mammals also simulates reductions in ungulate abundance caused by the encroachment of human populations, which is a critical conservation issue throughout East Africa (Happold 1995). KLEE excludes several combinations of native ungulates and livestock using six treatments (various combinations of +/– elephants and giraffes, +/– cattle, and +/– other native ungulates; Figure 1), which are established through a combination of regulated herding for livestock and electrified fencing for native ungulates. Because livestock are continuously accompanied while they graze at MRC, their movements can be controlled by herders. Native ungulates are excluded using two types of fencing, one of which excludes all ungulates (Figure 2), and the other of which excludes only the biggest ungulates (giraffe and elephants). Each treatment area is large—200 m × 200 m (4 ha)—and there are three replicates of each of the six treatments.

Effects of large mammals on the demography of small mammals

Because the focus of so much ecological research in East Africa has been on ungulates, one obvious question about small mammals is how their abundance and diversity are affected by large mammals. Because many small mammals are partially or totally herbivorous, it seemed likely that the removal of herbivorous large mammals, such as zebras and hartebeests, would increase the availability of food for some small mammals. If so, the densities of those small mammals should increase after removal of the large mammals. This type of experiment is the classic approach to determining whether organisms are competing for resources (Connell 1983, Schoener 1983).

As the KLEE fences were being completed in September 1995 (Young et al. 1998), I established 1-ha trapping grids in the center of two of the large-mammal exclusion areas—the treatment plots that excluded all ungulates and the control plots, which excluded none (Figure 1). Each grid contained 100 live-traps, and there were three replicates of each treatment. The most common small mammal on all the grids turned out to be the pouched mouse, *Saccostomus mearnsi*, a hamster-sized rodent (Figure 3) that is widespread in East Africa but had never before been reported in high local abundance (Keesing 1998b). At MRC, *S. mearnsi* represented approximately 80% of the small mammals captured in traps. Other small mammals captured included *Arvicanthis*, *Mastomys*, the pygmy mouse (*Mus minutoides*), the climbing mouse (*Dendromus melanotis*), and several species of shrews (*Crocidura* spp.).

An initial surprise of this experiment was the speed with which pouched mice responded to the exclusion of ungulates. By January 1996, just 4 months after the fences were installed, pouched mice were 20% more abundant where there were no large mammals than they were on control plots (Figure 4). Over the next 8 months the difference increased, so that by August 1996 there were twice as many pouched mice inside the fences as in the control areas (Figure 4). That difference has been sustained ever

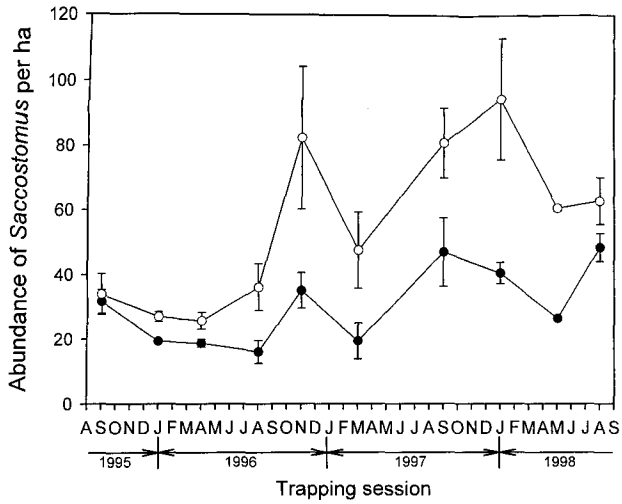


Figure 4. Abundance (individuals per ha) of the pouched mouse, Saccostomus mearnsi, *in the presence and absence of ungulates. Abundance was measured beginning in August 1995, when the large-mammal exclusion fences were installed. Differences in abundance between plots with (solid circles) and without (open circles) ungulates are statistically significant, based on a repeated-measures analysis of variance (treatment: $F_{1,4} = 13.97$; P = 0.02; treatment·time: $F_{8,32} = 2.38$; P = 0.07). Error bars represent standard errors.*

since, even during the pronounced seasonal fluctuations in abundance that are common in rodents. In effect, the carrying capacity of this habitat for pouched mice doubles when there are no ungulates.

How could removing ungulates double the carrying capacity of the habitat for rodents? The most likely mechanisms involve predation and competition. In the first case, the removal of large mammals could cause an increase in the amount of vegetative cover in the habitat. The amount of cover has been demonstrated to be important for protecting small mammals from predators, particularly raptors (Birney et al. 1976, Peles and Barrett 1996), which are abundant at MRC. Other predators at the site include small carnivores (mongooses, black-backed jackals) and snakes (e.g., puff adders [*Bitis arietans*] and cobras [*Naja* spp.]). None of these predators was excluded by the KLEE fences (Keesing 1998a). If cover increased when ungulates were removed, pouched mice would be less exposed to these predators, which could lead to an increase in their abundance. In the second case, ungulate removal could cause an increase in the quantity or quality of food resources available to the mice. This scenario would suggest that ungulates and pouched mice are competing for food in this habitat and that the removal of the ungulates caused an increase in their competitors, the mice.

Based on several lines of evidence, the doubling of mouse density does not appear to have been due to a relaxation of predation pressure when ungulates were excluded. First, surveys of vegetative cover on the plots 2 and 3 years after the fences were installed indicated that there was no significant difference in the amount of cover with or without ungulates for either year (paired t-test; 1997: $t_2 = 0.13$, $P = 0.91$; 1998: $t_2 = -1.317$, $P = 0.32$). Therefore, pouched mice were not more exposed to predators when ungulates were present (Keesing 1998a, Felicia Keesing, unpublished data). Second, survival rates of mice did not differ on treatment versus control plots (repeated-measures analysis of variance; treatment: $F_{1,3} = 0.00$, $P = 0.96$; time·treatment: $F_{8,24} = 1.25$, $P = 0.31$). If predation pressure was higher when ungulates were present, then fewer mice should have survived from one trapping session to the next in these areas as compared to areas without ungulates.

Competition appears to be the more likely explanation for the doubling of mouse density, based on analyses of space use and body condition of the mice on treatment and control plots. Patterns of space use by mice in the two areas were estimated from the trapping data, which indicated the maximum distances that individual mice traveled during any single 3-day trapping session. This "maximum distance traveled" is a linear index of the area of an individual's home range. Male mice moved significantly shorter distances on plots from which ungulates had been excluded (Figure 5). Differences for female mice were not statistically significant, although they showed a similar

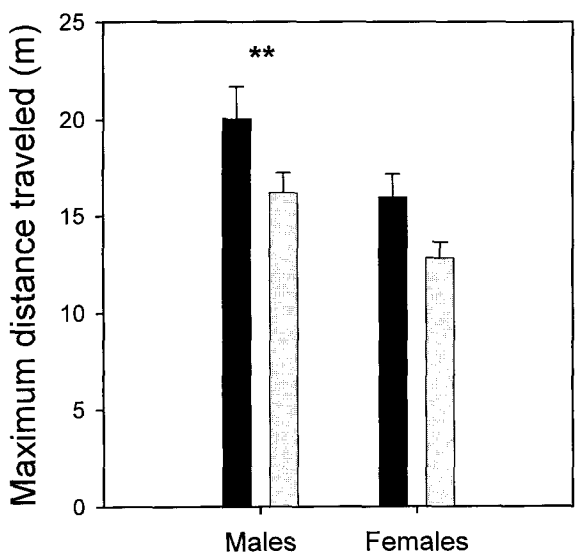


*Figure 5. Average maximum distance traveled by individual small mammals within a trapping session on plots with (solid bar) and without (shaded bar) ungulates. Males moved significantly shorter distances on plots without ungulates than on plots with ungulates. Averages were computed for all adults captured at least twice during a single trapping session over all trapping sessions, except the initial trapping session (in August 1995). For each sex, maximum distances traveled were compared using a two-way analysis of variance, with trapping session and treatment as factors (males: $F_{1,337} = 6.37$, P = 0.01; females: $F_{1,308} = 1.232$, P = 0.27). Error bars represent standard errors. ** indicates statistical significance.*

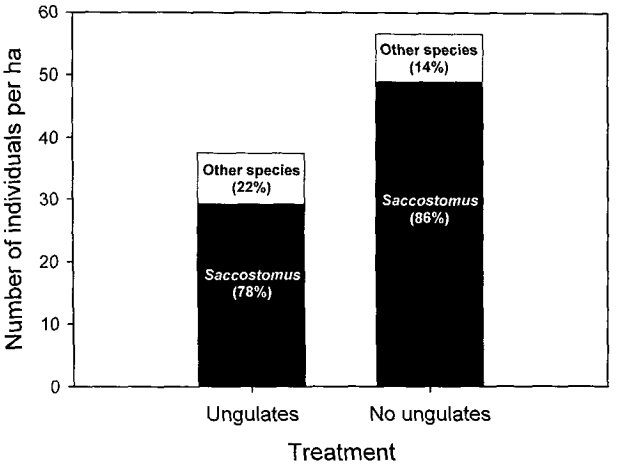


Figure 6. Average number of small mammals per hectare captured on plots with and without ungulates since August 1996. Differences between numbers were statistically significant based on a paired t-test comparing the average for each block ($t_2 = 5.34$; P = 0.03). The pouched mouse,* Saccostomus mearnsi, *accounted for most of the small mammals captured in each treatment.

trend (Figure 5). Overall, where mice were twice as dense because ungulates were absent (Figure 4), each mouse used less space. But this crowding had no adverse effect on body condition: male weights were not significantly different in the two treatments. (Females were not analyzed because undetected pregnancies could have confounded the results.) In other words, individual male pouched mice used less space where ungulates were excluded, but they maintained equivalent body weights. This observation strongly suggests that food quality was higher for mice in the absence of ungulates. Therefore, pouched mice appear to be competing with ungulates for food.

Effects of large mammals on diversity of small mammals

The exclusion of ungulates affects the relative abundance of small mammals as well as their absolute abundance. On average, the removal of ungulates resulted in a 60% increase in the total number of small mammals on the plots (Figure 6). Most of that increase was due to increases in the number of pouched mice. On plots with ungulates, pouched mice constituted 78% of the small-mammal community, whereas on plots without ungulates that percentage increased to 86%.

The species diversity of a community includes both species richness (the total number of species) and species evenness (the proportion of the community that is made up of each species). A community with high species richness might have low evenness if one of the species is much more abundant than the others. The Shannon Diversity Index incorporates both of these measures in a single value. During most of the first year, small-mammal diversity, as calculated using this index, was the same whether or not ungulates were present (Figure 7). However, at the end of the first year, diversity plunged on the control plots. Two species, *Arvicanthis* and *Mus*, were not trapped at all on control plots, although both species were still present on ungulate exclusion plots. The absence of these two species on control plots may have been the result of an unusually long dry season in 1996. Densities of small mammals at MRC typically decline as the dry season progresses from January through March (Figure 4), and by the time the rains began in 1996, densities of *Arvicanthis* and *Mus* on the plots with ungulates may have been so low that these two species went locally extinct.

Following the rapid decline in small-mammal diversity in August 1996, diversity rebounded to equivalent levels in both the presence and absence of ungulates (Figure 7). Since that time, however, there has been a steady long-term trend toward higher diversity in the presence of ungulates than in their absence. Plots with ungulates now have consistently greater representation of the less common species in the habitat, resulting in higher diversity. For example, following the rains, a greater proportion of shrews are captured on control plots than on ungulate exclusion plots.

Correlative evidence suggests that ungulates are playing the major role in this change in diversity—although through disturbance rather than through competition. At

Figure 7. Shannon Diversity Index of small mammals captured on plots with and without ungulates since August 1995. Since August 1997, diversity has been higher on the plots with ungulates (solid circles) than on the plots without ungulates (open circles), except for August 1996, when an unusually dry summer may have caused local extinction of some species on plots with ungulates. Diversity on the two sets of plots was compared using a repeated-measures analysis of variance (treatment: $F_{1,32} = 4.13$; P = 0.11; time: $F_{8,32} = 11.60$; P < 0.01; treatment·time: $F_{8,32} = 5.06$; P < 0.01). Error bars represent standard errors.

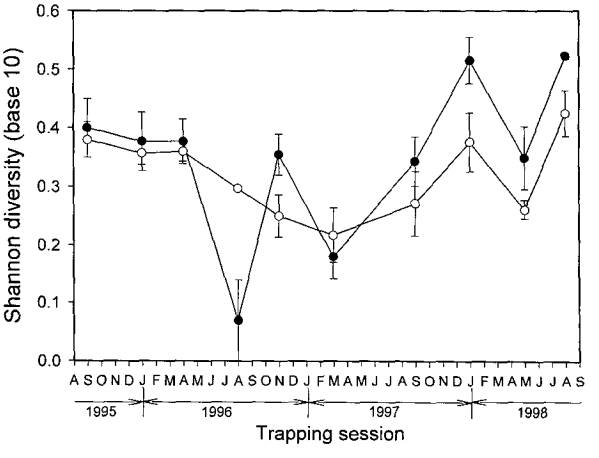


Figure 8. African elephant, **Loxodonta africana.** *Disturbance by elephants and other large mammals may result in higher species diversity of small mammals.*

MRC, ungulates, especially elephants (Figure 8), trample vegetation and disturb the soil surface along their travel routes (Felicia Keesing, unpublished data), and these paths have different topography and moisture levels from surrounding areas. Such changes in physical structure cause increases in some otherwise rare plant species, such as a sedge (*Kyllinga navosum*), which is abundant only in disturbed areas following the rains (Felicia Keesing, personal observation). Ungulates, especially megaherbivores, such as elephants and giraffe, may create disturbances that increase small-mammal diversity through their effects on vegetation and, possibly, on invertebrates. This scenario is in accord with the intermediate disturbance hypothesis, which suggests that moderate disturbance decreases competitive dominance of one or a few species, resulting in higher diversity (Sousa 1984, Reice 1994).

Ungulates, therefore, strongly influence the small-mammal community. When ungulates are present, small-mammal density is lower and small-mammal diversity is generally higher, although diversity has the potential to fluctuate rapidly. When ungulates are removed, small mammals, especially pouched mice, are more abundant and diversity is lower. Large mammals, then, are important determinants of small-mammal dynamics in this habitat. If large mammals became scarce or absent, could increases in the densities of small mammals have any important consequences for the savanna community?

Effects of small mammals on vegetation

Although heavy impacts of irrupting rodent populations on cereal crops have been documented in Africa (e.g., Leirs 1995), effects of rodents on native savanna vegetation are largely unknown. In temperate grasslands, herbivorous rodents can reduce aboveground plant biomass and alter species composition within plant communities (e.g., Batzli and Pitelka 1970). Similar interactions may occur between African small mammals and savanna plant communities.

To examine these impacts, I established nine small-mammal exclusion fences in August 1995 and paired these with nine unfenced control plots. The fences are each 3 m × 7 m, constructed of 1 m wide hardware cloth (1 cm mesh), and extending 0.5 m into the ground to prevent small mammals from burrowing underneath. Aluminum flashing attached to the top edge of the fence prevents animals from climbing over. The small-mammal exclusion fences were located within the fences that exclude ungulates because elephants destroyed pilot small-mammal fences wherever they had access to them. Consequently, any effects of small mammals on vegetation would represent the effects of high densities of small mammals, especially pouched mice.

The exclusion of high densities of small mammals resulted in a rapid and dramatic effect on aboveground plant biomass. Plant biomass was initially equivalent on both experimental and control sites (Figure 9). However, by the end of the first year the aboveground plant biomass in sites without small mammals was 40% greater than that in sites to which small mammals had access. By the end of the second year, this difference had increased to 50%, a difference that was sustained through the end of the third year (Figure 9).

The strong effect of small mammals on aboveground plant biomass is surprising, given that the pouched mouse, the dominant small mammal, has been reported to be an omnivore, with a strong preference for seeds (Kingdon 1974, Neal 1984). Although a seed eater could have an effect on plant biomass, such an effect would be expected to develop more slowly than the immediate impact I observed, especially because herbaceous vegetation at the study site does not appear to be seed-limited (many of the plant species propagate vegetatively and are perennials rather than annuals). To determine the actual diet of pouched mice at the study site, Margaret Metz, then a student at Princeton University, and I conducted "cafeteria trials" on field-caught pouched mice, in which they were offered an assortment of grasses, a common forb, and an array of mixed seeds (Margaret Metz, Felicia Keesing, in review). The mice chose almost exclusively green vegetation by weight (93%) and consumed few seeds (7%). Thus, this species is primarily a folivore, at least during some seasons, which may explain its rapid impact on aboveground plant biomass. This preference for green vegetation was apparent in the habitat as well, where we

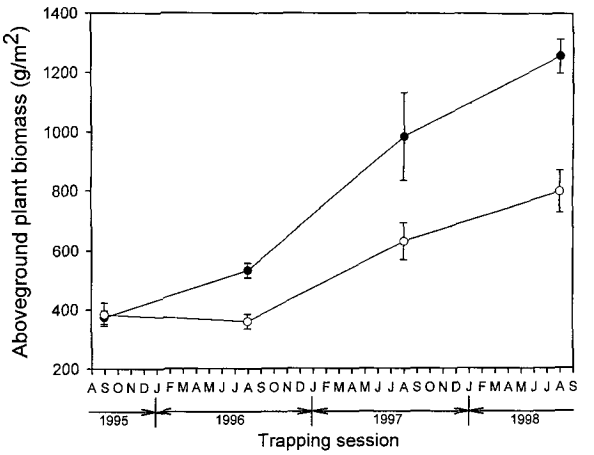


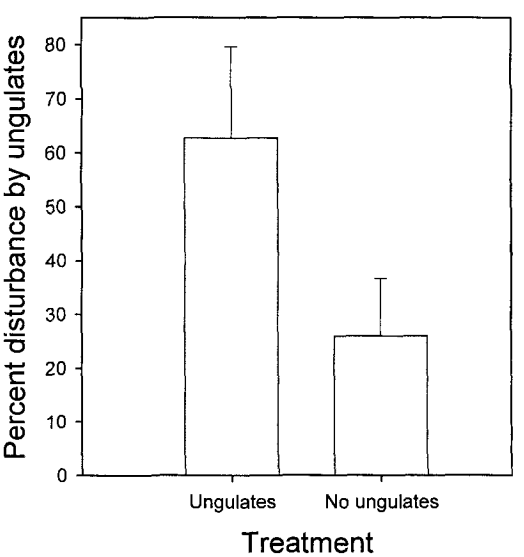
Figure 9. Effect of small mammals on aboveground plant biomass. Aboveground plant biomass, in g/m², was measured on 3 m × 7 m plots with (open circles) and without (solid circles) small mammals. The amount of aboveground plant biomass was, on average, approximately 50% higher on plots without small mammals than on plots with small mammals, and this difference was significant based on a repeated-measures analysis of variance (treatment: $F_{1,13} = 9.22$; P = 0.01; time·treatment: $F_{2,26} = 2.26$; P = 0.13). Higher-than-average rainfall in 1997 and 1998 resulted in an overall increase in plant biomass on all plots. Error bars represent standard errors.

found many piles of clipped vegetation similar to those made by voles (*Microtus* spp.) in temperate habitats. In both the lab feeding trials and surveys of clippings they made in the field, pouched mice consumed both forbs and grasses and showed distinct preferences for certain plant species (Margaret Metz, Felicia Keesing, in review).

Small mammals may also influence the spatial distribution of vegetation at the study site. Throughout the habitat, termite mounds are preferred sites for small-mammal burrows, and a single mound can be occupied by more than five pouched mice, in addition to other species of small mammals (Keesing 1998b). Because many animals begin their nightly foraging from a single, shared mound, preferred food items near the mound would be affected more heavily than those further from the mound (Keesing 1997). A 1996 study indeed demonstrated that experimental seeds (peanuts) placed near termite mounds were eaten at higher rates than those away from the mound. Within 6 m of the center of termite mounds, approximately 75% of the peanut halves were removed, whereas at distances of 6–15 m from the center of the mounds, only approximately 40% of the peanuts were removed (Figure 10; Keesing 1997). Because peanuts are both aromatic and non-native, it is not clear whether these results would apply to native seeds. Preliminary results of seed removal studies using seeds of the dominant tree, *A. drepanolobium*, demonstrate that, on average, small mammals consume 70% of available seeds over the course of a week and that there is pronounced spatial variation in removal rates, which seems to be related to the local density of rodents (Felicia Keesing, Richard S. Ostfeld, unpublished data). Recent research has demonstrated that 80% of *A. drepanolobium* seeds germinate within 1 week (Okello and Young in press). Therefore, rapid, intense predation by small mammals has the potential to influence both the recruitment and the spatial distribution of this tree.

Factors that affect recruitment of *A. drepanolobium* may in turn have cascading consequences for this savanna community. These trees form a virtual monoculture in the overstory, constituting 97% of the woody vegetation at the study site (Young et al. 1998). Typically, the trees are widely spaced, although there is considerable variation in their density (Young et al. 1998). Trees are important in savannas (Belsky et al. 1993, Belsky 1994, Belsky and Canham 1994) because the productivity of herbaceous vegetation is often higher under savanna trees than in surrounding areas (Belsky et al. 1993), probably as a result of shading and nutrient enrichment (Belsky 1994). *A. drepanolobium* trees, and the productive vegetation beneath them, could attract animals, which might further increase nutrient

Figure 10. The percentage of seeds removed from termite mounds as a function of the distance from the center of the mound. At each of six mounds, seed removal was determined by placing shelled peanuts at 40 random angles and distances from the center of the mound, up to a distance of 15 m. Fifteen meters represents the outer limit of the zone of visible impact on vegetation associated with mounds; it is equivalent to the average maximum distance traveled by female pouched mice (Saccostomus mearnsi) on the trapping grids. The frequency of seed removal varied significantly with distance, based on a chi-squared test of independence (df = 4; chi-square = 20.5; P < 0.01).



enrichment under the canopy through deposition of fertilizer (urine and feces). Because small-mammal density is determined in large part by ungulate density, and because rates of seed predation by small mammals seem to be determined by local small-mammal density, a positive feedback loop might connect ungulates to grass quality through their effects on small mammals. Some ungulates might be attracted to neighborhoods of thick tree cover, which could reduce local small-mammal density. Low small-mammal density might allow recruitment of tree seeds, further attracting ungulates.

The results of these experiments on seed removal and plant biomass show that the effects of herbivory by small mammals on savanna vegetation can be considerable, rivaling those of the better-known ungulates. Indeed, small mammals may, to a large extent, compensate for the exclusion of the dominant herbivores in this system. Surveys of the percentage cover of herbaceous vegetation in areas with and without ungulates indicated that, after 3 years of ungulate exclusion, vegetation cover inside the fences did not differ from that on control plots ($P = 0.32$; Felicia Keesing, unpublished data). This surprising result may reflect the doubling of density of small mammals caused by excluding ungulates and the consequent reductions in vegetation biomass.

Metabolic considerations support this interpretation of the effects of small mammals on vegetation biomass. Assuming that small mammals at MRC have metabolic rates similar to those of other small mammals of similar size, each individual small mammal uses oxygen at a rate of approximately 3.0 $mL \cdot g^{-1} \cdot hr^{-1}$ (Eisenberg 1981). Large ungulates—horses (*Equus caballus*), for example—use oxygen at a rate of only approximately 0.25 $mL \cdot g^{-1} \cdot hr^{-1}$ (Eisenberg 1981). Data such as these are the basis for the well-known inverse relationship between basal metabolic rate and body size of mammals (Vaughan 1986). The average biomass of small mammals in areas with ungulates present is 2.4 kg/ha. Based on metabolic estimates, this biomass consumes the metabolic equivalent of what is consumed by approximately 30 kg/ha of zebra-sized ungulates. In the absence of ungulates, the biomass of small mammals is 3.9 kg/ha, approximately 60% higher than the biomass in the presence of ungulates. The difference in biomass, 1.5 kg/ha, is—at the metabolic rates estimated above—approximately equivalent to that consumed by 18 kg/ha of zebra-sized ungulates. Therefore, when ungulates are removed, small mammals have the capacity to compensate for approximately 18 kg/ha of ungulates.

Does this compensation potential correspond to the biomass of ungulates excluded by the fences? Although the biomass of ungulates at the KLEE site has not been estimated directly, aerial surveys of ungulates throughout a 7000 km^2 area of Laikipia district, in which MRC is located, led to an estimate of 44 kg/ha of ungulates (LWF 1996, Keesing 1998a). However, considerable variation exists among different habitat types within the Laikipia district (LWF 1996). Whether the biomass at the KLEE site is lower than this average and approximates the compensation potential of the small mammals remains to be determined. Even when ungulates are present and small mammals are at normal densities, their metabolic consumption is 68% of that of their larger counterparts (30 kg/ha divided by 44 kg/ha). Although small mammals are cryptic, they may be almost as important to the dynamics of African savanna vegetation as the more conspicuous and better-known zebras, elephants, and gazelles.

Consequences for savanna communities

The findings discussed in this article demonstrate that savanna community dynamics at MRC are indeed dominated by large mammals, but in some unexpected ways. When ungulates are present, small-mammal densities are low, small-mammal diversity fluctuates rapidly but tends to remain high, and the impacts of small mammals on the plant community are relatively minor (Figure 11a). When ungulates are scarce or absent, small-mammal densities increase, small-mammal diversity is generally lower but more stable, and the small-mammal community can have a profound effect on the biomass and spatial distribution of the plant community (Figure 11b).

These cascading effects on the community in the absence of ungulates may have profound implications for ecological dynamics. For example, reducing or eliminating native ungulate populations in East Africa might have unanticipated consequences. If reductions in native ungulate populations increased small mammal densities, then higher densities of small mammals, particularly rodents, could lead to increased transmission of both human and livestock diseases for which rodents are reservoirs. And high small-mammal densities might also increase the abundances of predators that specialize on small mammals, including raptors, snakes, and small carnivores. Furthermore, if high densities of small mammals compensate for herbivory by native ungulates, then eliminating native ungulates might not increase range quality for livestock because small mammals could themselves reduce forage availability for cattle and other domesticated grazers.

Without more research on African savannas, it is unclear whether the community interactions among small mammals, large mammals, and vegetation seen at MRC are common elsewhere. The habitat in which my research has been conducted is widespread in East Africa. The soil and vegetation that characterize the KLEE site cover more than one-fourth (2700 km^2) of the Laikipia ecosystem (Young et al. 1997) and are found in many other parts of East Africa, including Nairobi National Park and the western section of Serengeti National Park (Young et al. 1998). Whether dynamics similar to those described in this article occur at these other sites has not been investigated, nor is it known whether similar patterns are found in savannas with different soils and vegetation.

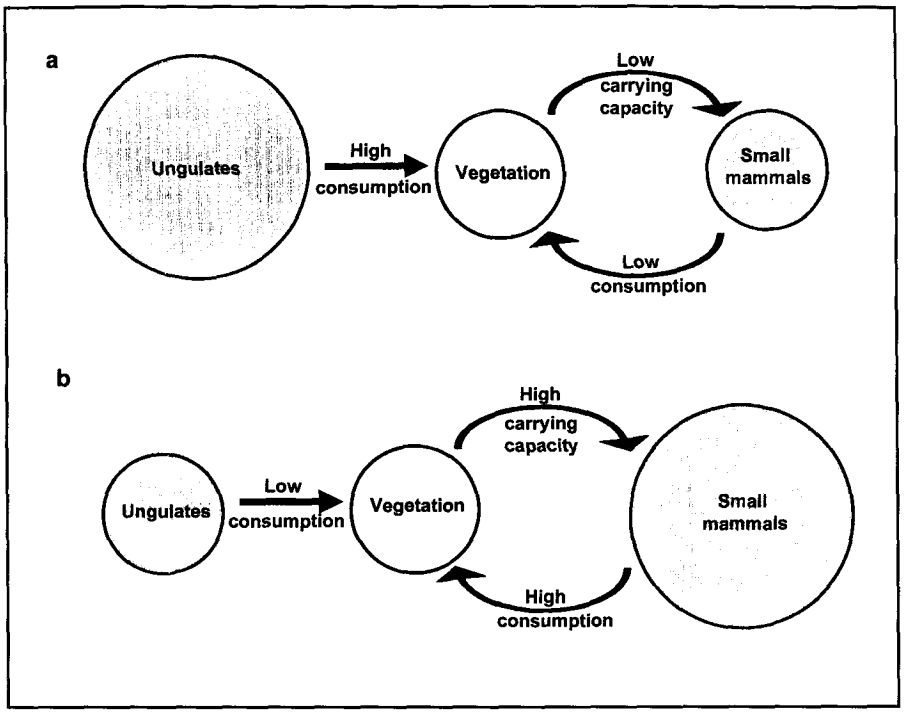


Figure 11. Conceptual model of compensation by small mammals. (a) When ungulates are abundant, they consume a high proportion of vegetation, which results in a low carrying capacity for small mammals. At low density, small mammals have a relatively small effect on vegetation. (b) When ungulates are scarce or absent, they consume little or no vegetation, resulting in a high carrying capacity for small mammals. These small mammals then compensate for herbivory by the large mammals, resulting in plant biomass equivalent to that when large mammals are abundant.

The small-mammal community at MRC may differ from that of other areas of East Africa in at least one major respect. Although the pouched mouse is the most abundant small mammal at MRC, it has not been reported as locally abundant at the few other sites for which small-mammal abundance has been estimated (Delany 1964, Neal 1984). Moreover, the pouched mouse itself has not been reported as a pest species. Whether it serves as a reservoir for human or livestock diseases remains to be determined. Such a role is possible, given that for other disease systems, the dominant small-mammal species in the community is frequently a highly competent reservoir for bacterial and viral diseases (Mills et al. 1992, Childs et al. 1994, Ostfeld 1997)

The two most common small mammals throughout East Africa, at least around human settlements, are *Arvicanthis* and *M. natalensis*, both of which occur at the KLEE site. Like the pouched mouse, *Mastomys* increased in abundance when ungulates were excluded (Keesing 1998a). However, the densities of both *Mastomys* and *Arvicanthis* are lower than the density of pouched mice in both the presence and the absence of ungulates. It is unknown whether, at sites where these two species dominate the small mammal community, ungulates affect them as dramatically as they affect pouched mice at MRC. This issue, too, could be critical to address in future studies because of the roles of these species as agricultural pests and disease reservoirs.

Another important area for future investigation is whether livestock and native ungulates affect small mammal abundance and diversity in similar ways. Much of the research on the effects of ungulates on small mammals in other habitats has focused on livestock (Grant et al. 1982, Bock et al. 1984, Heske and Campbell 1991, Douglass and Frisina 1993), and it is clear that heavy stocking rates affect vegetation cover and can cause dramatic alterations in the species composition and densities of small mammals. Whether livestock have these effects in East Africa is not known. In light of the interactions between ungulates, small mammals, and vegetation described in this article and the controversies about competition between native and domestic ungulates, determining impacts of cattle is critical for effective management of wildlife and habitats. I am currently investigating the separate and combined effects of livestock and native ungulates on small mammals at MRC; similar investigations in other areas of East Africa are warranted.

Studies of the ecology of African savannas have provided much of the framework for the general understanding of species interactions within ecological communities. The majority of these studies have focused on the most conspicuous members of savanna communities. However, some of the most important organisms and crucial interactions may be inconspicuous. Understanding cryptic connections in ecosystems may prove essential for adequately managing and conserving both natural and human-altered habitats.

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