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Impacts of ungulates on the demography and diversity of small mammals in central Kenya

Received: 28 December 1997 / Accepted: 11 May 1998

Abstract The impacts of ungulates on small mammals in an East African savanna habitat were investigated by monitoring the population and community responses of small mammals on replicated 4-ha plots from which ungulates had been excluded. The dominant small mammal in this habitat is the pouched mouse, *Saccostomus mearnsi*, a medium-sized murid rodent. Eight other small mammal species, including *Arvicanthis* sp., *Mus* sp., *Mastomys* sp., *Dendromus* sp., *Crocidura* sp., and, rarely, *Tatera* sp., *Aethomys* sp., and *Acomys* sp., were also captured. The dominant ungulates are elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), Grevy's and common zebra (*Equus grevyi* and *E. burchelli*), buffalo (*Syncerus cafer*), eland (*Taurotragus oryx*), Grant's gazelle (*Gazella granti*), and domestic cattle. Within 1 year, *S. mearnsi* populations had responded dramatically to the exclusion of large mammals by a two-fold increase in density, a difference that was maintained through pronounced seasonal fluctuations in the second year. Though individual pouched mice showed no significant differences in their use of space with and without ungulates, male *S. mearnsi* maintained significantly higher body weights in the absence of ungulates, indicating that habitat quality had increased. One other species, *Mastomys* sp., also increased in the absence of ungulates. Overall, the small mammal community maintained relatively constant species diversity on the plots to which ungulates did not have access. On the plots to which ungulates did have access, on the other hand, there was a rapid 75% decrease in diversity in the control plots during one trapping session. Ungulates are most likely affecting small mammals through

their effects on food quality, since there were no detectable differences in their exposure to predators, as determined by vegetative cover, in the absence of ungulates. These results demonstrate that ungulates can have strong and rapid impacts on small mammal abundance and diversity in East African savannas, an interaction which has not previously been given serious consideration.

Key words Competition · Small mammals · Ungulates · Savanna · *Saccostomus mearnsi*

Introduction

East African rodents are recognized as important agricultural pests and disease reservoirs affecting humans (Davis 1953; Taylor 1968; Fiedler 1988; Gratz 1988; Leirs et al. 1996; Mills et al. 1997). Periodic population outbreaks of several taxa (e.g. *Arvicanthis*, *Mastomys*) are widely reported and have been shown to have dramatic impacts on agricultural crops and stores (Taylor 1968; Fiedler 1988; Leirs et al. 1996). Until recently, studies of factors influencing population dynamics in East African rodents have been limited to investigations of the role of abiotic factors such as rainfall and the resulting density-independent population processes (Neal 1977; Hubert and Adam 1983; Leirs et al. 1996). Recent research in northern Tanzania has revealed an interplay between density-dependent and density-independent factors in the population dynamics of one widespread species, *Mastomys natalensis* (Leirs et al. 1997). However, the effects of community interactions such as competition and predation on the abundance and diversity of East African rodents have not been investigated.

Many rodents consume vegetation and thus have the potential to compete with other herbivores. In African savannas, ungulates are the predominant consumers of vegetation. If foraging by ungulates reduces the quantity or quality of food resources available to rodents, rodent

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populations should increase in the absence of ungulates. Competition between organisms of such vastly different body sizes as rodents and ungulates has rarely been investigated (but see Brown and Davidson 1977). In addition, because there are numerous species of ungulates in East African savannas, competitive effects of ungulates on rodents could be the result of diffuse competition (MacArthur 1972) rather than of pairwise species interactions. Diffuse competition could also play a role within the small mammal community. For instance, if one rodent species increased in density in the absence of ungulates, other rodent species might decrease due to increased interference competition with a competitive dominant. Thus, changes in ungulate abundance have the potential to influence small mammal community dynamics.

A second means by which ungulates may affect small mammals is via predation. In North American rangelands, trampling and grazing by ungulates have been shown to reduce vegetation cover for small mammals (Grant et al. 1982; Bock et al. 1984). Reductions in cover are assumed to increase their exposure to predation (Birney et al. 1976; Edge et al. 1995; Peles and Barrett 1996). Whether the presence of ungulates increases the exposure of small mammals to predators has not been investigated in East African savannas, but could have significant effects on their population dynamics. Ungulates may also influence other aspects of habitat quality for rodents through physical disturbance, such as trampling of soil.

To investigate the impacts of ungulates on East African rodents, I monitored small mammal abundance and diversity in both the presence and the absence of ungulates. I hypothesized that the exclusion of ungulates would result in an overall increase in small mammal abundance. I also monitored small mammal demography and space use, and changes in vegetative cover, to investigate the mechanism(s) underlying any effects. I report here the results of the first 2 years of this ongoing experiment.

Methods

Study site

This research was conducted between August 1995 and September 1997 at the Mpala Research Centre (0°17'N, 36°53'E), located in the Laikipia District of central Kenya at an altitude of 1800 m. This area is characterized as wooded grassland on "black cotton" vertisol soils with impeded drainage, and is dominated by a swollen-thorn acacia, *Acacia drepanolobium*. Other woody species present include *Balanites aegyptiaca*, *Cadaba farinosa*, *Acacia mellifera*, *A. brevispica*, *Rhus natalensis*, and *Lycium europaeum* (Young et al. 1997). The understory is dominated by the grasses *Themeda triandra*, *Pennisetum stramineum*, *P. mezianum*, *Lintonia nutans*, and *Brachiaria lachnatha*, and the herbs *Aerva lanata*, *Rhinacanthus ndorensis*, *Dyschoriste radicans*, and *Commelina* spp. (Young et al. 1997). This is the most common plant community in the Laikipia ecosystem, covering more than a quarter or 2700 km² of this region (Young et al. 1997).

The growing season for vegetation is highly seasonal. Rains generally begin in April and May, with an intense dry season from December to February. Average annual rainfall is 500–600 mm, though there is substantial spatial and temporal heterogeneity. During the first year of this study, rains were late, with lower than average precipitation falling before June and July 1996, following a long dry season (Fig. 1). In the second year of the study, there was much higher than normal rainfall during April 1997.

Ungulates in this habitat include elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), Grevy's zebra (*Equus grevyi*), Burchell's zebra (*E. burchelli*), Grant's gazelle (*Gazella granti*), Jackson's hartebeest (*Alcelaphus buselaphus*), eland (*Taurotragus oryx*), Beisa oryx (*Oryx gazella*), steinbuck (*Rhaphicerus campestris*), cape buffalo (*Syncerus cafer*), and domestic cattle. Mammalian carnivores include lion (*Panthera leo*), leopard (*P. pardus*), cheetah (*Acinonyx jubatus*), black-backed jackal (*Canis mesomelas*), ratel (*Mellivora capensis*), white-tailed mongoose (*Herpestes ichneumon*), and slender mongoose (*H. sanguineus*). Other conspicuous mammals include baboon (*Papio cynocephalus*), patas monkey (*Erythrocebus patas*), bushbaby (*Galago senegalensis*), and aardvark (*Orycteropus afer*). While a complete list of the herpetofauna has not been compiled, snakes encountered in this habitat are puff adders (*Bitis arietans*) and cobras (*Naja* sp.). The dominant raptor is the black-shouldered kite (*Elanus notatus*).

Ungulate exclusion

A long-term study to assess the interrelationships between large herbivores, livestock, and vegetation was established by T. P. Young in August 1995. This experiment consists of a stratified randomized block design, with three blocks of six treatments. Each treatment is 4 ha (200 m × 200 m); each block is 24 ha (400 m × 600 m). This research was conducted inside two of the six treatments: the total exclusion treatment, which excluded both native ungulates and cattle, and the control plots, which allowed free access by both native ungulates and cattle.

Full fencing for the total exclusion treatment consists of a 2.4 m fence with eleven strands of wire, with every other strand electrified at 3,000–7,500 V. The control plots are unfenced. Cattle presence on the control plots is managed by resident herders. During cattle grazing periods, project assistants record the number of cattle, date, and total time on each of the plots.

Prior to installation of the exclusion fences, the density and height of *Acacia drepanolobium* stands were mapped over a several

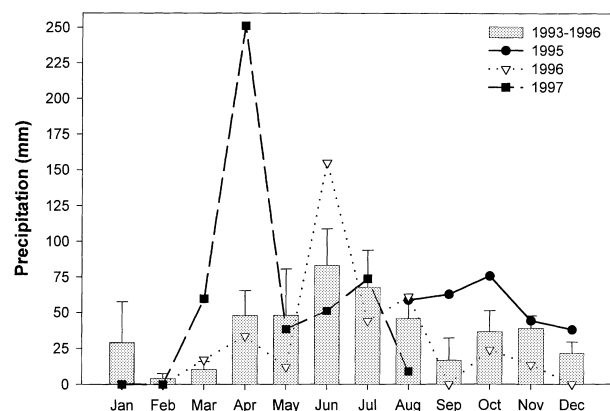


Fig. 1 Monthly average precipitation at Mpala Research Centre for 1993–1996 (bars) versus averages for 1995 (dashed line) and 1996 (solid line). There is a distinct dry season from December through February. Rains typically begin in April and continue through August, with peaks in June and July, though there is great heterogeneity from year to year. In 1996, significant precipitation did not begin until June. In 1997, there was unusually high precipitation in April

hundred hectare area (T. P. Young, personal communication). Locations for blocks were chosen to be as homogeneous as possible, avoiding sites of either very low tree density or low tree stature. Sites were also chosen to be as far as possible from the infrequently used private roads near the study site to minimize any disturbance by vehicles and edge effects.

Small mammal analyses

I established a permanent small mammal trapping grid inside each of the three replicates of the ungulate exclusion and control plots. Each 4-ha plot was set with a 10 by 10 grid with 10 m spacing. Grids were located in the central hectare of each plot, so that no trap was closer than 50 m to the nearest neighboring treatment. Trapping was conducted for three consecutive nights, using large folding Sherman traps, with one trap per station. Traps were baited with a mixture of peanut butter and oatmeal, and checked morning and evening. Captured individuals were marked for individual identification, and their weight, sex, and reproductive condition (males: testes scrotal or abdominal; females: vulva perforate or imperforate, pregnant or lactating) recorded.

I conducted seven trapping sessions during the 2 years of large-mammal exclusion: in September 1995 at the time of installation of the fences; in January 1996 at the beginning of the dry season; in April 1996 at the height of an unusually long dry season; in August 1996, after 1 year of large mammal exclusion; in November 1996; in March 1997; and in September 1997, after 2 years of ungulate exclusion. In November 1996, one of the control plots was trapped 1 month late, due to an abundance of lions and buffalo on and near the grid.

Abundances of all small mammal species were determined using direct enumeration, since all but one of the species were captured too infrequently for accurate mark-recapture analyses of abundance. Because the pouched mouse, *Saccostomus mearnsi*, was captured frequently its abundance was also estimated using mark-recapture algorithms. Trapping data for *S. mearnsi* were entered into Program CAPTURE (Rexstad and Burnham 1992) and the program's model selection procedure was invoked to choose the most appropriate model for each trapping occasion. The appropriate abundance estimator for the selected model was then used to calculate the CAPTURE population estimate. Program CAPTURE selects these models using algorithms which test for various possible sources of heterogeneity in the trapping data, including capture probabilities which vary with time, with the behavior of individual animals (e.g., trap avoidance after initial capture), or with combinations of these factors. Such heterogeneity could lead to bias in estimates of abundance; Program CAPTURE chooses the model which best accounts for this possible bias. To establish that model selection was not influencing the results, I also compared *S. mearnsi* abundance using direct enumeration of individuals.

Abundance data for small mammal species for the baseline trapping session in September 1995 were compared using a paired *t*-test, to establish that starting conditions were not significantly different. I used a factorial repeated measures ANOVA for all comparisons once treatments were in place, but did not include initial conditions to avoid spurious time \times treatment interactions. Spurious interactions could result from comparing conditions before experimental treatments were imposed with conditions after treatments were imposed. These analyses, therefore, provide a conservative estimate of treatment effects. All statistical tests were performed using StatView 4.1 (Abacus Concepts 1992) unless otherwise noted.

Demographic and space use data were calculated only for *S. mearnsi*, as other species were captured too infrequently for accurate analyses. To consider the effect of the two treatments on body condition of *S. mearnsi*, I compared male weights through time. Female weights were not compared to avoid possible bias due to undetected pregnancies. The minimum adult weight for male *S. mearnsi* was determined by taking the median of the ten smallest males that were reproductively active (scrotal testes), and was found to be 48 g and above. All juveniles (<48 g) were excluded

from subsequent calculations of body weight. Male weights from the baseline September 1995 trapping session were compared for treatment and control plots using a paired *t*-test; the six subsequent trapping sessions were compared using a factorial repeated measures ANOVA.

Survivorship of *S. mearnsi* was determined by calculating the proportion of individuals alive at trapping session *t* who survived until the following trap session *t* + 1. Recruitment, which subsumes both in situ reproduction and immigration, was calculated as both per capita recruitment and total recruitment. Per capita recruitment was computed by determining the proportion of individuals captured at trapping session *t* that had not previously been captured. Total recruitment was the total number of new individuals captured in a given plot during a particular trapping session. All of these demographic features were compared between treatments using a factorial repeated measures ANOVA.

To estimate differences in space use by individual pouched mice in response to changes in density in experimental and control treatments, I compared the maximum distances moved between captures for males and females that were captured more than once, based on the calculations of these distances by Program CAPTURE. I calculated the average maximum distance moved for all individuals on each grid, with the grid as the unit of replication. Baseline values were compared using a paired *t*-test; comparisons for the remaining six trapping sessions were compared using a factorial repeated measures ANOVA. To determine whether differences in pouched mouse density on the experimental and control treatments had an effect on pouched mouse space use, I conducted an ANCOVA (SYSTAT 7.0; SPSS 1997) for the maximum distance moved by each sex, with block (three levels) and treatment (ungulates, no ungulates) as factors and mouse density (as determined by program CAPTURE for each grid) as a covariate.

I calculated an index of small mammal species diversity for each plot for each trapping session using Shannon's equation, $H' = -\sum p_i \log_{10} p_i$ (Zar 1984). Because some species were captured too infrequently to make accurate mark-recapture estimates of density, I calculated the proportional contribution of a species (p_i) using direct enumeration of that species for each grid. Because repeated measures of diversity are usually normally distributed (Magurran 1988), I used parametric statistical tests to compare indices. I used a paired *t*-test to compare the baseline values, and a factorial repeated-measures ANOVA to compare the values through the remainder of the study.

Ungulate abundance

Though no precise estimates of native ungulate use of the plots are available, two censuses of the large mammals of the Laikipia District were conducted during the first year of this study, in February and September 1996, by the Laikipia Wildlife Forum (unpublished work). These censuses incorporated the location of the current study and measured the ungulate community that had access to the study plots. Because they conducted aerial surveys with direct enumeration of individuals, the results were conservative, with the February 1996 count yielding numbers 25% less than the previous sample count in 1994 (Laikipia Wildlife Forum, unpublished work). I estimated the biomass of native ungulates that had access to the study site by multiplying the number of each species, as determined from the count, by an estimate of average mass for that species (from Nowak and Paradiso 1983). I then divided that total biomass by the area of Laikipia District surveyed (7000 km²).

To estimate the average biomass of cattle on the study site, I determined the average number of cattle-hours per day on each 4-ha plot at the study site during 1996, as recorded by project assistants accompanying cattle herders (T. P. Young unpub. data). I converted this to kg/ha using an estimate of 600 kg/cow.

Vegetation cover

In August 1997, at the end of the second year of ungulate exclusion, I measured vegetative cover in both ungulate exclusion and control

plots using a 1 m pin frame with 20 pins. The pin frame was placed every 3 m along three transects through the central hectare of each plot for a total of 100 placements per plot. Transects were separated by 50 m, and were at least 50 m from the nearest neighboring treatment. At each placement of the pin frame, I recorded how many pins contacted vegetation and how many contacted bare ground. I then calculated the average proportion of bare ground in each plot and compared these values with a paired *t*-test.

Results

Small mammal responses

Between September 1995 and September 1997, I captured a total of 2,283 small mammals (approximately 20% trap success), comprising nine species (Table 1). The pouched mouse, *Saccostomus mearnsi*, a semi-fossorial, medium-sized murid rodent, was the most frequently trapped species, representing approximately 75% of all captures.

Capture probabilities of species other than *S. mearnsi* were too low to provide accurate mark-recapture estimates of abundance, and were not entered into Program CAPTURE. For *S. mearnsi*, Program CAPTURE chose the model of equal probability of capture *M*(o) for 18 of 24 trapping sessions, the model *M*(t) (time specific variation in trapping probabilities) one time, the model *M*(bh) (behavioral response with heterogeneity) one time, the model *M*(th) (temporal variation with heterogeneity) one time, and the model *M*(h) (unknown heterogeneity of trapping probabilities) three times.

The exclusion of ungulates resulted in a highly significant increase in the abundance of *S. mearnsi*. At the time of the installation of the fences in September 1995, there was no significant difference between treatment and control ($t_2 = -0.45$; $P = 0.70$) demonstrating that starting conditions were not different. By February 1996, the abundance of *S. mearnsi* in fenced plots was 40% higher than in the unfenced control plots, a result that was highly significant ($t_2 = -12.12$; $P = 0.007$) (Fig. 2). These differences were maintained and increased through the subsequent five trapping sessions, and showed a significant time × treatment interaction ($F_{5,20} = 2.68$; $P = 0.05$) (Table 2). By the 2nd year of ungulate exclusion, the abundance of *S. mearnsi* in fenced plots was twice as high as in control plots, and

this difference was maintained throughout pronounced seasonal fluctuations in abundance (Fig. 2). Abundance estimates based on direct enumeration of individuals were also significantly different, demonstrating effects of both treatment ($F_{5,20} = 12.91$; $P = 0.02$) and time × treatment ($F_{5,20} = 2.73$; $P = 0.05$).

There was no significant difference in either survivorship (time × treatment: $F_{5,20} = 1.37$; $P = 0.29$) or per capita recruitment (time × treatment: $F_{5,20} = 0.75$; $P = 0.60$) of pouched mice between treatment and control over the 2 years of the study (Fig. 3a,b). Both survivorship and per capita recruitment did show highly significant seasonal variation for both control and experimental treatments combined (survivorship: $F_{5,20} = 4.36$; $P = 0.01$; per capita recruitment: $F_{5,20} = 15.72$; $P < 0.0001$). In both years of the study, per capita recruitment rates for *S. mearnsi* in control and experimental treatments were lowest during the dry season and highest following the rains. The total number of individual recruits was significantly different between treatments ($F_{1,4} = 11.13$; $P = 0.04$) (Fig. 3c). During the final trapping session, there were 30% more recruits on the plots from which ungulates were excluded (control: 35.0 ± 2.0 ; experimental: 46.0 ± 1.2).

Male *S. mearnsi* had significantly higher body weights on the experimental grids ($F_{1,4} = 16.46$; $P = 0.02$),

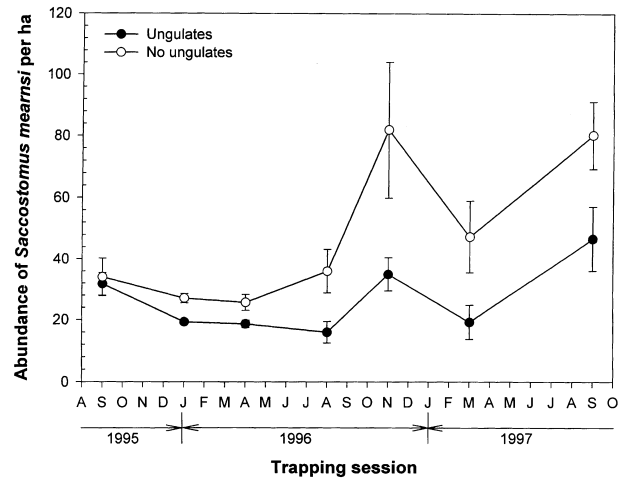


Fig. 2 Abundance of pouched mice, *Saccostomus mearnsi*, per hectare in ungulate exclusion (open circles) and control (solid circles) treatments. Error bars represent SEs

Table 1 Species list of the small mammals captured on the plots and the number of individuals of each species captured

Species	Order: Family	No. of individuals
<i>Acomys</i> sp.	Rodentia: Muridae	1
<i>Aethomys</i> sp.	Rodentia: Muridae	2
<i>Arvicanthis</i> sp.	Rodentia: Muridae	155
<i>Dendromus</i> sp.	Rodentia: Muridae	38
<i>Mastomys</i> sp.	Rodentia: Muridae	37
<i>Mus</i> sp.	Rodentia: Muridae	96
<i>Saccostomus mearnsi</i>	Rodentia: Muridae	1124
<i>Tatera</i> sp.	Rodentia: Gerbillidae	2
<i>Crociodura</i> sp.	Insectivora: Soricidae	20

Table 2 Repeated measures ANOVA for the abundance of *Saccostomus mearnsi* per hectare (using mark-recapture estimates) in the presence or absence of ungulates (Treatment) over six trapping sessions between January 1996 and September 1997 (Time)

	Source	df	Mean square	F	P
Between plots	Treatment	1	5112.25	6.33	0.066
	Error	4	807.31		
Within plots	Time	5	2037.09	15.22	< 0.001
	Time × treatment	5	370.25	2.77	0.05
	Error	20			

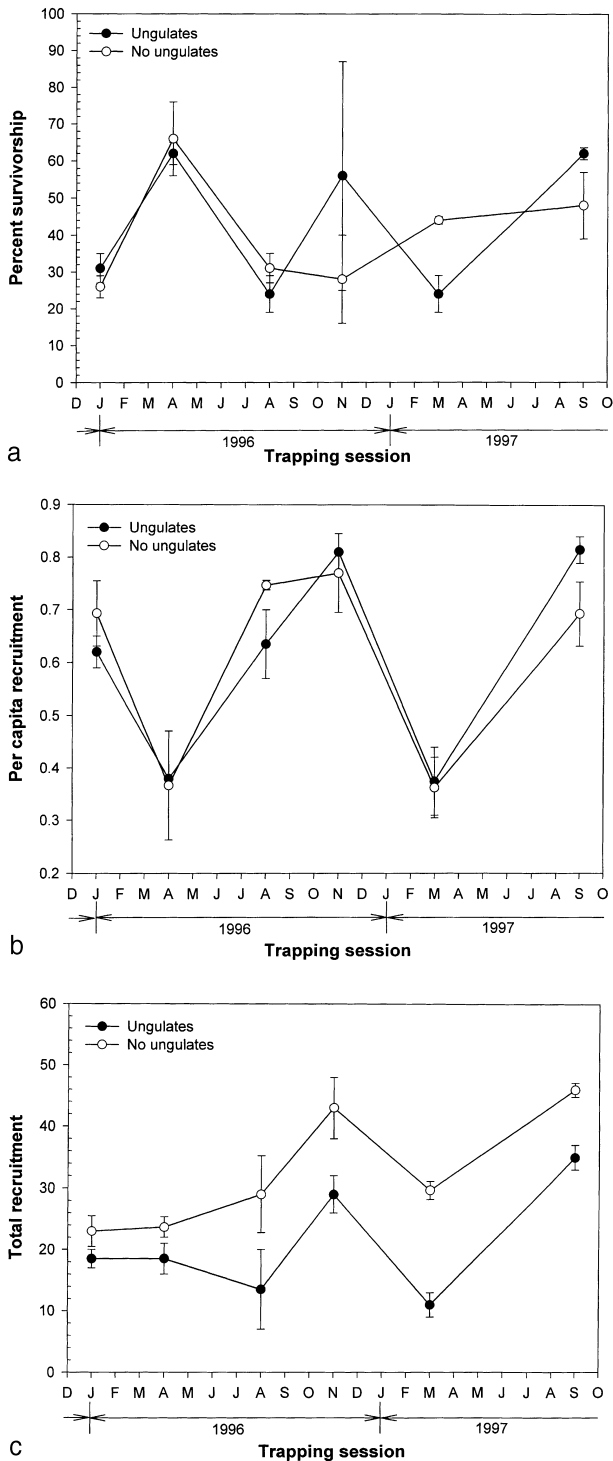


Fig. 3a-c Demographic responses of *Saccostomus mearnsi* on ungulate exclusion (open circles) and control (solid circles) plots. **a** Percent survivorship of individuals between trapping sessions; **b** per capita recruitment; and **c** total recruitment of individuals between trapping sessions. Error bars represent SEs

with weights an average of 4% higher in the absence of ungulates (control: 80.4 ± 2.0 g; experimental: 77.7 ± 2.3 g). There were also seasonal differences in average male body mass for both treatments combined ($F_{5,20} = 5.14$; $P = 0.003$), with the lowest weights

during the dry season and the highest weights following the rains.

Pouched mice showed no significant effect of treatment on the average maximum distance moved between captures for either males ($F_{1,4} = 1.3$; $P = 0.38$) or females ($F_{1,4} = 1.85$; $P = 0.31$). Though these results were not significant, males moved an average of 33% further in the control plots (26.1 ± 5.4 m) than in the plots from which ungulates had been excluded for 2 years (19.6 ± 2.7 m), while females moved 20% farther in the control plots (17.4 ± 1.6 m) than in the experimental plots (14.2 ± 1.5). Based on the ANCOVA, there was a significant effect of pouched mouse density on the average maximum distance moved by males ($F_{1,36} = 5.07$; $P = 0.03$), but with no effect of treatment ($F_{1,36} = 0.43$; $P = 0.51$). There was no effect of density for females ($F_{1,36} = 1.46$; $P = 0.24$), nor was there a treatment effect ($F_{1,36} = 0.48$; $P = 0.49$).

The abundances of small-mammal species other than *S. mearnsi* showed diverse responses to ungulate exclusion. Like *S. mearnsi*, after 2 years *Mastomys* sp. was significantly more abundant on plots from which ungulates were excluded (time \times treatment: $F_{5,20} = 3.08$; $P = 0.03$) (Fig. 4a). Two other small mammal species, *Arvicanthis* sp. and *Mus* sp., showed highly variable patterns of abundance over the two years (Fig. 4b,c). Though the abundance of *Arvicanthis* was generally higher in the absence of ungulates, neither *Mus* nor *Arvicanthis* exhibited significant effects of either treatment (*Arvicanthis*: $F_{1,4} = 5.161$, $P = 0.09$; *Mus*: $F_{1,4} = 0.497$; $P = 0.52$) or time \times treatment (*Arvicanthis*: $F_{5,20} = 8.4$, $P = 0.19$; *Mus*: $F_{5,20} = 12.4$; $P = 0.20$). The abundance of *Dendromus* sp. did not appear to respond to ungulate exclusion. *Dendromus* showed a steady and significant decline in abundance on both treatment and control plots from April through August 1996, and maintained low and relatively constant densities on both experimental and control plots through the second year (Fig. 4d) ($F_{5,20} = 8.0$; $df = 2$; $P = 0.01$).

Shannon species diversity of all small mammals showed a highly significant effect of time \times treatment ($F_{5,20} = 7.58$; $P = 0.0004$) (Table 3). In the ungulate exclusion plots, diversity remained relatively constant, exhibiting only gradual changes between trapping sessions over the 2 years of the study (Fig. 5). In the control plots to which ungulates had access, diversity also remained relatively constant from the September 1995 through the April 1996 trapping sessions. However, during the August 1996 trapping session, diversity in the control plots decreased substantially, coincident with a decrease in the abundance of *S. mearnsi*. This decrease in diversity was largely the result of the complete disappearance of *Arvicanthis* and *Mus* from the control plots (Fig. 4b,c). By the November 1996 trapping session, species diversity had rebounded in the control plots to levels higher than those in the ungulate exclusion plots. Diversity in both treatments was comparable for the remainder of the second year.

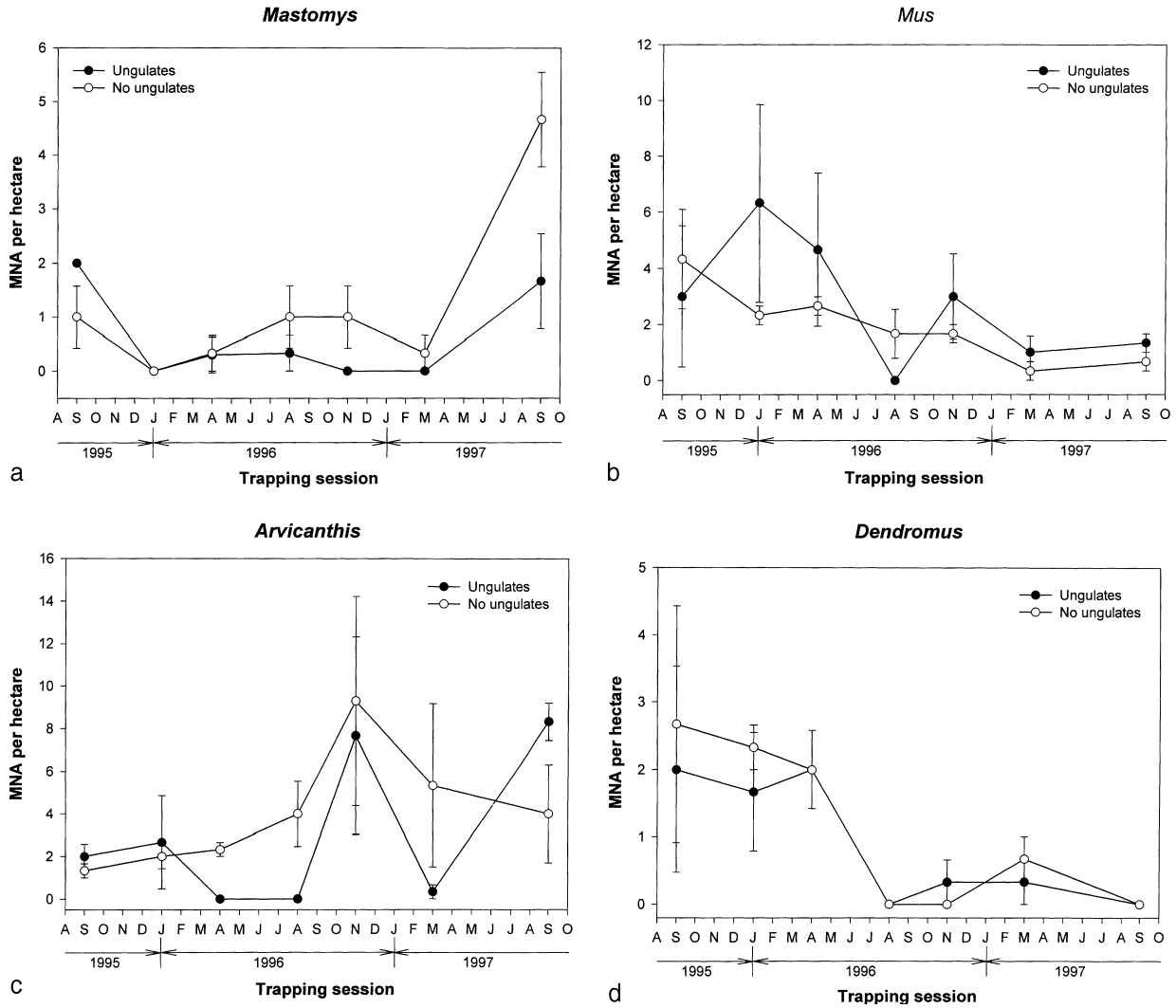


Fig. 4 Abundance (minimum number alive, MNA) of **a** *Mastomys* sp., **b** *Mus* sp., **c** *Arvicanthis* sp., and **d** *Dendromus* sp. per hectare on ungulate exclusion (open circles) and control (solid circles) plots. Error bars represent SEs

Table 3 Repeated measures ANOVA for Shannon diversity of the small mammal community in the presence or absence of ungulates (Treatment) over six trapping sessions between January 1996 and September 1997 (Time)

	Source	df	Mean square	F	P
Between plots	Treatment	1	0.001	0.11	0.760
	Error	4	0.005		
Within plots	Time	5	0.039	7.58	<0.001
	Time × treatment	5	0.021	4.04	0.011
	Error	20			

Ungulate abundance

Livestock grazing on the control plots was low during the first year. The mean cattle presence on the three control plots was 632 cattle h year⁻¹ (±146; range 411–

909), which is the equivalent of one animal grazing on a 4 ha plot for less than two hours each day, or a biomass of approximately 10 kg ha⁻¹ day⁻¹. I calculated a large mammal biomass for Laikipia District of 44 kg ha⁻¹ for all native ungulate species combined. This biomass estimate is probably low because the study site is in a region of Laikipia with a greater density of wildlife than other areas more populated by humans (Laikipia Wildlife Forum, unpublished work). Nonetheless, this conservative estimate yields a biomass of native ungulates on the study site approximately 4.5 times greater than the biomass of livestock. Therefore, the effects reported here are primarily caused by native ungulates rather than livestock.

Vegetative cover

At the end of the 2nd year of the study, there was no significant difference in percent cover in the presence (77.0 ± 2.1%) versus the absence (77.2 ± 2.5%) of ungulates (*t*₂ = 0.13; *P* = 0.91).

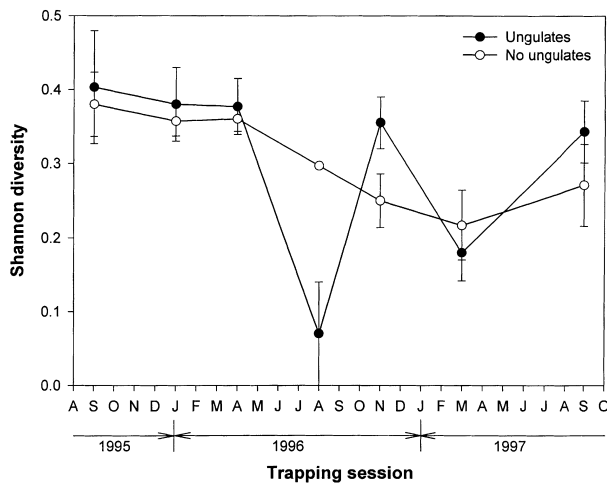


Fig. 5 Shannon species diversity (base 10) of small mammals captured in the ungulate exclusion (open circles) and control (solid circles) plots. Error bars represent SEs

Discussion

The exclusion of ungulates resulted in a substantial increase in *S. mearnsi* abundance, a modest increase in the abundance of *Mastomys*, and the avoidance of an episodic decline in overall small mammal diversity that occurred in the presence of ungulates. The rapid and pronounced increase by *S. mearnsi* when ungulates were removed demonstrates a strong interaction between these taxa. This effect could have resulted from three primary mechanisms – a decrease in habitat disturbance, a decrease in the exposure of small mammals to their predators, or a decrease in competition between ungulates and small mammals.

If ungulates cause habitat disturbance through trampling, small mammals could be affected either directly or indirectly. Small mammals could suffer the direct effect of being squashed, though this is unlikely given the relatively low probability of encounter and the abundance of refugia. Soil compaction could cause cave-ins or changes in water infiltration of burrows, though these effects seem unlikely to be a major factor and would be expected to appear after a longer time period. Or soil compaction could have an indirect effect on small mammals by causing changes in vegetation, though this would also be expected to have a delayed impact on small mammal populations. None of these factors seems to account for the rapid response of pouched mice to the removal of ungulates.

Second, the removal of ungulates could increase vegetative cover, thereby decreasing the exposure of small mammals to their predators. Studies in North American rangelands have demonstrated that trampling and grazing by ungulates can reduce cover for small mammals (Grant et al. 1982; Bock et al. 1984), which is assumed to increase their exposure to predation (Birney et al. 1976; Edge et al. 1995; Peles and Barrett 1996). At

this site, however, differences in vegetative cover were not significant in the presence vs. the absence of ungulates. Heske and Campbell (1991) found a similar increase in rodent abundance inside long-term livestock enclosures in Arizona despite no detectable differences in vegetative cover. In addition, survival of pouched mice was not significantly higher in the absence of ungulates, a difference which would be expected if their risk of predation were lower.

Finally, the removal of ungulates could cause an increase in the quantity or quality of food available to small mammals, since pouched mice are herbivores (Keesing, 1998; F. Keesing and M. Metz, unpublished work) and potentially compete with ungulates for food resources. Indirect evidence from this study suggests that this was indeed the case. The home ranges of male pouched mice were not significantly different in size in the absence of ungulates, as indicated by their average maximum distances travelled. Yet despite their using the same amount of space, males managed to maintain significantly higher body weights in the absence of ungulates, suggesting that habitat quality was higher for pouched mice when ungulates were removed.

If ungulates and small mammals are sharing food resources in this habitat, this would be an example of exploitative competition. Competition has typically been identified through experiments in which the exclusion of one species results in an increase in the abundance of another (Connell 1983; Schoener 1983). By this criterion, ungulates and *S. mearnsi* are competing in this habitat. However, these data demonstrate only a one-way effect of ungulates on small mammals. A more inclusive definition of competition requires a two-way negative interaction (Lidicker 1979). Whether small mammal abundance also has a negative effect on ungulate abundance remains to be determined, though results from other research in this habitat demonstrate that small mammals have an effect on both the quality and the quantity of the vegetation available to ungulates (Keesing 1997). This suggests that competition with ungulates, as defined by either criterion, may be the dominant mechanism affecting the abundance of *S. mearnsi* in this habitat.

It is possible that the fence might have excluded the predators of small mammals in addition to the ungulates, so that the increases in *S. mearnsi* abundance might have resulted from the exclusion of their predators in addition to the exclusion of ungulates. While it is difficult to quantify the degree to which predators may have been affected by the ungulate exclusion fences, it is unlikely that this effect was substantial. The major predators of small mammals in this habitat are snakes, raptors, and small carnivores. The bottom strand of the fence was not electrified, allowing unimpeded access by snakes. Raptors had aerial access to the plots and were therefore unlikely to have been affected by the fences. Some small carnivores may have been deterred by the fence; however, small carnivores, such as mongooses, jackals, and ratels, were known to access the exclusion

grids, as indicated by tracks, trap disturbance, and diggings.

The demographic factors responsible for the increase in *S. mearnsi* abundance in the absence of ungulates are not clear. There was no indication of higher survivorship in the experimental treatments, nor was there a detectable difference in per capita recruitment. Each female appears to have been producing, on average, the same number of young whether or not ungulates were present. Total recruitment, however, did differ, with an average of about twice as many new individuals appearing on the ungulate exclusion plots during each trapping session of the second year. There are two likely explanations for these demographic patterns. First, females may have been producing on average equal numbers of offspring on both treatments, but there were more females on the ungulate exclusion plots, so that they produced a greater number of total recruits. This explanation is supported by the trend toward higher survivorship on the exclusion plots during the first year (April 1996 and August 1996), which could have initiated the increase in numbers of females on the ungulate exclusion plots. Alternatively, these results may indicate habitat selection by individuals within the experimental and neighboring areas. Under this scenario, demographic differences between experimental and control plots would have been due to dispersal from surrounding areas onto ungulate exclusion grids. Though the size of the exclusion plots (4 ha) was large relative to *S. mearnsi* home ranges (males: 0.19 ha; females 0.05 ha; Keesing, 1998), individuals may have dispersed from areas of higher ungulate activity to the experimental areas without ungulates. This hypothesis is supported by the significant increase in total recruits, which may have been dispersers from neighboring areas, despite no detectable differences in per capita recruitment or survivorship of individuals on the grids. In either case, plots without ungulates supported small mammal densities twice as high as plots to which ungulates had access, demonstrating that ungulates have dramatic effects on the abundance of pouched mice.

The sudden decrease in small mammal diversity in the control plots between the April and August 1996 trapping sessions suggests that ungulates, either as competitors or as agents of disturbance, can cause local extinctions of uncommon savanna small mammal species. In a long-term experimental study in a temperate desert rodent assemblage, Valone and Brown (1995) found that the removal of a dominant competitor increased the species diversity of the remaining small mammal community. They demonstrated that this was due to higher colonization and lower extinction rates of these species in the absence of a competitively dominant species. The maintenance of small mammal diversity in the absence of dominant competitors (ungulates) in this savanna system may be the result of similar processes.

The results of this study indicate that there may be unanticipated consequences of decreases in savanna ungulate densities, whether due to natural or anthropogenic influences. An consequent increase in small

mammal abundance could impact humans through rodents' roles as agricultural pests and disease reservoirs. On the other hand, an increase in small mammal abundance might be beneficial for small carnivores and raptors by providing increased prey resources. Low ungulate densities might also serve as a buffer for maintenance of small mammal diversity. However, if increases in small mammal density result in compensatory consumption of vegetation, this could have the unexpected effect of decreasing grassland forage quality. Even moderate densities of small mammals in this habitat have been shown to have pronounced and rapid effects on both the biomass and the species composition of savanna vegetation (Keesing 1997). These interactions between ungulates and small mammals have not previously been seriously considered, but may be important for management of mammalian biodiversity in East African savannas.

Acknowledgements I thank the Office of the President of the Republic of Kenya and the Kenya Wildlife Service for their cooperation and assistance in the conduct of this research. I gratefully acknowledge financial assistance from the National Geographic Society, the Museum of Vertebrate Zoology, the Museum of Paleontology, and the Department of Integrative Biology at the University of California at Berkeley, the American Society of Mammalogists, Sigma Xi, The University of California Vice Chancellor's Fund for Research, the Patricia Robert Harris Fellowship fund, and the ARCS Foundation. I benefited greatly from the logistical assistance of S. Takata, R. Ostfeld, J. Wasike, T. Young, D. Kinyua, W. Z. Lidicker Jr., G. Small, the UC Berkeley Museum of Vertebrate Zoology, the Mpala Research Centre, and the Institute of Ecosystem Studies. This research could not have been completed without the installation of the large mammal exclusion fences for which acknowledgement is due to T. Young, A. Smith, the National Geographic Society, the Mpala Wildlife Foundation, and the Smithsonian Institution. This manuscript was greatly improved by the comments of R. Ostfeld, W. Z. Lidicker, Jr., D. McCullough, J. Patton, D. Morris, and two anonymous reviewers.

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