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Author(s): Felicia Keesing

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ECOLOGY AND BEHAVIOR OF THE POUCHED MOUSE, *SACCOSTOMUS MEARNSI*, IN CENTRAL KENYA

FELICIA KEESING

Department of Integrative Biology, University of California, Berkeley, CA 94720

*Present address: Department of Biology, Siena College, 515 Loudon Road,
Loudonville, NY 12211-1462*

I investigated the ecology and behavior of *Saccostomus mearnsi*, a medium-sized semi-fossorial murid rodent for 15 months in a tropical savanna of central Kenya. This poorly known species is the dominant small mammal in this widespread habitat, although it has never before been reported in high local abundance. On three replicated 1-ha grids, *S. mearnsi* exhibited a 2.5-fold change in abundance over 15 months from 16 ± 3.5 (SE) to 42 ± 7.5 individuals/ha. *S. mearnsi* had strongly seasonal reproduction, with almost all females in breeding condition following the rainy season, while only 10% were in breeding condition during the dry season. Eighty-five percent of males, however, remained in breeding condition throughout the year. Adults of both sexes exhibited great variation in body weight (males, 48–121 g; females, 39–94 g). There was significant seasonal variation in body weight for both sexes. Home ranges of males (0.21 ± 0.02 ha) were three times the size of those of females (0.06 ± 0.01 ha), and the average of the maximum distances moved by males between captures varied significantly between seasons. Analyses of stomach contents showed that *S. mearnsi* was omnivorous, consuming primarily forbs during the dry season and seeds following the rains. Adults share burrow entrances in termite mounds; whether or not they nest individually or communally remains to be determined.

Key words: *Saccostomus mearnsi*, pouched mouse, ecology, behavior, Kenya

Savannas cover one-third of the land surface of the earth and account for ca. 50% of the area of Africa (Okigbo, 1985; Werner et al., 1990). In Africa, these biomes harbor a mammalian fauna unparalleled in either biomass or species richness. Distinctive vertebrates of these areas have long been studied (Bell, 1970; Jarman, 1974; Kruuk, 1972; Schaller, 1972; Swynnerton, 1958), but research on savanna mammals has focused almost exclusively on the ecology and behavior of larger species, primarily ungulates, primates, and carnivores (Altman et al., 1995; Cheney and Seyfarth, 1983; Sinclair and Arcese, 1995; Sinclair and Norton-Griffiths, 1979). Smaller mammals are comparatively poorly known. Recent research, however, has demonstrated that savanna rodents can interact strongly with other members of the community, including ungulates and vegetation (Keesing,

1997). In the absence of ungulates, density of small mammals increased two-fold, and these small mammals had a significant effect on vegetation, reducing plant biomass by 40% and altering composition of plant species (Keesing, 1997). Therefore, small mammals may have a pronounced effect on both quantity and quality of vegetation available to ungulates. Knowledge of the ecology and behavior of small mammals may be critical for understanding community dynamics of African savannas.

Previous research on East African rodents has established that a number of savanna species experience seasonal peaks in abundance (Delany, 1986; Delany and Monro, 1986; Delany and Roberts, 1986; Martin and Dickinson, 1985; Neal, 1981) and that several taxa, including *Arvicanthis* and *Mastomys*, undergo occasional population increases (Hubbard, 1972; Leirs et

al., 1996; Poulet and Poupon, 1978; Taylor, 1968). Because of impacts of these population increases on agricultural crops and stores (Fiedler, 1988; Leirs et al., 1996; Taylor, 1968), the majority of work on small mammals of the African savanna has focused on population biology and factors that may trigger peaks in density. Several studies have suggested that timing and quantity of precipitation in the year preceding a population increase are the most important factors (Leirs et al., 1996; Neal, 1977; Taylor and Green, 1976), although the effect of variation in rainfall on availability of resources for rodent populations has not been quantified. Seasonal shifts in diet also are well documented for several species of rodents in East Africa (Delany, 1986; Delany and Monro, 1986; Neal, 1981, 1984; Taylor and Green, 1976). The behavioral ecology of one widespread common species, the grass rat (*Arvicanthis niloticus*) has been the subject of two studies (Packer, 1983; Senzota, 1990).

As part of a larger project on the role of small mammals in savanna ecosystems (Keesing, 1997), I investigated the ecology and behavior of the pouched mouse, *Saccostomus mearnsi*, a medium-sized semifossorial murid rodent. *S. mearnsi* is a poorly known species, which only recently has been separated taxonomically from its congener, *S. campestris* (Hubert, 1978), a widespread but uncommon species from southern Africa (Gliwicz, 1985; Happold and Happold, 1991; Linzey and Kesner, 1997; Swanepoel, 1981). In central Kenya, *S. mearnsi* is the dominant small mammal in several habitats (Keesing, 1997), although it has never before been recorded in high local abundance (Delany, 1964; Neal, 1984). Because of its pronounced interactions with ungulates and vegetation, *S. mearnsi* is an important member of this mammalian community (Keesing, 1997). I report the results of a 15-month study of its abundance, survival, reproduction, home range, diet, and burrowing behavior. This study provides a baseline for long-term

monitoring of population dynamics of this species and for understanding its role in community structure and dynamics of savannas.

MATERIALS AND METHODS

Study site.—This research was conducted August 1995–November 1996 at the Mpala Research Centre (0°17'N, 36°53'E) in the Laikipia District of central Kenya at 1,800 m above sea level. The study site is characterized as wooded grassland on black-cotton vertisol soils with impeded drainage and is dominated by a swollen-thorn acacia, *Acacia drepanolobium*. This is the most common plant community in the Laikipia ecosystem, comprising >25% or 2,700 km² of this region (Young et al., 1997). Other woody species present include *Balanites aegyptiaca*, *Cadaba farinosa*, *Acacia mellifera*, *A. brevispicata*, *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 lachnantha* and the herbs *Aerva lanata*, *Rhinacanthus ndorensis*, *Dyschoriste radicans*, and *Commelina* (Young et al., 1997).

Ungulates in the study area include African elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), Grevy's zebras (*Equus grevyi*), Burchell's zebras (*E. burchelli*), Grant's gazelles (*Gazella granti*), Jackson's hartebeests (*Alcelaphus buselaphus*), elands (*Taurotragus oryx*), Beisa oryx (*Oryx gazella*), steinbucks (*Raphicerus campestris*), cape buffalos (*Syncerus cafer*), and domestic cattle. Mammalian carnivores include lions (*Panthera leo*), leopards (*P. pardus*), cheetahs (*Acinonyx jubatus*), black-backed jackals (*Canis mesomelas*), ratels (*Melivora capensis*), white-tailed mongooses (*Herpestes ichneumon*), and slender mongooses (*H. sanguineus*). Other conspicuous mammals include olive baboons (*Papio cynocephalus*), patas monkeys (*Erythrocebus patas*), bushbabys (*Galago senegalensis*), and aardvarks (*Orycteropus afer*). In addition to *S. mearnsi*, small mammals captured include *Arvicanthis*, *Mus*, *Dendromys*, *Mastomys*, and *Crocidura*. While a complete list of the herpetofauna has not been compiled, snakes encountered in this habitat are puff adders (*Bitis arietans*) and cobras (*Naja*). The dominant raptor is the black-shouldered kite (*Elanus caeruleus*).

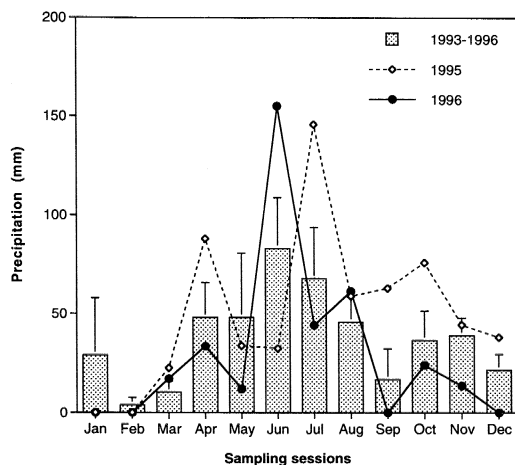


FIG. 1.—Annual average precipitation at Mpala Research Centre for 1993–1996 (bars) versus averages for 1995 (dashed line) and 1996 (solid line). There is a distinct dry season from December through February. Rains typically begin in April and continue through August, with peaks in June and July, although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

Termitaria are a conspicuous feature of the landscape. These low-lying roughly circular mounds vary in size, averaging ca. 5 m in diameter, and support a distinctive vegetative cover, dominated by the grass *Pennisetum stramineum*. Each mound has numerous burrow entrances constructed by small mammals.

Rains generally are concentrated in April–July, with an intense dry season in December–February. Average annual rainfall is 500–600 mm, although there is substantial spatial and temporal heterogeneity of rainfall. Daily rainfall has been recorded at Mpala Research Centre since July 1992 at a site 5 km east of the exclosures. Since January 1996, daily rainfall has been recorded at a rain gauge placed centrally at each of the three exclosure blocks. Rainfall during 1995 peaked in July, with moderate amounts of precipitation from August through December 1995 (Fig. 1). During January–March 1996, there was low or no precipitation. April and May 1996 had lower than average rainfall, resulting in a prolonged dry season, while there was higher than average rainfall in June 1996. Rains decreased through September, and there

was almost no precipitation through the rest of this study.

Demography.—Trapping to determine seasonal abundance of small mammals was conducted on three control plots as part of a larger study on effects of exclusion of ungulates on small mammals (Keesing, 1997). Each of these unfenced plots was set with traps on a permanent 10-by-10 grid with 10-m spacing. Grids were set so that no trap was closer than 50 m to the nearest exclusion treatment of ungulates (Keesing, 1997). Trapping was conducted for 3 consecutive nights, using large folding Sherman traps (7.6 by 8.9 by 22.9 cm), 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, location, and reproductive condition recorded (males, testes scrotal or abdominal; females, vulva perforate or imperforate, pregnant or lactating).

Five trapping sessions were conducted: September 1995; January 1996 at the beginning of the dry season; April 1996 at the height of an unusually long dry season; August 1996 after the late rains; November 1996. During the November 1996 trapping session, only two of the grids were trapped due to an abundance of elephants and lions on the third grid.

Trapping data 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 estimator for the selected model was then used to calculate the CAPTURE estimate of abundance. To quantify variation in abundances among trapping sessions, I computed a one-way factorial analysis of variance (ANOVA) on abundance data with trapping session as the factor and each grid as a replicate. All statistical tests were performed using StatView 4.1 (Abacus Concepts Inc., 1992). Although I was repeatedly sampling some of the same individuals, this test was appropriate because repeated sampling would tend to show reduced variation between trapping sessions (Connell and Sousa, 1983); any differences detected are, therefore, conservative.

Survivorship was determined by calculating the proportion of individuals alive at a trapping session t who survived until the following trapping session $t + 1$. Per-capita recruitment was

calculated by determining the proportion of individuals captured at a trapping session t that had not been captured previously. Total recruitment is the total number of new individuals captured in a given plot during a particular trapping session. To quantify variation in survival and both per-capita and total recruitment among trapping sessions, I computed a one-way factorial ANOVA on those data with trapping session as the factor and each grid as a replicate.

Minimum weight of adults was determined by taking the median of the 10 smallest animals of each sex that were reproductively active (male, scrotal testes; female, perforate vulva). For males, weight of adults was determined to be ≥ 48 g; it was ≥ 39 g for females. I compared weights of adults in two ways. To determine if there were significant differences between weights of males and females, I calculated average weight for all adult individuals of each sex captured during each trapping session with weights from all three grids combined. Only weight at first capture of each individual was included in the analysis. I compared those results using a paired t -test. To quantify seasonal variation in body weight for each sex, I compared weights of adults through time for each sex using grids as replicates. Those data were tested using a one-way factorial ANOVA with trapping session as the factor.

Home range.—To minimize trampling in permanent grids, I established a different grid, located ca. 800 m from the nearest permanent grid, to estimate size of home range. In March 1996, a 14-by-14 trapping grid with 10-m spacing was set for 13 days. Traps were opened for 5 consecutive days and checked morning and evening. For 3 subsequent days, traps were left in place but not opened, and then, traps were opened for another 5 days. Individuals were marked and weighed, and their reproductive condition and site of capture were recorded. Sites of capture for each individual were entered into program RangesV (Kenward and Hodder, 1992), which I used to calculate size of home range using the minimum-convex-polygon method. Only individuals that were captured at least three times in at least three different capture sites were included in estimates of size of home range. Sizes of home ranges of males and females were compared using an unpaired t -test. Using program RangesV, I also computed an overlap matrix for

each sex to assess the degree to which home ranges of males and females overlapped.

As a seasonal index of size of home range, I computed the maximum distance (as calculated by program CAPTURE) moved between captures by each individual on permanent grids that was trapped at least two times during any 3-day trapping session. Those results were averaged by sex for each grid for each trapping session and compared using a one-way ANOVA with trapping session as a factor. I also compared maximum distance moved by males and females, averaged for each grid, through the year using a repeated-measures ANOVA, with sex as the between-factor variable.

To test the hypothesis that individuals of larger body size move greater distances on the grid, I computed a simple regression for each sex between body weight and maximum distance moved by each individual. I considered only individuals that had been captured three times during each trapping session. I computed two regressions, one for combined distances moved for trapping sessions in September 1995 and August 1996, following rains, and one for the dry-season trapping sessions in January and April 1996, for a total of two regressions for each sex.

Occupancy of termite mounds.—Because preliminary observations revealed that termitaria were centers of activity for small mammals, I set Sherman traps around 12 marked termite mounds for 3 consecutive days each in March 1996 to determine patterns of occupancy of burrows. Captured animals were marked, weighed, sexed, and released, and the specific burrow entrance into which they returned was recorded.

Diet.—In March and August 1996, I trapped 10 animals in Sherman traps baited with smooth peanut butter and euthanized them with halothane anaesthesia. Stomachs were collected and preserved whole in ethanol and sent to the Composition Analysis Laboratory, Colorado State University, Fort Collins, for microhistological analysis. Each sample was bleached to make cellular characteristics more visible and then washed in warm water to remove bleach and any peanut-butter bait contaminating samples. Five subsamples were taken from each sample and mounted on microscope slides in Hoyers' mounting medium. There were about three identifiable food fragments per microscope field when viewed at a 100 \times magnification. Food fragments were categorized as arthropods, seeds,

grasses, or leaves of herbaceous or woody plants by using cellular and morphological characteristics. Some plant fragments were identified to genus. A total of 20 microscope fields, or ca. 60 identifiable food fragments, was counted for each of the five subsamples per sample. Relative density and standard deviation were calculated for each identifiable food category.

RESULTS

Demography.—On permanent grids, I captured 333 *S. mearnsi* 825 times in a total of 4,500 trapnights (ca. 18% trapping success for *S. mearnsi*). Program CAPTURE chose the model of equal probability of captures (M_0) 12 of 14 times, the model of heterogeneity of trapping probabilities in the population (M_h) one time, and the model of time specific variation in trapping probabilities (M_t) one time. Overall, mean probability of capture was 0.51 ± 0.04 SE.

Following a peak of 32 ± 3.7 individuals/ha in September 1995, density of *S. mearnsi* on grids dropped ca. 40% to 19 ± 0.3 in January 1996 and decreased only slightly during the following 7 months (Fig. 2). By August 1996, densities were one-half those of the preceding year (16 ± 3.5). Densities rebounded to 42 ± 7.5 by November 1996, the highest density during the study.

Survivorship was higher in November 1996 than in preceding trapping sessions, with an average of >50% of individuals surviving from August, although that difference was not significant possibly due to high variation among grids ($F = 1.3$, $d.f. = 3$, $P = 0.36$; Fig. 3a). Lowest survivorship occurred in April–August 1996 trapping sessions, following the delayed rains (Fig. 3a). Based on trapping records, four individuals survived on grids for the entire 15 months of this study, and one more for ≥ 1 year; all five of those mice were large adults at the time of first capture. Twelve additional individuals survived ≥ 9 months.

Per-capita recruitment varied significantly through time on the three grids ($F = 4.9$, $d.f. = 3$, $P = 0.04$). The highest per capita

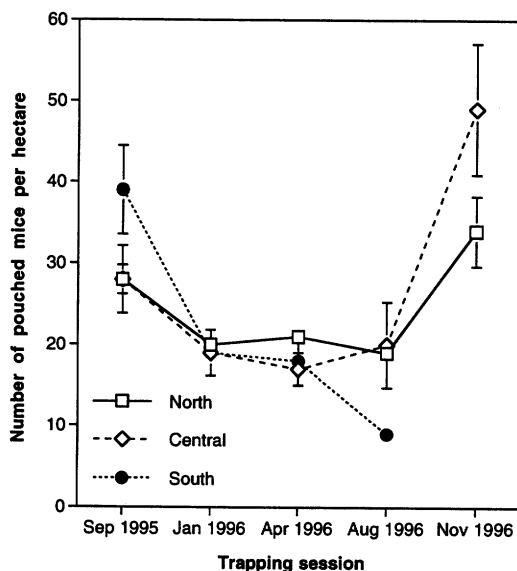


FIG. 2.—Abundance (\pm SE) of *Saccostomus mearnsi* over 15 months on each of the three grids. The third replicate was not trapped during the November 1996 trapping session (see Materials and Methods).

recruitment was August–November 1996 at 0.81 recruits/individual, and the lowest was during the dry season trapping sessions with an average of 0.37 recruits/individual (Fig. 3a). Total recruitment did not vary significantly through time when all trapping sessions were considered together ($F = 2.3$, $d.f. = 3$, $P = 0.16$), although there was a significant difference between August and November 1996 (Fisher's Protected Least Significant Difference, $P = 0.04$; Fig. 3b). The greatest number of new individuals appeared in November 1996. This followed a decline from a peak in January 1996 of 18.3 ± 0.9 new individuals/grid to a low in August 1996 of 13.3 ± 3.8 new individuals/grid.

Adult male and female pouches mice had body weights that covered a considerable range. Minimum and maximum weights of adult males differed by a factor of two within each trapping session (Table 1). Weights of adult females also varied by a factor of two within several trapping ses-

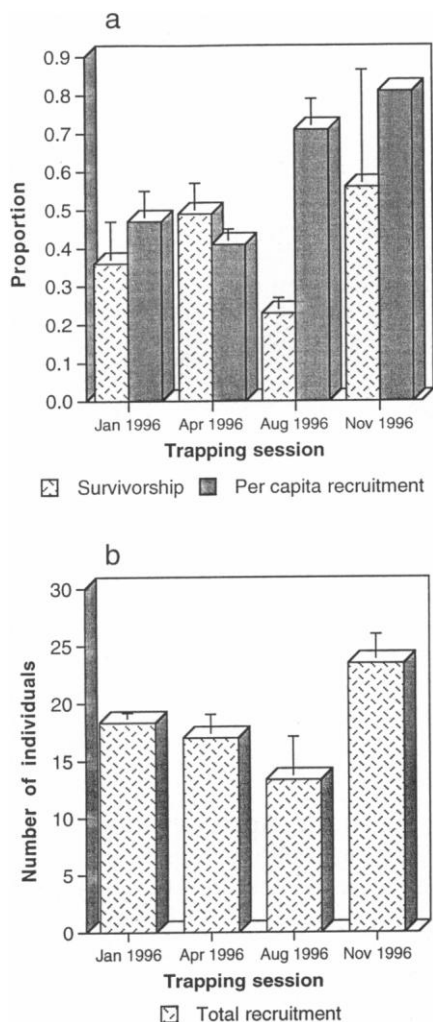


FIG. 3.—Means (\pm SE) of a) the proportion of individuals of *Saccostomus mearnsi* surviving from the preceding trapping session and the number of per-capita recruits, and b) the total number of new individuals for the three grids.

sions (Table 1), although it is possible that some of the heavier individuals were pregnant but were not detected as such. Weights of adult males and females were significantly different ($t = 11.2$, $d.f. = 4$, $P < 0.001$), with the average weight of males for the whole year (79.5 ± 3.2 g) 25% greater than that of the average female (62.3 ± 2.0 g). Average weights of males ($F = 3.5$, $d.f. = 4$, $P = 0.01$) and females ($F =$

3.2 , $d.f. = 4$, $P = 0.02$) varied significantly through the year, with averages in August and November 1996 $>10\%$ greater for both sexes than that at other times of the year (Table 1).

Adult females showed seasonal changes in reproductive condition (Fig. 4b). Almost all adult females were reproductively active (perforate, pregnant, or lactating) in September 1995 and August and November 1996 following periods of rainfall. An increasing proportion of adult females were reproductively inactive (imperforate) as the dry season progressed from January through April 1996, so that by April only ca. 10% of females were in reproductive condition. In August 1996, after unseasonal rains, almost one-half of adult females were pregnant or lactating, and this proportion increased through November 1996. The proportion of juvenile females captured peaked at ca. 20% during January and April 1996, while only 5% of captured females were juveniles in August 1996.

Adult males showed much less seasonality in breeding condition; $\geq 85\%$ of adult males were in reproductive condition (scrotal testes) over the entire year (Fig. 4a). The greatest proportion of adult males (13%) were reproductively inactive (undescended testes) in April 1996, coincident with the lowest proportion of females being in breeding condition. The proportion of juvenile males captured varied more for males than for females, from a high of 38% of all captures of males in January 1996 to a low of no juveniles captured in April 1996. Neither males nor females exhibited seasonal torpor, as has been observed in *S. campestris* from southern Africa (Ellison, et al., 1993b).

Home range.—Home ranges of males averaged 0.21 ± 0.02 ha and were significantly larger than those of females, which averaged 0.06 ± 0.01 ha ($t = -7.6$, $d.f. = 14$, $P < 0.001$). Home ranges of males were broadly overlapping; of 68 possible combinations of overlapping ranges between pairs of males, average overlap was $8.2 \pm$

TABLE 1.—Mean, minimum, and maximum weights for adult male and female *Saccostomus mearnsi* captured during each trapping session in central Kenya.

	September 1995	January 1996	April 1996	August 1996	November 1996
Male					
$\bar{X} \pm 1 SE$	77.7 \pm 2.5	73.1 \pm 3.2	73.9 \pm 2.3	90.8 \pm 2.9	82.1 \pm 4.2
Minimum	48	49	51	60	50
Maximum	106	97	95	121	120
Female					
$\bar{X} \pm 1 SE$	59.6 \pm 2.0	58.2 \pm 2.7	61.1 \pm 2.1	69.1 \pm 4.8	65.3 \pm 2.0
Minimum	40	39	49	39	53
Maximum	83	83	76	94	80

2.0%. Of those 68 home ranges that could have overlapped, 25 actually did and the average of those 25 was $22.2 \pm 4.0\%$. Home ranges of females showed almost no overlap. Of 12 pairs of home ranges of females that could have overlapped, average overlap was $1.4 \pm 1.4\%$. Of those 12, only two actually overlapped, and the average overlap of those two was $8.6 \pm 8.4\%$.

The average maximum distance moved by males on each grid showed a significant effect of time ($F = 4.2$, $d.f. = 4$, $P = 0.03$); males traveled a smaller distance between captures during the trapping session in January 1996 than during any of the other sessions (Table 2). Females showed no such effect ($F = 1.0$, $d.f. = 4$, $P = 0.47$). Average maximum distances traveled by males (23.8 ± 3.5 m) and females (18.7 ± 1.3 m) differed ($F = 28.5$, $d.f. = 1$, $P = 0.03$) and showed a significant distance-time interaction ($F = 5.8$, $d.f. = 4$, $P = 0.02$), with the greatest difference during the trapping session in August 1996 (Table 2). There were no significant relationships between body size and maximum distance traveled for either sex or for either of the two combined trapping periods (males, September 1995–August 1996, $r^2 = 0.01$, $P = 0.85$; January 1996–April 1996, $r^2 = 0.05$, $P = 0.61$; females, September 1995–August 1996, $r^2 = 0.09$, $P = 0.42$; January 1996–April 1996, $r^2 = 0.13$, $P = 0.33$).

Occupancy of termite mounds.—The

number of pouched mice occupying each termite mound in March 1996 ranged from one to five, with a mean of 2.4 ± 0.4 individuals/mound. No individuals appeared stressed by handling or presence of the handler and often spent a considerable amount of time getting oriented after release before returning to a particular burrow entrance. The majority of the time, the entrance to which they returned was not the closest entrance available to them upon release, suggesting that they were choosing preferred entrances rather than the most immediate ones. Fifteen individuals returned to at least two different burrow entrances in the same mound upon being released on subsequent days, and the mean for all 31 individuals was 1.5 ± 0.1 entrances used. Of 36 entrances used by at least one individual, eight were used by more than one pouched mouse, and three entrances were used by three or more mice. Of those eight multiply used entrances, one was used by three juveniles and one was used by a juvenile female and an adult male; the remaining six were used by various combinations of adult males and females.

Diet.—*Saccostomus mearnsi* had a highly seasonal diet. During the dry season in February 1996, its diet was composed almost entirely of forbs ($55 \pm 3\%$) and arthropods ($35 \pm 3\%$; Fig. 5). Grasses and seeds together comprised $<10\%$. In August 1996, 2 months after the rains had begun, the diet of

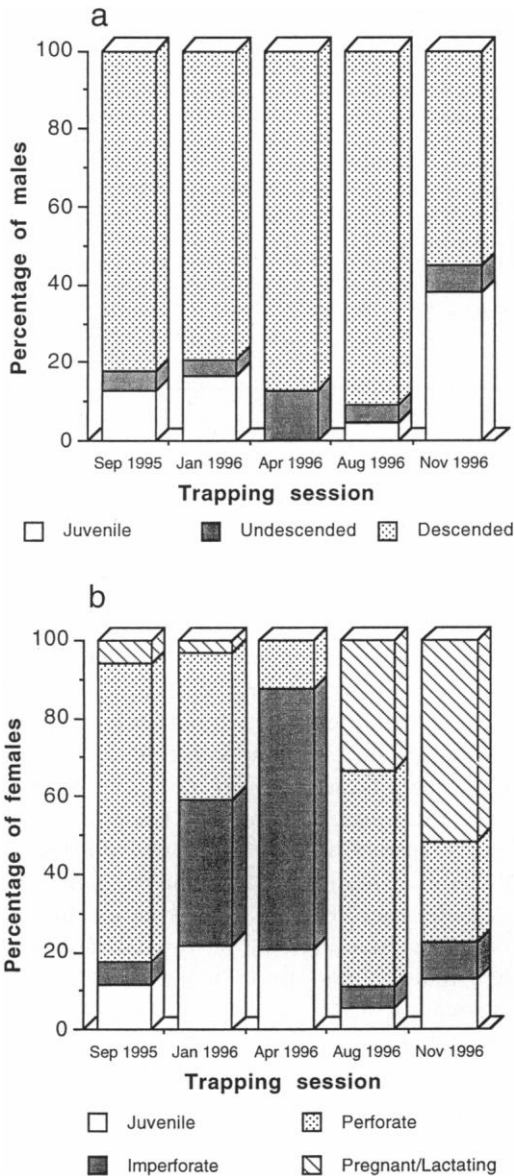


FIG. 4.—Percentage of a) males and b) females of *Saccostomus mearnsi* in each reproductive category during each trapping session.

S. mearnsi consisted almost exclusively of seeds ($94 \pm 3\%$), with grasses, herbs, and arthropods together accounting for $<6\%$.

DISCUSSION

Saccostomus mearnsi exhibited significant seasonal variation in abundance, with

more than a 2.5-fold difference in density within 3 months. The degree of population fluctuation in *S. mearnsi* during the 15 months of this study, however, was low compared with fluctuations seen in some temperate species of rodent (Batzli, 1992). Continued monitoring at this site will establish if that relative stability in density of *S. mearnsi* is characteristic of this habitat, or was only a short-term pattern. *S. mearnsi* also showed seasonality in weight, diet, distance traveled by males, and reproductive behavior of females. There appears to be no strong direct or lagged correlation between abundance and rainfall. Although the peak in abundance in September 1995 occurred 3 months after the greatest rainfall, the greatest densities of *S. mearnsi* during this study were recorded in November 1996, 5 months after the height of the 1996 rainy season.

Demography.—Females showed pronounced seasonality in reproductive activity between the dry season when few adults were in breeding condition and the rainy months when almost all adults were perforate, pregnant, or lactating. Most adult males remained in breeding condition year-round. Seasonality in breeding condition, as with females of *S. mearnsi*, is common in mammals (Bronson, 1989) and has been demonstrated in studies of rodents elsewhere in East Africa (e.g., Delany, 1986; Neal, 1981; Taylor and Green, 1976). The degree of asymmetry in reproductive activity of male *S. mearnsi*, however, is surprising. While it is usual for male small mammals to be in breeding condition longer than females (Keller, 1985), pronounced differences in this study were sustained over several months.

Seasonal increases in abundance seem to be the result of significant pulses in recruitment, although results for per capita and total recruitment differed. Per-capita recruitment was at its lowest during the dry season, while total recruitment was lowest just

TABLE 2.—Average maximum distance moved ± 1 SE (m) between trapping occasions for *Saccostomus mearnsi* captured at least twice during each trapping session in central Kenya.

	September 1995	January 1996	April 1996	August 1996	November 1996
Male	24.7 \pm 4.4	14.3 \pm 4.4	33.0 \pm 16.3	39.5 \pm 6.7	15.5 \pm 1.2
Female	21.9 \pm 6.2	16.2 \pm 2.3	16.2 \pm 1.0	15.4 \pm 7.0	18.8 \pm 2.7

after the rains. That trough in total recruitment coincided with lowest abundance and lowest survivorship on grids, suggesting that there was high mortality during May–July 1996, possibly as a result of the delayed rains.

The wide range in body weights of adult *S. mearnsi* is unusual. Both males and females had maximum and minimum weights that differed by a factor of two during trapping sessions. Both *Arvicanthis* (Neal, 1981) and *S. campestris* (Ellison et al., 1993b) differ greatly in body size between locations, which is correlated with variations in rainfall for *S. campestris*, but these

differences at a single locality have not been described previously. Like *S. mearnsi*, *S. campestris* has been found to be sexually dimorphic in most studies (Skinner and Smithers, 1990; Speakman et al., 1994); however, Ellison et al. (1993a) examined specimens from the Transvaal Museum in South Africa and found no significant difference between sexes, nor did weights show as much variation as those in this study. Seasonal variation in body weight of *S. mearnsi* has been found in temperate (Stewart and Barnett, 1983; Ure, 1984) and tropical (Ellison et al., 1993a; Korn, 1989) rodents. Using museum specimens, Korn (1989) found a 28% decrease in average body weight of South African *S. campestris* during the dry season, with weights of males and females combined.

Home range.—Although estimates of size of home range have not been reported previously for East African rodents in natural habitats (Delany and Monro, 1985, reported range lengths but not sizes of home ranges for *Arvicanthis*), the three-fold difference between sizes of home ranges of males and females is similar to those in some temperate studies of small mammals (Cockburn, 1988; Ostfeld, 1990). Maximum distances moved by individuals on permanent grids supports these estimates of home range. During the trapping session in April 1996, which offers the closest comparison to estimates of home range from March 1996, males traveled an average maximum distance 40% greater than that of females. Bowland and Perrin (1989) found a higher mean distance traveled between captures by *S. campestris* in South Africa, with a combined average for males and fe-

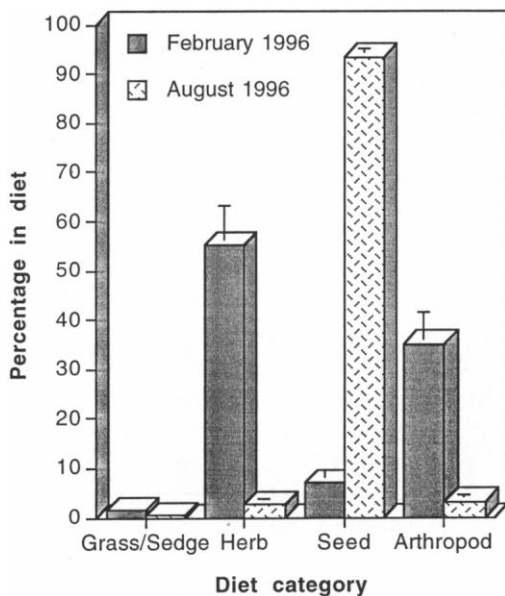


FIG. 5.—Percent composition (\pm SE) of stomach contents of *Saccostomus mearnsi* in the dry season (February 1996) and late wet season (August 1996).

males of 35 ± 13 m—70% higher than results presented here. *S. campestris* also was at much lower density in their study area, which may partially account for differences in distance traveled.

The least difference between distances traveled by males and females occurred during September 1995 and November 1996 and the greatest difference was in August 1996. During September 1995 and November 1996, density was at its highest on the grids, which may have inhibited use of space by males. Also, during those times, the greatest proportion of females were pregnant or lactating, so that males may have been defending their young (Ebensperger, 1997), or no longer searching for mates if females were giving birth to their last litters of the season. In August 1996, by contrast, the greatest proportion of females were in breeding condition, but not pregnant or lactating, so that males may have increased their distances traveled to gain access to females.

Distances traveled by females varied much less through the year than those traveled by males, with the low (January 1996) and high (September 1995) averages differing by 50%, while averages of males differed by more than a factor of three. Studies of reproductive behavior of small mammals have suggested that males are limited by access to mates, while females are limited by access to resources (Ostfeld, 1985). Those data would support such a scenario for *S. mearnsi*, because females seem to be maintaining relatively constant sizes of home range despite seasonal changes in density and reproductive condition. However, distance traveled by females was actually lowest in the dry season (January and April 1996) when resources would seem to be low. *S. mearnsi* is omnivorous, and it is possible that its dry season diet of insects is of high quality, which leads to a reduction in distance traveled by females.

Occupancy of termite mounds.—Burrowing behavior of *S. mearnsi* has not been described previously. In southern Africa, *S.*

campestris has been described as both solitary and communal (Ellison, 1993), although Ellison (1993) excavated 11 burrows and found all of these occupied by single individuals, or by mothers with young, suggesting that *S. campestris* is solitary. Results from the present study indicate one of two possibilities for *S. mearnsi*. Because adult males and females are sharing burrow entrances, *S. mearnsi* may be communal, in contrast to the solitary *S. campestris*. If so, the taxonomic conflation of these two species until recently may have led to confusion in the literature. Indeed, this situation could be even more confusing because recent work suggests that the southern African *S. campestris* may actually be two separate species, based on extensive chromosomal variation (Gordon, 1986). Second, *S. mearnsi* may be sharing burrow entrances but occupying separate nests. Burrowing in the clay-like soil of this habitat probably is difficult, so that pouched mice appear to be restricted to favorable microsites for burrow construction, such as termite mounds and bases of trees. This may necessitate an increased tolerance of conspecifics, a situation that could be an early evolutionary step toward communal nesting. Whether or not individuals are nesting individually or communally warrants further investigation.

Diet.—*Saccostomus mearnsi* at my study site were omnivorous, consuming mostly seeds following rains and forbs during the dry season. At another site in central Kenya, Neal (1984) collected stomachs from 23 *S. mearnsi* (identified as *S. campestris* in his study) and also found evidence for a strongly seasonal diet. Pouched mice studied by Neal (1984), however, consumed a diet that was 22% arthropods and 33% seeds during the dry season and mostly forbs and browse (83%) during the wet season. Those results differ from those presented here, where *S. mearnsi* consumed arthropods and forbs during the dry season and seeds following rains. Differences between sites and between years may account for the discrep-

ancy. However, further studies are warranted to determine inter-annual and intra-annual variability in diet, particularly given the impact of *S. mearnsi* on both biomass and species composition of vegetation at this site (Keesing, 1997).

Saccostomus mearnsi was the dominant small mammal in this widespread habitat over the 15 months of this study, although neither it nor its congener *S. campestris* has been reported in high local abundance. Its strong interactions with ungulates and vegetation indicate that it is an important member of this savanna community (Keesing, 1997), both as a consumer and potentially as prey for raptors, snakes, and small mammalian carnivores, such as white-tailed mongooses (*Ichneumia albicauda*) and black-backed jackals (*Canis mesomelas*). An understanding of its ecology and behavior is crucial for understanding the structure and dynamics of this savanna ecosystem.

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