Spatial patterns in *Mastomys natalensis* in Tanzania (Rodentia, Muridae)

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Summary. – We investigated habitat preference, dispersal and movement patterns of *Mastomys natalensis* in fallow land and maize fields in Tanzania. During periods of low densities, the animals seemed to avoid open spaces and were concentrated in areas with rich vegetation cover. A high turn-over rate, even in periods without reproduction, indicated a high degree of dispersal. Resident animals had a limited home range with most movements within 30 m of the burrow ; however, excursions and movements over large distances were observed. Animals living on the border of maize fields and fallow land are active in both habitats and may have their burrow in any of them. Home ranges overlap both intra- and intersexually and there is no indication for territoriality. The obtained results are disappointing for the development of new pest control strategies.

Résumé. – Nous avons étudié la préférence d'habitat, la dispersion et les mouvements de *Mastomys natalensis* dans des jachères et des champs de maïs en Tanzanie. Pendant les périodes de faibles densités, les animaux semblaient éviter les espaces ouverts et étaient concentrés dans les zones à riche végétation. Les taux de remplacement élevés, même en dehors des périodes de reproduction, indiquaient un degré élevé de dispersion. Les animaux résidents avaient des domaines vitaux plutôt limités avec la plupart de leurs mouvements limités à moins de 30 m du terrier ; cependant, occasionnellement des excursions et des mouvements à grande distance étaient observés. Les animaux vivant aux abords des champs et des jachères étaient actifs dans les deux habitats, ayant leur terrier dans l'un ou l'autre de ces deux habitats. Les domaines vitaux se recouvraient entre individus de même sexe ainsi qu'entre mâles et femelles ; il n'y avait aucune indication de territorialité. Les résultats obtenus sont plutôt décevants pour le développement de nouvelles stratégies de contrôle de ces rongeurs très nuisibles.

INTRODUCTION

Multimammate rats of the genus *Mastomys* are common rodents in subsaharan Africa. They are common in fallow land and agricultural fields, where they are considered a pest ; densities are highly variable and sometimes peak to real outbreaks (Fiedler 1988). The temporal dynamics of these rats have been reported extensively and the

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underlying mechanisms of reproductive seasonality have been investigated (Bronner *et al.* 1988, Leirs *et al.* 1994, Swanepoel 1980). The spatial dynamics of *Mastomys* are much less well known and the existing information is often sparse, collected in unusual populations or unpublished (*e.g.* Bronner 1986, Duplantier and Granjon 1988, Sheppe 1972, Willan 1982). However, knowing the patterns of space use is important in order to design a sound ecological basis for pest management. In the present paper, we attempt to answer the following questions with regard to spatial patterns that may be of relevance in this perspective : 1° Are the *Mastomys* found in fields a resident population ? 2° Are *Mastomys* likely to rapidly colonize vacant habitats ? 3° Are habitat alterations likely to reduce the presence of *Mastomys ?* 4° Could *Mastomys* living around a maize field "socially fence" that field against new immigrants ?

MATERIAL AND METHODS

The data were collected during a capture-mark-recapture (CMR) study in a mosaic landscape of maize fields and fallow land in Morogoro, Tanzania (06°51'S, 37°38'E). A one hectare grid (grid 1) with trapping stations 10 m apart was set up in November 1986 and maintained until February 1989 ; this study area consisted of an old maize field that had been harvested in mid 1986. A second one hectare grid (grid 2) was set up 100 m away in an older fallow land ; this grid was run from April 1987 to August 1988. In early September 1987, the whole area was burned by a savanna fire which destroyed all dry grasses, leaving the area very open with bare soil except for an area of 2100 m^2 in grid 2 which was covered by a short weed, *Tridax* sp. In July 1988, a detailed vegetation map of both grids was drawn, using seven vegetation types : open area with (nearly) bare soil ; *Brachiaria biscenta* grass ; *Pennisetum polystachium* grass ; *Cymbopogon* spp. grasses ; *Rothboellia conchinchinensis* grass ; *Panicum* spp. grasses ; bushes. From the vegetation map, the area covered by the different vegetation types was estimated in each grid cell (10 m × 10 m) ; in a multiple regression analysis, the relation between the vegetation cover of each grid cell and the numbers of rats captured in there early in the dry season in July-August 1988 (low population density, Minimum Number Alive on grid 1 = 32) and at the end of the dry season in November 1988 (high population density, MNA = 401) was investigated. On the same site a 300 m × 100 m grid was started again in March 1994 and remained still in use in December 1995 ; this time, the area consisted mainly of fallow land but included a 80 m × 80 m maize field in the middle, surrounded by fallow land for at least 60 m in every direction ; in addition, a 30 m × 60 m corner of the area was part of a farmer's maize field.

Three-day trapping sessions were conducted monthly. During the 1986-89 period, trap density varied between 1 and 4 traps per trapping station, depending on the number of rodents trapped, in an attempt to avoid low trappability due to trap shortage. During 1994-1995, the trap density was always one trap per trapping station. Traps were baited with a mixture of peanut butter and maize scrap and left in the field overnight. Trapped animals were taken to the field laboratory, weighed and marked by toe clipping ; their sexual condition was recorded and they were released on the capture position. During the first period, 8509 captures of 3531 individual *M. natalensis* were realised. Analyses of reproduction and growth patterns in this study have been published elsewhere (Leirs *et al.* 1990, 1994). During the second period, 6455 captures of 2556 individuals were realised.

In November 1994 and March-April 1995, on the same site, 40 animals were equipped with radio-tags (Televilt, Sweden and Biotrack, UK). Their movements were tracked by recording positions, to the nearest meter, 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 daily. For the purpose of this study, it seemed more relevant to calculate home ranges as inclusive boundary convex polygons, including localisations during occasional excursions, rather than as probabilistic estimates. Home ranges were calculated only for animals for which > 20 telemetric localisations were obtained, since in this group there was no significant correlation between polygon size and number of observations ($r^2 = -0.027$, $n = 21$). Polygon areas were also calculated with capture data for animals that were trapped more than 5 times within 5 months. From the capture data, information on movements was also analysed as the distance between consecutive captures within one month, or as the distance between activity centres (geometric mean of capture positions) in consecutive months.

RESULTS

In July-August 1988, the vegetation cover explained 18-36 % of the variation in rat capture distribution ; in November this was less (Table 1). Rodent numbers were negatively correlated with open space and positively with the presence of high, dense grasses. After the fire in early September 1987, rodents tended to be more concentrated in an area with short *Tridax* weed which was not burnt, while there were relatively few animals in that part of the grid before the fire (Fig. 1). Nevertheless, animals also occurred in the burnt area (Fig. 1) and local survival to the next month was not different in the two parts of the grid (Table 2).

Nearly all distances between capture points during the same month were less than 30 m (Fig. 2). Males generally move a bit further than females ; seasonal patterns are hard to discover due to scarce data for low-density months (Fig. 3 a). Only 96 animals moved further than 40 m (the 95 th percentile). Of these, 41 were trapped more than once, but none of them moved such large distances again. Distances between activity

TABLE 1. – Results of multiple regression analyses of rat captures per grid cell on areas of different vegetation types in that grid cell (100 grid cells). Regressions based on rodent captures in July-August 1988 in both study areas and in November 1988 in grid 1. Partial correlation values for vegetation types included in the model are underlined (* $p < 0.01$; ** $p < 0.001$).

period	Grid 1 7-8/88	Grid 2 7-8/88	Grid 1 11/88
number of captures	115	173	630
multiple R	.423**	.606**	.324 *
partial correlations			
open or very sparse	-.331**	-.038	.023
Brachyaria biscenta	-.050	.157	-.062
Pennisetum polystachium	-.054	.010	.294 *
Cymbopogon sp.	-.048	.162	-.114
Rothboellia conchinchinensis	.148	.212	-.005
Panicum spp.	.100	.589**	-.037
bushes	.114	-.090	-.028

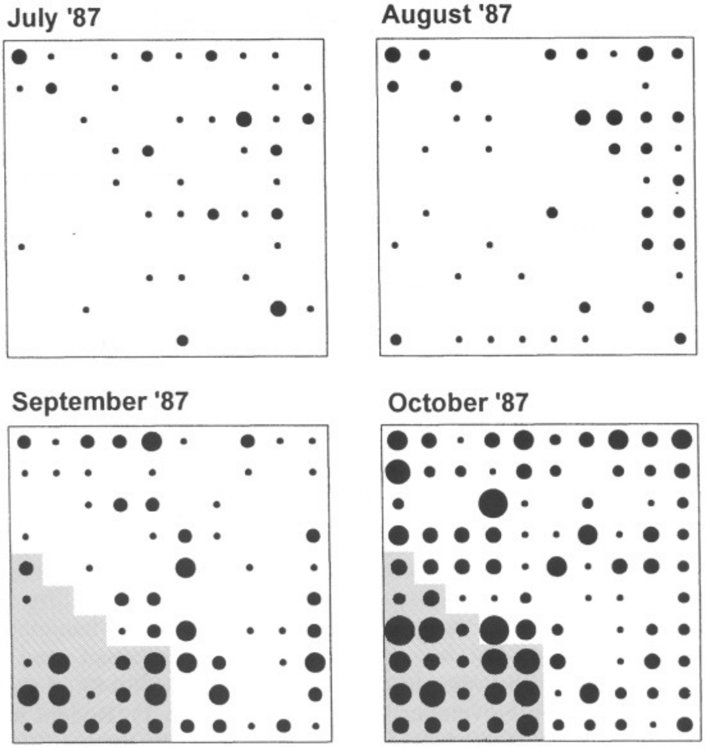

Fig. 1. – Capture densities per trapping station on grid 2 (1 ha) between July and October 1988. Dot size increases with number of captures (1-6). The shaded area remained unburnt during the savanna fire in early September 1987.

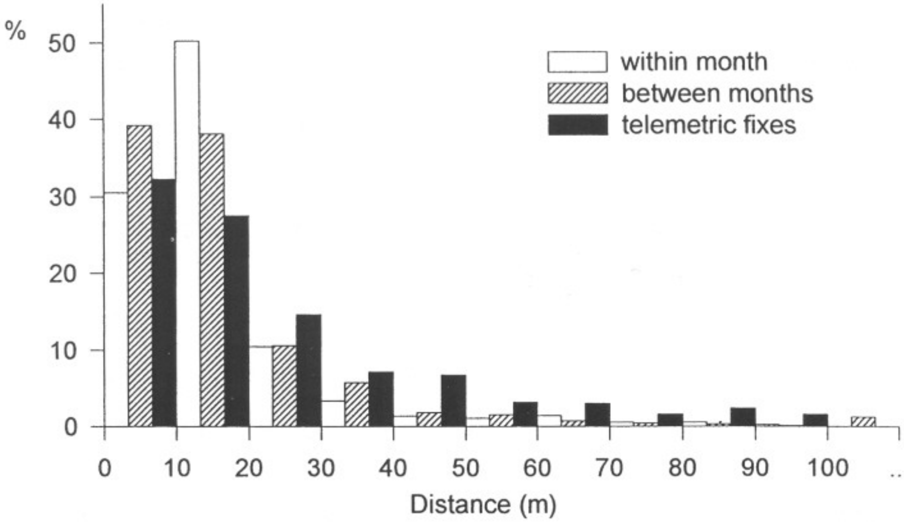

Fig. 2. – Frequency distribution (%) of distances between consecutive captures within a month (white, n = 2078), distances between activity centres in consecutive months (grey, n = 1707), distances of telemetric fixes to the burrow (black, n = 505).

TABLE 2. – Local survival of individuals in burnt (barren) and unburnt (covered with *Tridax* weed) areas after a fire. Statistical significance of the differences was tested in a contingency table.

	burnt area		unburnt area			
	n	surv	*n*	surv	χ^2	*p*
Sep-Oct 1987						
males	37	0.189	14	0.357	1.592	0.207
females	38	0.447	12	0.500	0.102	0.750
Oct-Nov 1987						
males	84	0.214	32	0.219	0.003	0.958
females	73	0.205	34	0.176	0.124	0.725

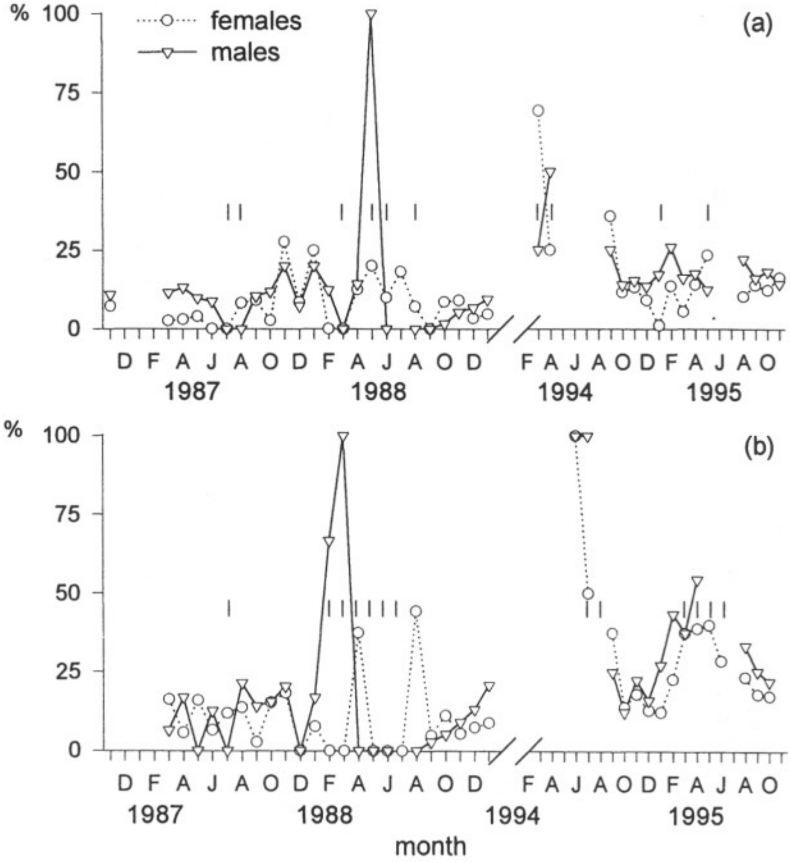

Fig. 3. – Monthly percentage of distances greater than 30 m ; (a) distances between consecutive captures within a month ; (b) distances between activity centers in consecutive months. Small vertical lines indicate months for which less than five distances were obtained per sex.

centres in consecutive months showed similar results (Figs. 2, 3 b). Home ranges calculated from capture data were consequently small with most of the animals not moving more than one trapping station away (Table 3). Distances from an individual's burrow to telemetric fixes were often larger than this (Fig. 2) and also home ranges were more than double those of the capture study (Table 3). Home ranges were not different between sexes or seasons.

Home ranges based on telemetric data in March-April showed considerable overlap between individuals, also between members of the same sex (Fig. 4). Many home ranges consisted partly of maize field, partly of fallow land. Out of 477 individuals that were trapped at least twice and at least once in the maize field, 145 were never trapped in the fallow land ; of the others, 189 were trapped in the maize field only once.

TABLE 3. – Convex polygon home range estimates for both sexes in the CMR-study (breeding and non-breeding season) and the telemetric study (breeding season only). Differences between seasons and sexes are tested with a Mann-Whitney-U-test.

	Breeding season		Non-breeding season		
	n	median	n	median	
Trapping study					
♀♀	48	593	125	441	p=0.059
♂♂	30	412	144	462	p=0.213
		p=0.044		p=0.209	
Telemetric study					
♀♀	13	1212 (range: 221-2025)			
♂♂	8	1119 (range: 458-2578)			
		p=0.51			

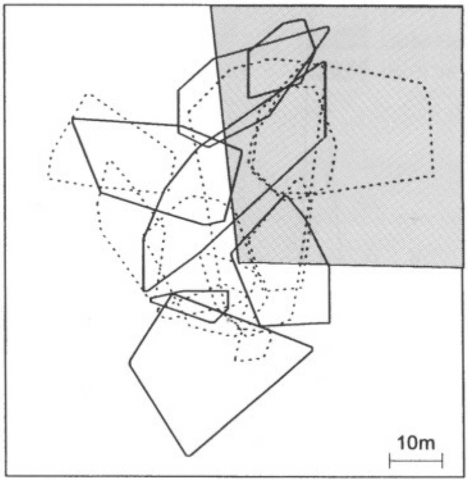

Fig. 4. – Convex polygon home ranges for 17 males (solid lines) and females (dotted lines) at the border of the maize field (grey) and fallow land (white) in April 1995.

Throughout the year, a considerable part of the population consisted of new, previously uncaptured, animals (Fig. 5). Outside the breeding season, such new animals are necessarily immigrants ; many of these new animals were never recaptured again (Fig. 6).

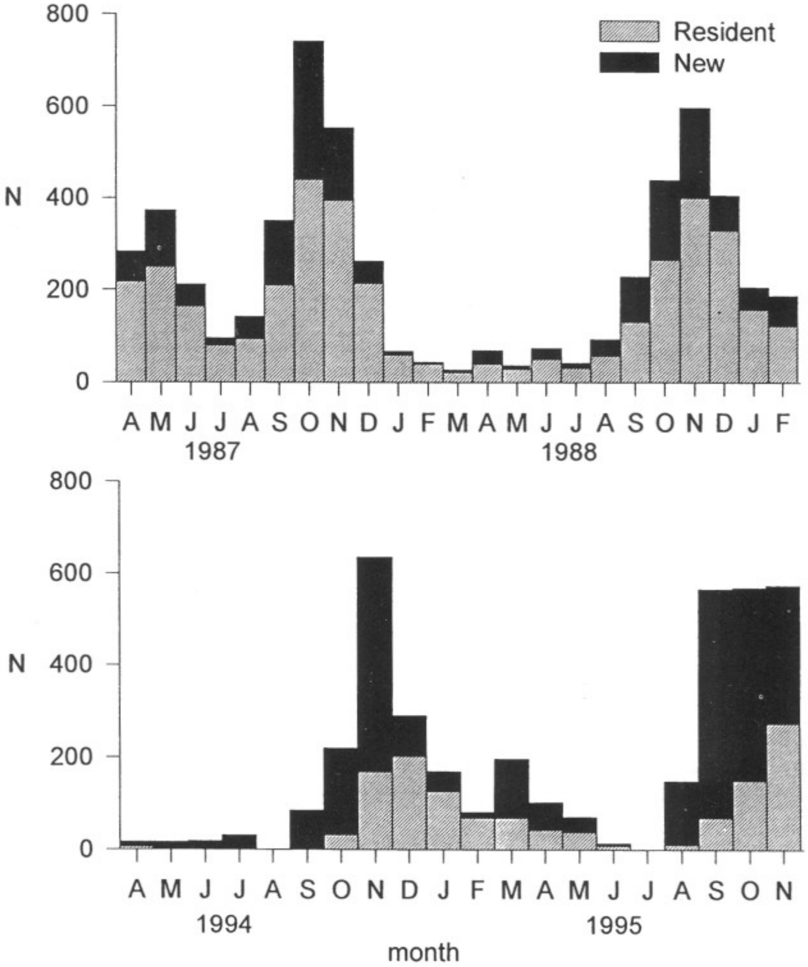

Fig. 5. – Number of residents and new animals per month.

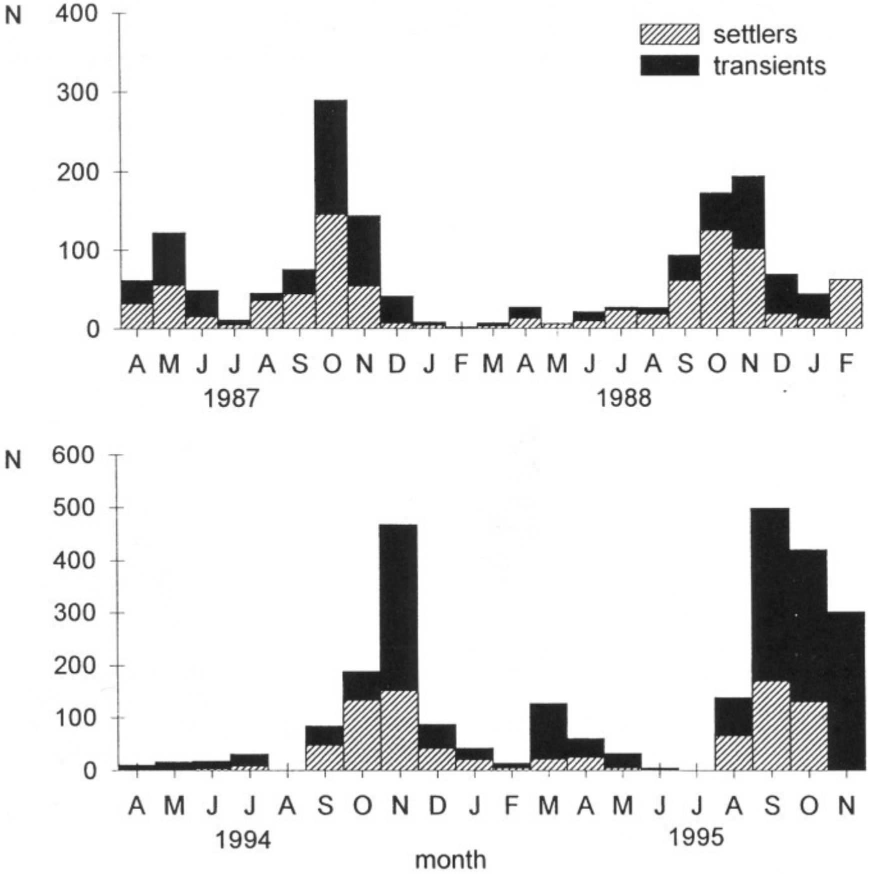

Fig. 6. – Number of settlers (new animals that were captured in at least one later month) and transients (new animals that were never captured in a later month).

DISCUSSION

The data show that densely covered sites were preferred ; also in other areas, *Mastomys* sp. was commonest in sites with many bushes or tall grasses (Dieterlen 1967, Neal 1970, Martin and Dickinson 1985). Yet, our data also showed that high densities can exist on open areas and survival there is not always reduced. Green and Taylor (1975) experimentally removed vegetation but found that *M. natalensis* was less responsive to this than other rodent species. Chidumayo (1980, 1984) observed a distinct decrease of *Mastomys* sp. populations after fire, while areas with a permanent bush vegetation showed very little changes in population numbers. In other studies, *Mastomys* sp. numbers remained unchanged immediately after burning or even increased sharply (Neal 1970, Cheeseman and Delany 1979, Martin and Dickinson 1985, Bronner

1986). Sheppe (1972) found *Mastomys* sp. reproducing on dry soil with new fresh growth, and peak populations in high grass ; when the grass grew even higher and became more impenetrable, the catch was lower. These divergent results show that the preference for dense vegetation is not simple and probably is dependent on population density and the availability of alternative vegetation types.

Overall, most animals moved very little between two captures. Also in fields in Burundi, the mean distance between consecutive trappings was 20 m and 85 % of the animals moved less than 25 m (Giban 1977). These distances are much shorter than the few anecdotical data from the Zambian floodplains (about 60-90 m there vs 10-20 m in this study), but that peculiar population showed strong migration patterns (Sheppe 1972).

Distances observed in the telemetric study were larger than those obtained from capture data. However, a more detailed look into the telemetric data shows that the long distances were made during short excursions (data will be presented elsewhere). Such excursions are less obvious in the capture study, which could be caused by several reasons. Animals may be intercepted by traps before they leave their normal activity range for short excursions. Alternatively, animals may be more trap shy during excursions than in their familiar surroundings. However, it is clear that animals do make excursions that can readily be more than 50 m, and thus extend well outside their normal home range. This may also explain the high proportion of animals that were trapped only once in the maize fields, and before or afterwards in the fallow land. It indicates that many of the animals that were encountered in a maize field, spent a lot their time in the surrounding fallow land. The subpopulation possibly damaging crop may thus originate from relatively far outside the actual field.

Our data showed that immigration and emigration were continuous processes in which a large part of the population participated. The result of this was a very high turn-over rate with many animals constantly appearing and disappearing. The very high proportion of new animals in the 1994-95 data set, in comparison with the 1987-89 period (Fig. 5), may be explained by a different degree of trap saturation in both studies or by the mosaic field-fallow pattern of the study area since 1994. Myllymäki (1987) already anticipated dispersal to be a major problem in *Mastomys* field control strategies and the present study supports this hypothesis with a large data set. Cheeseman and Delany (1979) had a very small data set (n = 48) but even in their study it was apparent that animals did not remain resident for many months. A high proportion of transients was also recorded in *M. erythroleucus* populations, and the number of settling immigrants was even lower there (Hubert *et al.* 1981).

The large home range overlaps give no indication for territoriality. Although *M. natalensis* has been reported to be rather aggressive in Senegal at the edge of its geographic range (Granjon *et al.* 1986), most studies do not report a high degree of aggression (Delany and Happold 1979, Isaacson 1975, Veenstra 1958). There is also little evidence for aggressiveness in our study : since 1986, we trapped only eight animals with damaged ears in our CMR-study. Since aggressiveness is a necessary condition for a "social fence" to function (Hestbeck 1982), it is unlikely to exist in *Mastomys.*

The high dispersal and turn-over rate certainly contributes to the good colonizing ability that is attributed to *Mastomys* (Meester *et al.* 1979, Willan and Meester 1989). Together with the generalized opportunism (Leirs *et al.* 1994) and high reproductive capacity (Leirs *et al.* 1993), it explains why multimammate rats are so successful in rapidly establishing populations on pioneer sites such as post-fire habitats or fallow land (Willan and Meester 1989). The same can be expected on agricultural fields from which rodents are removed by control actions. Moreover, *M. natalensis* from surrounding fallow land are likely to briefly visit maize fields, without settling there. The preference of *M. natalensis* for dense vegetation would suggest that removing vegetation around fields would alleviate rodent problems, but the very high densities that are sometimes observed on open places, make this effect rather dubious. Using behavioural characteristics in pest control is also unlikely to be successful. In conclusion, the results obtained are rather disappointing for the development of alternative strategies for integrated pest management of *M. natalensis* rats.

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