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SPATIAL DYNAMICS OF *MASTOMYS NATALENSIS* IN A FIELD-FALLOW MOSAIC IN TANZANIA.

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Abstract. The population dynamics of *Mastomys natalensis* rats is reported for a 3-year study of monthly CMR-trapping in a small scale maize field-fallow land mosaic in Tanzania. The seasonal evolution of rodent presence was the same in both habitat types and it was not affected by agricultural activities in the fields. About one week after planting, there was a short increase of rodent captures in the maize fields, but this disappeared again after a few days. Recolonisation of fields was achieved very fast after a rodent control operation. Radiotelemetry indicated that many individuals were active in the maize field as well as in the fallow land. We concluded that, in a small scale set-up, the field and fallow land rodent populations are not separated and the latter should not be considered as necessary refuges. This renders several rodent control approaches unsuitable.

Key words: rodents, population dynamics, refuge habitat, pest control, Africa.

INTRODUCTION

Agricultural fields are situated in a matrix of surrounding habitat which, in an African smallholder setting, is most often fallow land. Since habitat quality of the fields is dramatically changing during the year, it can be expected that the population dynamics of organisms living there will contain an important spatial component. Rodents that are causing damage in the fields may be expected to leave the fields periodically and return only during the attractive crop stages. Such movements are often assumed to be an important process in rodent damage in field crops (*e.g.* FIEDLER & FALL, 1994) but rarely has this assumption been supported by data on movements of individuals rodents. In African rats of the genus *Mastomys*, seasonal invasion of the fields has been long assumed (*e.g.* HARRIS, 1937; ROBERTSON, 1938; FIEDLER, 1988). Yet, the only well documented instance of *Mastomys* sp. population movements originates from temporarily flooded habitats (SHEPPE, 1972).

In the present paper, we investigate population dynamics of *Mastomys natalensis* (Smith, 1834) in a mosaic of fallow land and agricultural fields in Tanzania. We test the hypothesis that the rodent populations in the fields are temporary and die out or dissipate in the fallow land periodically and we verify whether agricultural activities affect the population dynamics of rodents in the fields. Also, we examine experimentally how quickly rodents from surrounding populations in fallow land recolonise maize fields following rodent control operations.

MATERIAL AND METHODS

The study site was located on the campus of the Sokoine University of Agriculture in Morogoro, Tanzania (06°51'S 37°38'E). The population ecology of *M. natalensis* at this site has been described extensively (see LEIRS, 1994). In April 1994, we selected a 100 m x 300 m area of fallow land containing two plots of maize; a central 70 m x 70 m field which was purposedly ploughed and a corner (approximately 30 m x 70 m) in which local farmers penetrated as part of a larger maize field; we later took over the maize field in the corner ourselves (Fig. 1). All other sides of the area were separated from other fields by a zone of at least 30 m of fallow land. The size of the maize fields in our study area is common for smallholder farms in Tanzania.The maize fields were planted in a standard way (planting lines 1 m apart, plant holes 50-60 cm apart, three seeds per planting hole) after heavy rainfall in April and October 1994, April and November 1995 and March 1996. Seeds germinated in all planting seasons but only the crops planted in March-April received enough rainfall to produce a harvest. In late October 1996, the whole area was burned by a bushfire.

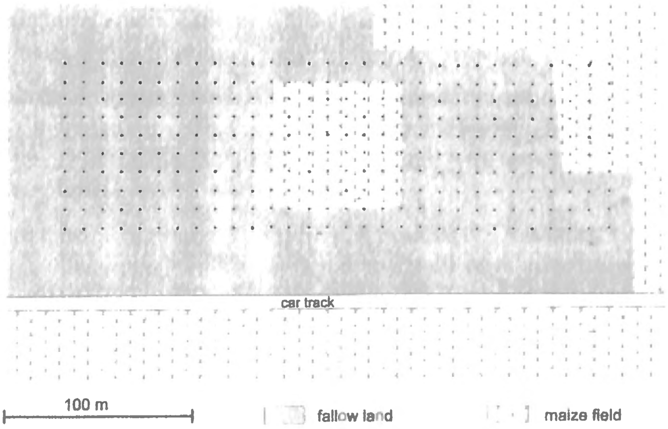

Fig. 1. – Schematic overview of the study area with maize fields and fallow land. Trap stations (dots) are situated in a 10 m x 10 m grid pattern.

A grid was laid out of 30x10 trapping stations, each 10 m apart. Out of 300 trapping stations, 54 were situated in the maize fields, at least 5 m from the border of the fields. We trapped every month for three consecutive nights with one Sherman trap per trapping station, baited with a mixture of peanut butter and crushed maize. Additional trapping sessions were organised in the week before and after each planting and harvesting session. The present study extended from April 1994 and March 1997. Captured animals were marked individually by toe-clipping; trapping station number, weight and sexual condition were recorded; afterwards each animal was released at its trapping station. We did this for all species of small mammals captured in the study area, but here we report only on M.natalensis. We used trapping success index, i.e. number of individuals trapped per trap night and adjusted for trap saturation as suggested by CAUGHLEY (1977), to assess the presence of animals in the different habitats.

Information on movement patterns was obtained from telemetry, using 2g transmitters from Televilt (Sweden) and Biotrack (UK). We radiotagged a total of 88 *M.natalensis* individuals, trapped after planting time (in March-April and November 1995 and March and May 1996). In November, nearly all tagged animals were trapped in the maize field (39/41) but in March-May (both years pooled), low densities necessitated also captures in the fallow land near the borders of the field and only 25/47 animals were trapped in the field itself. Activity status (moving/not moving) and positions (to the nearest metre) of the tagged animals were recorded several times per night, using a Televilt RX8910HE receiver with a built-in foldable 2 element YAGI-antenna; observations were made every night during periods of three hours; the timing of this three hour period was changed nightly. For each individual, all telemetric localisations were obtained within a three-week period. Spatial concentrations of activity were deduced for each individual from isoplethe shapes in a kernel analysis, carried out in Ranges V (KENWARD, 1996). Since we were interested in movements between habitats, we were not concerned about sample-size dependence of home range and used all individuals for which we had at least two localisations at different positions.

A recolonization experiment was carried out in March 1995. The two maize fields in our permanent CMR-grid were used as controls; for this purpose, we enlarged the corner field to a 70 m x 70 m field since the large field was not yet in use at that moment; two additional 0.5 ha-plots were selected at less than 100 m from the area. All plots were surrounded by at least 30 m fallow land bushes and tall grass. Animals were trapped during one night, marked and released. Maize was planted in all fields on 6 March; in the two experimental fields, a poisoning operation was carried out on the planting day by distributing 1.5 % zinc phosphide in a mixture of maize scrap and cooking oil in small heaps (approx. 20g) every 10 m in the field and extending 10 m in the surrounding fallow land. Carcasses picked up the following morning and autopsied confirmed the efficacy of the poisoning operation. On the day after planting, one night of live-trapping (releasing the captured individuals) was organised in all four fields with 100 Sherman traps per field and this life trapping was repeated four more times within the following two weeks.

RESULTS

In total we realised 35840 trap-nights, resulting in 11470 captures of 4355 individuals; 86% of these were *Mastomys natalensis*, 8.5 % *Tatera robusta* (Cretzschmar, 1830) and

5.5% *Lemniscomys rosalia* (Thomas, 1904); we trapped a single *Mus minutoides* Smith (1834) and 11 shrews *Crocidura* sp.

Trapping success varied greatly throughout the year (Fig. 2). In most trapping sessions, trap success was higher for rats in the fallow land than for those in the maize fields (Sign test, $Z=3.349$, $p<0.001$) but the differences were small and not consistent. There was no increased trapping success in the maize fields in comparison with the fallow land, during or just after the planting week. Trapping success index did differ significantly between seasons with and without crop on the fields ($F=14.34$, $p<0.001$), but not between both habitat types ($F=0.32$, $p=0.573$) and there was no interaction season-habitat ($F=0.02$, $p=0.882$, 2-way ANOVA). There was no obvious effect of the bushfire in October 1996, but we have no control treatment in this «natural» experiment.

We trapped 1071 individuals at least once in the maize fields but 480 of them were trapped also in the fallow land. Documented moves from the fallow land to the maize fields (animals that were trapped for the first time in the maize fields after a previous capture history in the fallow land, *i.e.* the movement direction which is relevant for the study of invasion of the fields) followed a similar seasonal pattern as overall abundance (Fig. 2).

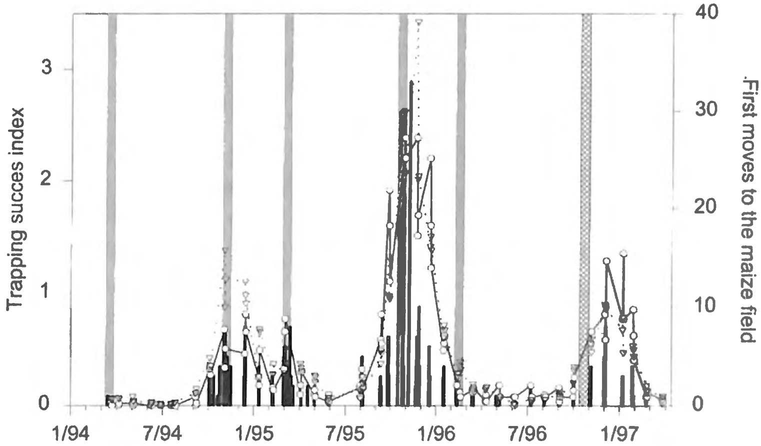

Fig. 2. – Trapping success for each trapping day in the maize field (solid line, solid circles) and fallow land (dotted line, open triangles) between March 1994 and March 1997. The thick grey vertical lines indicate planting periods. The column in October 1996 indicates a savanna fire which destroyed the grass layer in the study area. The narrow black columns indicate the number of individuals that moved from fallow land to maize field.

The number of transient animals (animals that were trapped only once in the study) increased during the October planting seasons, but this happened both in fallow land and in maize fields (Fig. 3). During the March planting season, this increase was not observed. The proportion of transients was higher ($\chi^2=24.5$, $p<0.001$) among animals that were only trapped in the maize field (369/591=62 %) than among animals that were only trapped in the fallow land (1360/2656=51 %). Reproductive activity was highly seasonal but similar in both habitat types (Fig. 4).

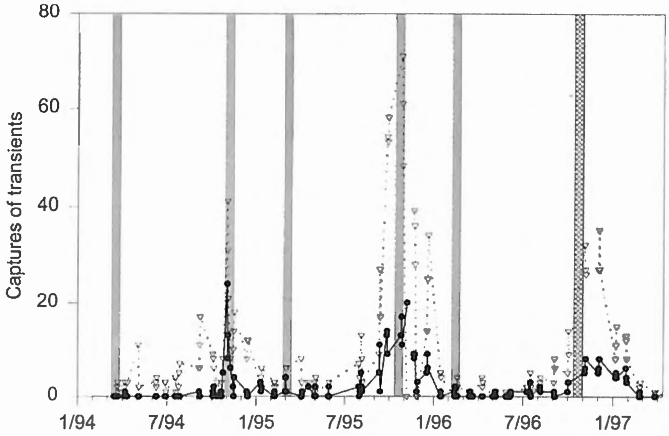

Fig. 3. – Number of transient animals (animals trapped only once) for each trapping day in the maize field (solid line, solid circles) and fallow land (dotted line, open triangles). The thick grey vertical lines indicate planting periods.

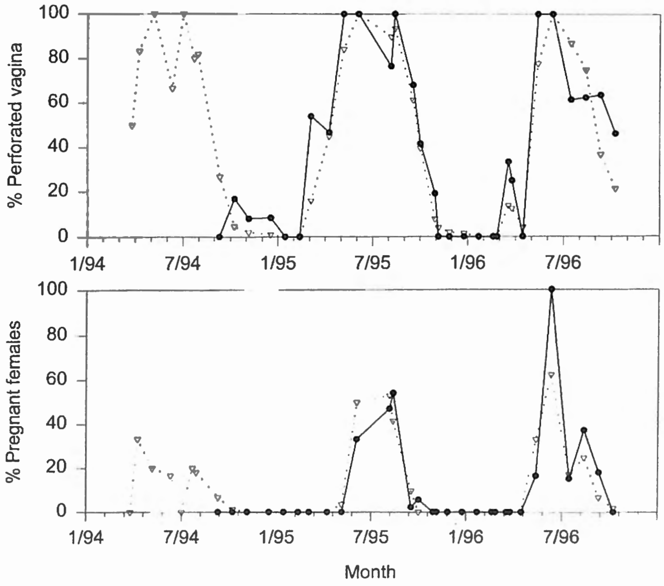

Fig. 4. – Percentage of females with perforated vagina (upper graph) or visible pregnancies (lower graph) per month in the maize field (solid line, solid circles) and fallow land (dotted line, open triangles).

Number and location of activity concentrations could be calculated for 63 of the radio-tagged animals. The 25 other animals died or disappeared before enough telemetric localisations could be collected. Many animals showed a bi- or even polynuclear activity range. In such cases, most animals displayed activity concentrations in the maize fields as well as in the surrounding fallow land (Table 1). This pattern was more obvious when analyses were restricted to localisations during which the individual was moving (Table 1). There was no relation between the number of activity centers and the total number of localisations for an individual (p=0.25) or the total length of the period during which an individual was followed telemetrically (Spearman Rank correlation, p=0.40). There are relatively more activity concentrations in the maize fields in November, but this corresponds to the bias in capture place of the tagged animals in that month.

TABLE 1

Number and habitat distribution of spatial activity concentrations for 88 radiotagged Mastomys natalensis, *trapped in the maize fields or on the maize field borders in March-May or November (different years pooled). All positions= activity ranges calculated with all telemetric localistations; Moving positions only= activity ranges calculated only with localisations when animals were clearly moving around.*

		Number of individuals			
		All positions		*Moving positions only*	
# activity centers	*Habitat*	*Mar.-May*	*Nov.*	*Mar.-May*	*Nov.*
1	Fallow	7	4	5	3
	Maize	4	12	2	8
≥2	Fallow only	3	2	4	1
	Maize only	2	7	3	8
	Fallow+Maize	6	18	6	19
Insufficient data	-	14	11	15	14

Prior to the recolonization experiment, rat densities were low in all fields (Fig. 5). One day after planting, densities dropped in all fields but in the untreated areas, they started

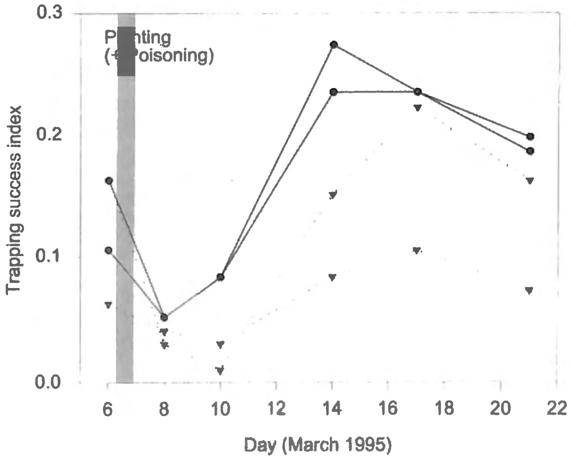

Fig. 5. – Evolution of trapping success in 2 fields where planting was accompanied by a poisoning action (dotted line, triangles) and 2 control fields (solid line, circles). All fields were planted on 6 March (grey vertical column).

increasing again immediately. In the poisoned fields, numbers remained low for at least three days. After that period, densities became high again, both in the treated and untreated fields, although one of the treated fields always remained at a relatively low level. In the untreated field, peak densities were reached at day 14 and they were higher than in the treated fields (one-sided t-test after arcsine-transformation, $p=0.037$).

DISCUSSION

On a seasonal time scale, we found no differences in the amount of rodent activity in fallow land and maize fields. There were animals in the maize fields throughout the year and their relative abundance varied seasonally just like that in the surrounding fallow land. Neither did we find indications of seasonal mass displacements or evidence that the field population disappears or becomes extinct in some seasons and reestablishes itself later on. There is a large turnover in the field population, but the same is happening in the fallow land population. The higher proportion of transients in the maize field could indicate temporary invasions of the fields, even more so because some of the apparent transients in the fallow land could actually be visitors attracted to the fields but intercepted by the traps in the surrounding fallow land. Yet, the seasonal pattern of the presence of transients cannot be explained by the crop seasons. The seasonal effects of rainfall as reported earlier for this population (TELFORD, 1989; LEIRS *et al.,* 1996a) thus seem to be stronger than the effects of agricultural activities or events like savanna fires. The observation that damage by *M. natalensis* in maize fields is highly seasonal and concentrated at planting and harvesting time (TAYLOR, 1968 and many unpublished reports), may therefore be the result of changing feeding behaviour dependent on crop stage, rather than differences in rodent abundance and spatial dynamics.

On a much shorter time scale, within the first week after planting and therefore not obvious in the three-year data series, we did observe effects of agricultural activity in our recolonization experiment. Interestingly, rodent densities in the fields sharply decreased immediately after ploughing and planting, also in the fields where no rodent control was applied, suggesting that the disturbance of the field has an impact, albeit a brief one, on rodent abundance. Numbers, however, then rapidly increased for a few days, reaching a maximum when the germinated seedlings were above the ground, after which they decreased again. We have no similar data on rodent densities in the surrounding fallow land during the same short period, but the fact that we observed the peak and consecutive decline also in fields where the local population was removed at the moment of planting, indicates that indeed a short invasion happened. We have no indications of the long range movements of colonizing animals, but rather long dispersal and excursion distances are not uncommon in *M. natalensis* (LEIRS *et al.*, 1996b; CHRISTENSEN, 1996). Clearly, poisoning would be needed in a band wider than the 10 m we applied around the fields in order to prevent quick recolonisation. This has important consequences for control since widening this band increases the total surface to be treated quadratically, rendering poison treatments economically less profitable. MYLLYMÄKI (1987) already indicated that the dispersal capacities of *M.natalensis* prevented a long-term effect of local control actions, but he suggested that treatments synchronised with planting could protect the seedlings over a short period. In our experiment, recolonization occurred so quickly, even at low densities, that even a short-term effect seems doubtful.

The short invasion of a field should not necessarily be a move of animals between separate populations. There is a higher proportion of transients in the maize field but that may be biased by the fact that the maize fields have relatively more area close to the border of the trapping area. Most non-transients in the maize fields were trapped at earlier or later occasions in the fallow land and our telemetric data show that individuals regularly moved between both habitats. That most animals spend considerable time in both habitats suggests that rats benefit from some complementarity between maize fields and fallow land. This does not mean that *M.natalensis* are homogeneously distributed at a small scale. It has been shown several times that *Mastomys* sp. individuals prefer sites with specific microhabitat characteristics from studies elsewhere (DIETERLEN, 1967; NEAL, 1970; MARTIN & DICKINSON, 1985; DUPLANTIER & GRANJON, 1988) and from our own study area (TELFORD, 1989; LEIRS *et al.*, 1996b). Observations that fields are first damaged at their borders (*e.g.* EVERARD,1966; TAYLOR, 1968) are not necessarily indications of invasions by rodents, but may be the result of a microhabitat preference of the rodents (near to more lush cover) in their usual home range. Rodent damage is often patchy in the maize fields (unpublished observations) and we observed also that radiotagged animals tend to be localised more in the surroundings of small weedy patches or left-over bushes in the field. Our telemetric data show that many individuals have disjunct activity centres, contrasting with earlier assumptions that *M.natalensis* has a simple circular home range (*e.g.* CHRISTENSEN, 1996).

The invasion of fields by rodents from surrounding populations is a general assumption in rodent pest ecology and several rodent strategies proposed for managing rodent damage have attempted to minimize influx of animals by fencing (*e.g.* SINGLETON, 1997), diversionary feeding (PELZ, 1989), perimeter poisoning (KAY *et al.*, 1994), buffer or capture crops and periphery environmental control (FITZWATER, 1988). Often, however, the evidence for large population movements into fields comes from studies which were carried out in very large scale agricultural landscapes, like the work on house mice in Australia (*e.g.* NEWSOME, 1969; TWIGG & KAY, 1995; KREBS *et al.*, 1995; CHAMBERS *et al.*, 1996) or the invasions of *Arvicanthis niloticus* (Desmarest, 1822) in the sahelian savanna during outbreak years (POULET & POUPON, 1978). When the different habitat patches are smaller, the evidence for seasonal movements is much weaker, a rare exception being the study by CUMMINGS & VESSEY (1994) who showed that individual *Peromyscus leucopus* (Rafinesque, 1818) change habitats seasonally in a small-scale patchy agricultural landscape in Ohio. Our present data indicate that, in fine-grained habitat typical for many African smallholder farms, the distinction between refuge and field populations disappears and consequently it can be assumed that management techniques based on the existence of both spatially and temporarily distinct populations will be of limited use there.

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