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SHORT COMMUNICATION

Impacts of density and large mammals on space use by the pouched mouse (*Saccostomus mearnsi*) in central Kenya

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Rodents in tropical Africa have been recognized for decades both as important pests of agriculture and as reservoirs of numerous diseases that affect humans and livestock (Keesing 2000). Despite this recognition, however, little is known about the ecology and behaviour of these abundant and widespread animals. Because the impacts of small mammals as pests are expected to be some function of their population density, most ecological research on African rodents has focused on their population dynamics (Delany 1972, 1986; Leirs *et al.* 1994, 1996a).

In temperate and boreal habitats, population density both influences the way small mammals use space and is influenced by space use. For example, territorial behaviour by some rodents is thought to regulate density, but when high population density is achieved, territorial systems often break down (Stenseth 1986, Tamarin 1983). Space use can also potentially describe spatial patterns by which rodents exploit resources (Bowers & Dooley 1993, Gill & Marks 1991, Manson & Stiles 1998, Manson *et al.* 1999, Ostfeld *et al.* 1997, 1999; Pusenius *et al.* in press). For example, white-footed mice (*Peromyscus leucopus* Rafinesque) in old-fields of eastern North America are most commonly found in shrub-dominated microhabitats, and predation on tree seeds by mice is highest in these areas (Manson *et al.* 1999; Ostfeld *et al.* 1997, 1999). Despite their potential interactions with both resource use and population density, patterns of

space use by small mammals in African savannas have rarely been documented (Keesing 1998a, Leirs *et al.* 1996b).

In parts of central Kenya, the pouched mouse (*Saccostomus mearnsi* Heller) is the dominant small mammal, representing about 85% of the small-mammal community (Keesing 1998a, 1998b, 2000). This murine rodent consumes both seeds and green vegetation (Keesing 1998a, Metz & Keesing in press) and fluctuates in density in response to the presence of ungulates (Keesing 1998b, 2000). When ungulates were experimentally removed from large, replicated areas, the abundance of pouched mice was twice as high as on control plots to which ungulates had access (Keesing 1998b, 2000).

Our goal in this study was to describe the spatial distribution of *S. mearnsi*, and to assess possible causes of variation in their distribution. Therefore, we investigated the effects of (a) mouse population density and (b) the presence of large mammals on patterns of space use by pouched mice based on 5 years of small-mammal trapping at the Mpala Research Centre in central Kenya. We determined whether the mice showed clumped, random or uniform spatial distributions on 1-ha grids. We then determined whether these patterns differed for males and females, and whether they were affected by either mouse density or the experimental removal of ungulates.

This study was conducted between 1995 and 1999 at the Mpala Research Centre (MRC) in the Laikipia District of central Kenya. MRC is the location of the Kenya Long-term Exclusion Experiment (KLEE), in which different combinations of large mammals are excluded from replicated 4-ha (200-m × 200-m) plots. KLEE consists of a randomized block design, with three blocks of six treatments (Keesing 2000, Young *et al.* 1998). The treatments manipulate the presence or absence of megaherbivores (giraffes and elephants), other native ungulates and cattle in a semi-factorial design (Young *et al.* 1998).

We focused our investigation on two of the six large-mammal treatments: one treatment excluded all ungulates; the other excluded no ungulates and served as a control. In August 1995, when the KLEE fencing was completed, we established small-mammal trapping grids in each of the three replicate plots for both treatments (six grids altogether). On the central hectare of each 4-ha treatment area, we established a 10×10 grid with 10-m spacing. All traps were therefore located ≥ 50 m from the edges of the large mammal treatment. At each of the 100 grid points, we placed a folding Sherman live-trap (5.1 cm × 6.4 cm × 15.2 cm), baited with a mixture of oatmeal and peanut butter. Traps were set in the evening and checked the following morning for three consecutive days. Captured individuals were identified to species, weighed, sexed, assessed for reproductive condition, marked with an individual numbered eartag if not previously marked, and released at the point of capture.

Analyses of density and space use were performed only for *S. mearnsi* because it was the only species in which individuals were recaptured frequently. Because average survivorship of *S. mearnsi* is < 1 year (Keesing 1998a), we

included only year-end trapping data in our analyses of space use, so that space use by individuals was not pseudoreplicated (Hurlburt 1984). Densities of *S. mearnsi* were estimated from year-end trapping data using Program CAPTURE (Rexstad & Burnham 1992). We used the program's model selection procedure to determine the appropriate population estimator.

We quantified the spatial distribution of *S. mearnsi* on the two treatments during each of the year-end trapping sessions in two ways. First, to assess whether individual animals were clustered on grids, we recorded the x–y coordinate of the first capture of each animal on each 10 × 10 grid, with each point on the grid representing a trap station. To assess whether total mouse activity was clustered on the grids, we recorded the x–y coordinate of *all* captures of mice on the grid during a trapping session, including cases in which the same animal was captured more than once. We considered captures of males and females separately and together for both types of analyses. We divided each grid into contiguous 100-m^2 areas circumscribed by the four trap stations at the corners. We then counted the total number of captures that were recorded for each 100-m^2 square on each grid. Values for grid-squares could range from 0 (no individuals captured in any of the four surrounding traps for 3 d) to 12 (a mouse captured in each of the four surrounding traps for each of 3 d). Grid squares were comparable in size to the home ranges of pouched mice (Keesing 1998a), and were therefore at a scale more biologically relevant than that of the individual trap station.

For each 10 × 10 grid, there were 81 grid-square values, from which we calculated the variance/mean ratio ($\overline{S^2}/X$) for the grid (Zar 1999). $\overline{S^2}/X$ values greater than 1.0 suggest a clumped distribution, values approximately equal to 1.0 suggest a random distribution and values less than 1.0 suggest a uniform distribution.

All statistical tests were performed using SYSTAT (SPSS 1997). Year-end densities of mice were compared using a repeated measures ANOVA, with treatment (± ungulates) and year as factors. To determine whether individual mice had clumped distributions, we conducted an ANOVA with square-root-transformed $\overline{S^2}/X$ as the dependent variable, considering only first captures on each grid, with treatment (± ungulates) and sex (males, females, both males and females) as factors. Because density has been shown previously to vary among treatments (Keesing 1998b, 2000), we also conducted an ANCOVA on the same data, with density as a covariate. To determine whether total mouse *activity* was clumped on grids, we conducted both an ANOVA and an ANCOVA on the square-root-transformed $\overline{S^2}/X$ considering *all* captures on each grid.

We used linear regression analyses to consider the effects of density on space use by mice, with density as the independent variable and square-root-transformed $\overline{S^2}/X$ as the dependent variable. We conducted this analysis for first captures of individuals only and for all captures of individuals. For each of these analyses, we considered males and females both separately and together.

For each grid during each trapping session, we compared the actual distribution of grid-square values to a Poisson distribution using a chi-square goodness of fit test to determine whether the spatial distribution of captures deviated significantly from random (Zar 1999). We then tested whether the frequency of non-random spatial distributions was independent of treatment (± ungulates) using a 2 × 2 contingency table (Zar 1999). Because significant deviations from random could represent either clumped or uniform distributions (Zar 1999), we also determined which of the grids that were non-random were clumped and which were uniform, and then repeated the chi-square analysis on the frequency of clumped and of uniform distributions.

Patterns of space use by mice on a grid may be influenced by intrinsic spatial variation in habitat quality within the grid. To assess whether the grids differed in their spatial variability, we conducted an ANCOVA with each of the six grids (three replicates each of plots with and without ungulates) as a treatment, each year's $\overline{S^2}/X$ on that grid as the dependent variable, and density as a covariate. We treated each year-end $\overline{S^2}/X$ value as independent because of nearly complete turnover of the mouse population on each grid. We included density as a covariate because the grids were known to vary in density due to the presence or absence of ungulates (Keesing 1998b, 2000). We conducted this test for first captures and for all captures, and, in each case, for the sexes both separately and together.

The average August density of *S. mearnsi* varied from a low of 13.5 ha^{-1} in 1999 to a high of 63.5 ha^{-1} in 1997. Densities on plots without ungulates were significantly higher than those on plots with ungulates ($F_{1,4} = 10.6$, $P = 0.03$; Figure 1), with an average density 53% higher on grids without ungulates (ungulates: 30.1 ± 11.3 (mean ± SE); no ungulates: 46.1 ± 7.8).

When only the first capture of each individual was included in the analyses, there were significant differences between patterns of space use by males, females and the two sexes combined ($F_{2,81} = 8.5$, $P < 0.01$). On average, females had variance/mean ($\overline{S^2}/X$) ratios <1.0 (0.89 ± 0.03), indicating generally uniform spatial distributions; males had $\overline{S^2}/X$ ratios approximately equal to 1.0 (1.04 ± 0.04), indicating random spacing; and both sexes together had a $\overline{S^2}/X$ of 1.33, indicating a clumped distribution. There were no significant effects of either the presence of large mammals or mouse density on $\overline{S^2}/X$ for either sex, or for both sexes combined.

When all captures of individuals were included in the analyses, there were no significant differences between average $\overline{S^2}/X$ for males, females, and both sexes combined ($F_{2,81} = 2.2$, $P = 0.12$). The presence of large mammals had no significant effect on mouse space use when the effects of large mammals on density were factored out. However, there was a significant negative relationship between density and the $\overline{S^2}/X$ of both sexes together ($r^2 = 0.22$, $P = 0.01$), such that mouse activity was more clumped when mice were at lower density. There was no such effect on the sexes considered separately (males: $r^2 = 0.01$,

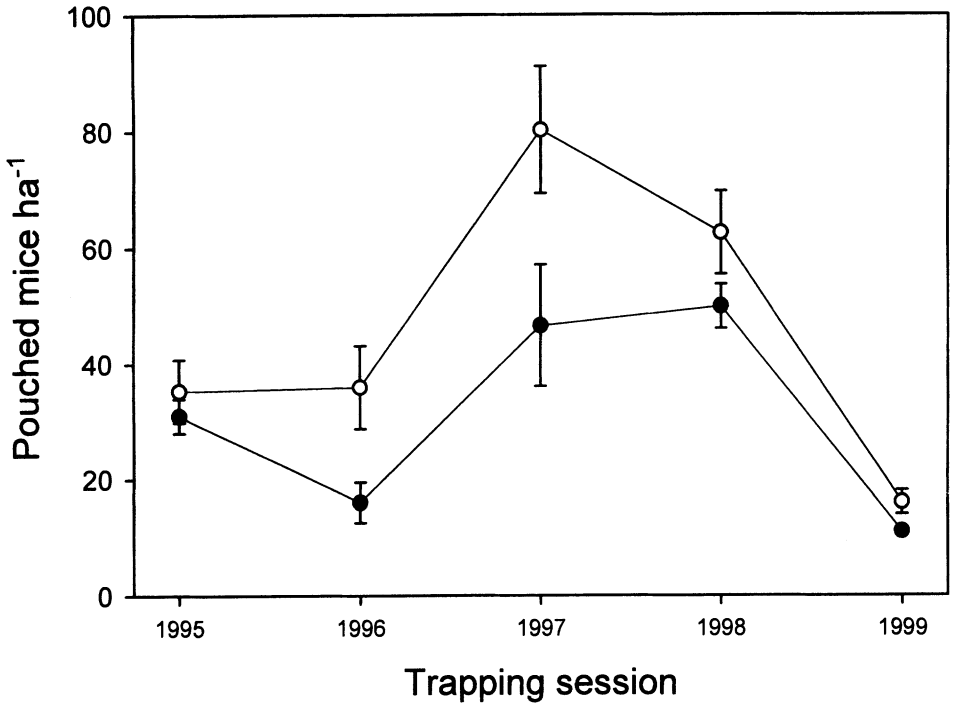

Figure 1. Abundance of pouched mice per hectare (mean ± SE) with (•) and without (o) the presence of large mammals. Abundances were determined in August of 5 consecutive years (1995–99) based on mark-recapture trapping on three pairs of 1-ha grids.

P = 0.67; females: r^2 = 0.07, P = 0.18). For males, plots with ungulates were more likely to have clumped distributions than plots without ungulates, when all captures were considered (Pearson chi-square: df = 1, P = 0.03). Neither females nor both sexes combined showed a similar effect.

Males on some grids showed consistent patterns of space use from year to year ($F_{5,22}$ = 4.93, P << 0.01), suggesting that there were some underlying habitat characteristics on the grids influencing their distributions. Females had no such tendency ($F_{5,22}$ = 0.43, P = 0.82), nor did both sexes together ($F_{5,22}$ = 0.93, P = 0.48).

Our analyses of space use by pouched mice considered two aspects of their distributions. First, we considered the spacing behaviour of individuals by analysing only the first capture of each animal. Second, we analysed the spatial pattern of total mouse activity on the grids using all captures, including multiple captures of the same individual. The results from these two analyses differed. Individual spacing behaviour, using first captures only, varied depending on the sex of the mice. Females showed a uniform pattern of space use, whereas males showed a random pattern. On the other hand, spatial patterns of total mouse activity differed based on the overall density of mice on the grid, but there were no significant differences between males and females.

At high density, the spatial pattern of activity (including all captures of both males and females) tended to be uniform; at low density, activity tended to be clumped. Mice reached high densities only on plots from which ungulates had been excluded.

The uniform spacing by female *S. mearnsi* suggests that they may be territorial, which may mean that they are protecting access to resources (Ostfeld 1985, 1990). Male pouched mice, on the other hand, did not appear to be territorial, as their distributions were random rather than uniform. Considering both males and females together, the distribution of individual mice was clumped. Thus, males appear to be superimposing their areas of activity on those of females, which is consistent with results from other studies of small mammals (Ostfeld 1990).

When we considered all captures of individuals, we found a significant negative effect of density on $\overline{S^2}/X$. At low densities, captures were clumped, whereas at higher densities, activity was distributed more evenly across the habitat. Clumping at low densities might have resulted from either of two causes. First, clumping might reflect the clustering of mice in favourable microsites. Second, clumping might represent repeated captures of the same individuals within their home ranges. In either case, as density increased, mice apparently filled interstitial areas, thereby generating a more uniform spatial distribution. High densities of small mammals have been reached in this habitat only in areas from which large mammals have been excluded (Figure 1; Keesing 2000). There was no independent effect of the presence of ungulates on mouse space use beyond that explained by differences in density.

Small mammals in this habitat are known to have a considerable impact on vegetation (Keesing 2000, unpubl. data). In treatments from which ungulates were excluded, the biomass of herbaceous vegetation was 50% higher on plots from which small mammals had been excluded compared to the biomass on plots to which they had access (Keesing 2000). Small mammals also consume tree seeds at a high rate. As many as 75% of the seeds of the dominant overstorey tree, *Acacia drepanolobium* Harms ex Sjostedt, have been removed within one week (Keesing, unpubl. data). If the activity of pouched mice is clumped in areas of low mouse density, we would expect that their effect on both seeds and herbaceous vegetation should be highly heterogeneous in these areas, potentially resulting in 'safe-sites' (Harper 1977) for survival and establishment. At high densities, on the other hand, we predict that their effects on the plant community should be both more uniform and of greater magnitude. As a result, determinants of the abundance and distribution of savanna rodents may indirectly influence patterns of plant establishment.

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