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Spatio-temporal patterns in the distribution of the multi-mammate mouse, *Mastomys natalensis*, in rice crop and fallow land habitats in Tanzania

Abstract: An understanding of the dispersion patterns of a pest is an important pre-requisite for developing an effective management programme for the pest. In this study, rodents were trapped in two rice fields and two fallow fields for three consecutive nights each month from June 2010 to May 2012. *Mastomys natalensis* was the most abundant rodent pest species in the study area, accounting for >95% of the trapped rodent community. *Rattus rattus*, *Dasymys incomtus*, *Acomys spinosissimus* and *Grammomys dolichurus* comprised relatively small proportions of the trapped population. Morisita's index of dispersion was used to measure the relative dispersal pattern (aggregate, random, uniform) of individuals across each trapping grid as a means of comparing rodent distribution in rice and fallow fields over time. This analysis revealed that the rodents in rice fields generally exhibited an aggregated spatio-temporal distribution. However, the rodents in fallow fields were generally less aggregated, approaching a random distribution in some habitats and seasons. Heat maps of trapping grids visually confirmed these dispersal patterns, indicating the clumped or random nature of captured rodents. ANOVA showed that the parameters of habitat (rice, fallow), crop stage (transplanting, vegetative, booting, maturity) and cropping season (wet, dry) all significantly impacted the number of rodents captured, with the vegetative, dry season, fallow habitat having the highest number of rodents; and the transplanting, wet season, rice habitat with the least number of rodents. Therefore, such spatio-temporal patterns can serve as a tool for developing stratified biodiversity sampling plans for small mammals and decision making for rodent pest management strategies.

Keywords: aggregate distribution; dispersion; irrigated rice; pest management; small mammals.

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Introduction

Agricultural cropping patterns in Tanzania typically consist of a relatively small-scale matrix of agricultural fields and fallow land (Odhiambo et al. 2005). Habitat quality for small mammals, particularly for rodent pest species, will likely vary according to such changes in land use, and it is expected that the population dynamics of resident animals will exhibit important spatio-temporal differences that can potentially affect crop damage patterns and severity. Despite existing knowledge on the population dynamics and breeding patterns of *Mastomys natalensis* (Smith 1834) in irrigated rice agro-ecosystems in Tanzania (Mulungu et al. 2013), the spatio-temporal distribution of rodent pest species in this kind of habitat in Africa is not well-known (Ludwig 1979).

The study of how animals are distributed within habitats has inspired many ecologists to understand and predict species distribution (Dungan et al. 2002, McGeoch and Gaston 2002, Perry et al. 2002). Seeking food, shelter and mating opportunities are considered as the primary factors controlling species distribution (Leirs et al. 1997).

Distribution of individuals and their relative aggregation change over time, where dispersal is determined by a combination of species biology, behaviour, abundance and environmental heterogeneity (Dungan et al. 2002, Perry et al. 2002). Indeed, distribution reflects the inherent variation in the distribution patterns of individuals across space and time (He et al. 2002).

Populations of rodents are often patchily distributed, indicating the heterogeneous distribution of suitable habitats (Wiens 1976, Steen et al. 1996). However, more uniform spatial distributions have been reported for *Thomomys talpoides* (Richardson 1828) with an increase in population density (Hansen and Reemega 1961) and for *Ctenomys* species under high-density conditions or in poor habitats (Rossi et al. 1992). A random population distribution has been observed for *Ctenomys australis* (Rusconi 1934) in sand dunes, which are considered an ecologically homogeneous habitat (Zenuto and Busch 1998). Thus, changes in population density or habitat heterogeneity may lead to a more even dispersion of individuals, which in turn may promote changes in other behavioural or demographic parameters.

By understanding the population structure of a species, important insights into ecological relationships can be elucidated. For example, decision-making on ecologically based rodent management strategies is based on information about pest population density and the distribution pattern of their population (Pedigo and Buntin 1994). Analysis of distribution is considered as an essential procedure for pest population studies and it provides basic information for designing efficient and cost-effective sampling plans for population estimation and pest management (Southwood and Henderson 2000, Esfandiari and Mossadegh 2007). Prior to recommending appropriate strategies for rodent management in a particular ecosystem, there is a need to analyse the distribution patterns of the target pests. Thus, the aim of this study was to investigate the spatio-temporal distribution patterns of *Mastomys natalensis* in rice and fallow-land habitats in Tanzania to develop appropriate management strategies.

Materials and methods

Study area

This study was conducted at Hembeti village (06° 16′S, 37° 31′E), in Mvomero District, Morogoro, Tanzania. The study area has a bimodal rainfall pattern with short rainy season from October to December and long rainy season from March to June. Farmers in the study area produce two rice crops per year. The first cropping season occurs during the wet season from January to June, and the second crop is grown during the dry season from July to December, exclusively under irrigation. For wet and dry seasons, respectively, land preparation and rice transplanting are done in January and July, the rice booting stage occurs in April and October, the rice crop reaches physiological maturity in May and November, and farmers harvest in June and December.

Trapping of rodents

A capture-mark-recapture study was conducted from June 2010 to May 2012. A total of four 70×70 m trapping grids (two in rice fields and two in fallow land) were established, where the field edges defined by raised field bunds coincided with the size of each grid. Rice fields had ongoing rice crop cultivation throughout the study period, whereas fallow fields had no cultivation during and for at least 1 year prior to the study. The distance from one experimental field to another was >100 m. Each grid consisted of seven parallel lines, 10 m apart, and seven trapping stations per line, also 10 m apart, making a total of 49 stations per grid. Evidence from several studies (Christensen 1996, Leirs et al. 1996a,b, Hoffmann and Klingel 2001, Monadjem et al. 2011) in southeastern Africa has indicated that this grid size (3600 m^2) is adequate to account for the home-range sizes of *Mastomys natalensis*, where the majority of a population (80%) typically does not move by more than 50 m from their burrows, with average home-range sizes of 200 to 4000 m^2. Agricultural fields typically have home ranges at the lower end of this spectrum (Leirs et al. 1996a,b). One Sherman LFA live trap (8×9×23 cm; H.B. Sherman Traps Inc., Tallahassee, FL, USA) was placed at each trapping station and all were set for three consecutive nights at intervals of 4 weeks. Traps were baited with peanut butter mixed with maize bran/maize flour, set in the afternoon, and inspected in the morning. During flooding, the traps were placed on top of dried grass mounds at the same grid locations.

Processing of captured rodents

All the captured animals were taken to the field laboratory and identified to species level following Kingdon (1974). On the first day of capture, all the captured animals were individually marked by toe clipping. The animals were then released at the same station of capture. New animals captured on subsequent days and during subsequent rounds of trapping were similarly marked, recorded and released.

Data collection and analysis

Rodent species were identified in the field to determine their relative abundance. Using the total number of *Mastomys natalensis* captured per trapping station during each trapping session as subquadrats, the spatial distribution patterns were calculated using Morisita's index of dispersion. This index calculates a distribution coefficient of I_d (Morisita 1962) using the following equation:

$$I_d = n\left[\frac{\sum x^2 - \sum x}{\left(\sum x\right)^2 - \sum x}\right]$$

where I_d=Morisita's index of dispersion
n=sample size
Σx=sum of the quadrat counts.

Subquadrats are areas so small that they can only be occupied by one subject (animal) at a time. Thus, p becomes the probability of an animal occupying a subquadrat. This probability will be the same for each subquadrat in the field or pasture. For example, if there are 20 animals and 100 subquadrats, p is $0.05 = x_1 + x_2 + x_3$. Thus, Σx^2 is the sum of the quadrat counts squared $= x_1^2 + x_2^2 + x_3^2$.

A value of $I_d<1$ indicates a uniform dispersion, $I_d=1$ indicates random dispersion and $I_d>1$ indicates an aggregated dispersion. The Morisita index of dispersion values were tested statistically for departure from randomness using the following formula (Morisita 1962):

$$\chi^2 = \frac{n\sum X^2}{N} - N$$

where χ^2=chi-square distribution
n=total number of plots
X=number of individuals in a single plot
ΣX^2=sum of all values of X^2
N=total number of individuals in all plots.

Monthly trapping data of *Mastomys natalensis* from each grid were used to produce a mean dispersion index according to habitat (rice, fallow), season (wet, dry) and crop stage (transplanting, vegetative, booting, maturity). To visualize the potential variation in dispersion, heat maps were produced (Tableau 8.1, http://www.tableausoftware.com/; Tableau Software, Seattle, WA, USA) for each trapping grid using the total number of *M. natalensis* captured per trap station and according to the same three parameters of habitat, season and crop stage. Statistical analysis using ANOVA with Fisher LSD was performed in XLSTAT version May 2, 2010 (Addinsoft, Paris, France) to compare the effects of habitat, season and crop stage using Morisita's index of dispersion and the mean number of *M. natalensis* captured per trapping station per cropping session (July 10 to December 10, January 11 to June 11, July 11 to December 11 and January 12 to June 12).

Results

A total of 3382 individuals belonging to five rodent species were captured (Table 1). *Mastomys natalensis* was the dominant rodent pest species in the area accounting for more than 99.5% of all captures in both habitats (Table 1), with slightly higher diversity found in fallow land. The other rodent species captured and their proportional contributions to the trapped community were *Dasymys incomtus,* Sundevall 1847 (0.18%), *Grammomys dolichurus,* Smut 1832 (0.03%), *Rattus rattus,* Linnaeus 1758 (0.24%), and *Acomys spinosissimus,* Peter 1852 (0.03%). Their numbers were too low to determine any differential effects of season or cropping stage on diversity (ANOVA, $p>0.05$), and their low numbers prevented their inclusion in any further analysis on species-level dispersion patterns.

For *Mastomys natalensis*, Morisita's index of dispersion showed that there were differences in dispersion patterns, particularly between rice and fallow-field habitats (Figure 1). Dispersion values of 1, or close to 1, were calculated for the fallow-land habitat, indicating that rodents were generally randomly distributed. Relatively higher dispersion values were calculated for the rice-field habitat showing that rodents were more aggregated, with the highest aggregation occurring when rice crops were at maturity (Figure 1). A χ^2 analysis to evaluate whether the Morisita values significantly departed from random

Table 1 Total number and percentage of rodent species captured according to habitat.

Species	Rice fields, n (%)	Fallow land, n (%)	Total, n (%)
Mastomys natalensis	1302 (99.85%)	2064 (99.33%)	3366 (99.53%)
Rattus rattus	2 (0.15%)	6 (0.29%)	8 (0.24%)
Dasymys incomtus	–	6 (0.29%)	6 (0.18%)
Acomys spinosissimus	–	1 (0.05%)	1 (0.03%)
Grammomys dolichurus	–	1 (0.05%)	1 (0.03%)
Total	1304 (100%)	2078 (100%)	3382 (100%)
Trap nights	7056	7056	14,112
Trap success (%)	18.48	29.45	23.97

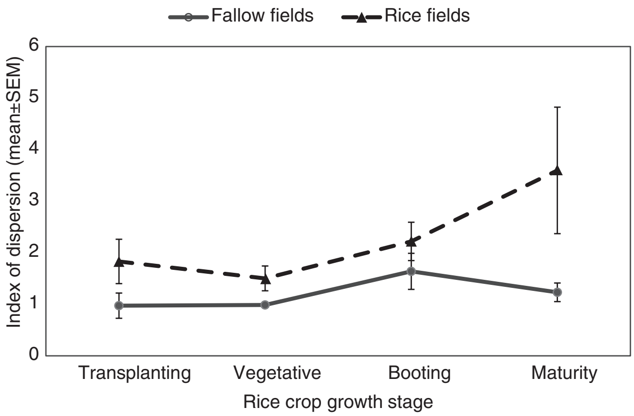

Figure 1 Morisita's index of dispersion where Y=1 indicates a random dispersion, Y<1 indicates a uniform dispersion and Y>1 indicates an aggregated dispersion. Data from wet and dry cropping seasons are combined (n=4).

Table 2 Analysis of variance (ANOVA) using Morisita's index of dispersion and the number of rodents captured per trapping grid according to parameters of habitat (rice, fallow), season (wet, dry) and crop stage (transplanting, vegetative, booting, maturity).

Category	Mean number of rodents	Morisita's index of dispersion
Transplanting*dry*fallow	2.19[EF]	1.13[CD]
Transplanting*dry*rice	0.82[JK]	2.39[ABCD]
Transplanting*wet*fallow	1.10[IJ]	0.81[D]
Transplanting*wet*rice	0.52[KL]	1.27[BCD]
Vegetative*dry*fallow	6.52[A]	0.86[D]
Vegetative*dry*rice	4.39[B]	1.13[CD]
Vegetative*wet*fallow	3.75[C]	1.11[CD]
Vegetative*wet*rice	1.67[GH]	1.86[BCD]
Booting*dry*fallow	2.76[D]	1.35[BCD]
Booting*dry*rice	2.36[DE]	1.93[BCD]
Booting*wet*fallow	0.92[IJK]	1.92[BCD]
Booting*wet*rice	0.37[L]	2.50[ABC]
Maturity*dry*fallow	1.80[FG]	1.30[BCD]
Maturity*dry*rice	1.28[HI]	4.23[A]
Maturity*wet*fallow	2.07[EFG]	1.12[CD]
Maturity*wet*rice	0.99[IJ]	2.95[AB]

ANOVA with Fisher LSD at 95% confidence where mean values in the same column followed by the same letter are not significantly different from each other.

was interpreted on the basis of a critical value of 65.17 for p=0.05 for n–1 (48) degrees of freedom. All χ^2 values above 65.17, therefore, indicated the Morisita index was significantly different from 1.0, where 1.0 equals a random distribution. All Morisita dispersion values above 1.5 were shown to be significantly different, thus indicating aggregated dispersion. Significant values were more predominant in the rice habitat (55%, 27 out of 49 values), with few significant values in the fallow fields (16%, 8 out of 49 values). Mature rice crops were observed to have the highest Morisita values (1.3–9.3), closely aligning with observations in Figure 1. Statistical analysis (ANOVA with Fisher LSD) of dispersion index values showed that all three parameters of season, habitat and crop stage had significant, albeit limited, effects on rodent dispersion patterns (ANOVA df=15, F=1.9, p=0.035; Table 2), confirming the finding that rodents in the rice crops were relatively more aggregated than in the fallow fields, particularly at the time of maturity.

Heat maps showing the total number of *Mastomys natalensis* captured at each trap station for each monthly cropping session visually indicate the aggregated nature of rodent presence in the rice fields at different crop stages (Figure 2). Heat maps for fallow habitats (Figure 3) suggest more random dispersion/limited aggregation with relatively higher numbers of rodents compared to the rice habitat. However, both habitats generally follow the same patterns of rodent abundance according to crop stage, with the vegetative stage showing the highest number of rodents in both habitats. Generally, it can be observed in the heat maps that rodents were often aggregated around the field edges, a factor that can be attributed to common geographic features of rice fields where raised bunds provide harbourage and nesting sites for rodents, as was the case in our study design where each grid was surrounded by a raised bund (Brown et al. 2001, 2006). Observations from these heat maps are supported by statistical analysis (ANOVA with Fisher LSD) performed on the number of rodents caught at each trap station over each of the four cropping cycles (July 10 to December 10, January 11 to June 11, July 11 to December 11 and January 12 to June 12), which showed that there were significant effects in the distribution of *M. natalensis* among crop stage, habitat and season (ANOVA df=15, F=103.3, p<0.0001; Table 2). The data show a particularly strong interaction between the vegetative stage and dry season during which the highest number of rodents was observed.

Discussion

The data collected in the present study revealed that two species of rodents were found in the rice fields, whereas five species were captured in the fallow-land habitats relatively nearby (100–500 m). *Mastomys natalensis* was clearly the most abundant species in both habitats. These findings are consistent with those reported by Sluydts et al. (2009) in monoculture agriculture habitats and in maize fields (Massawe et al. 2005). *M. natalensis* has

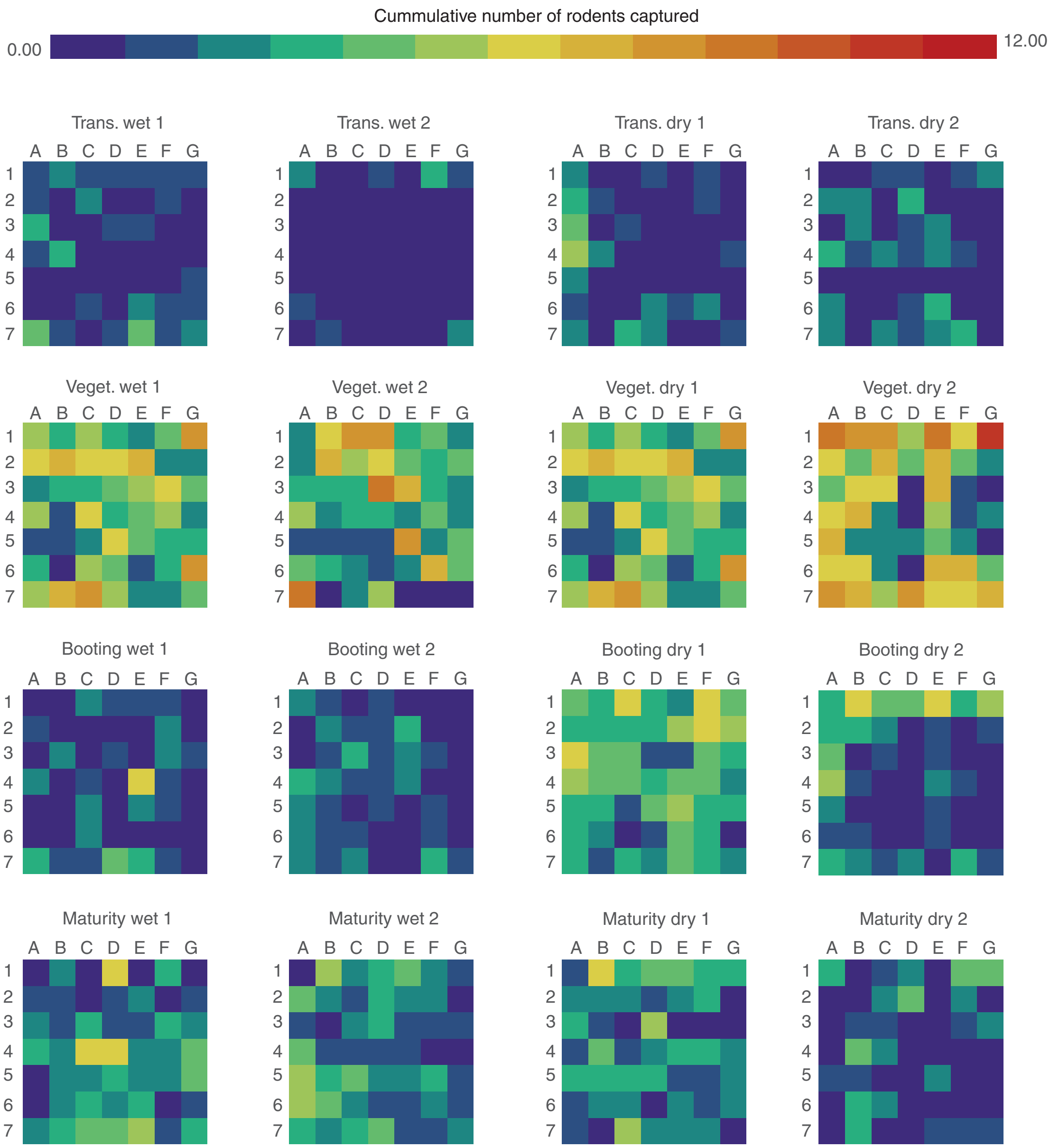

Figure 2 Heat maps showing the total number of rodents captured per trap grid location for the two rice field grids at different crop growth stages. Wet season crops were grown from January to June and dry season crops were grown from July to December, i.e., two cropping sessions per wet and dry seasons.

been recorded in high densities in disturbed landscapes and agricultural fields throughout East African countries (Leirs et al. 1996a,b). Under natural conditions its ecological requirements are essentially grasslands, but it is also found in different kinds of habitats including savannahs, woodland, secondary growth, forest clearings, houses and cultivated fields (Granjon et al. 2008). Due to its wide distribution across sub-Saharan Africa, the species has broad habitat tolerances – a fact that makes it a pioneer species in the colonization of disturbed habitats (Ferreira and Van Aarde 1996).

The aggregated distribution pattern of rodents in the rice fields in this study is consistent with those presented by Leirs (1994), who reported that aggregated distribution patterns were a characteristic of rodent communities, whereas uniform distribution patterns were rare and mainly found in populations where there was strong competition among individuals. The more random distribution of rodents in fallow land may be attributed to relatively larger home ranges (Leirs et al. 1996a, Monadjem et al. 2011), more weeds and generally higher plant diversity providing differential coverage and food resources.

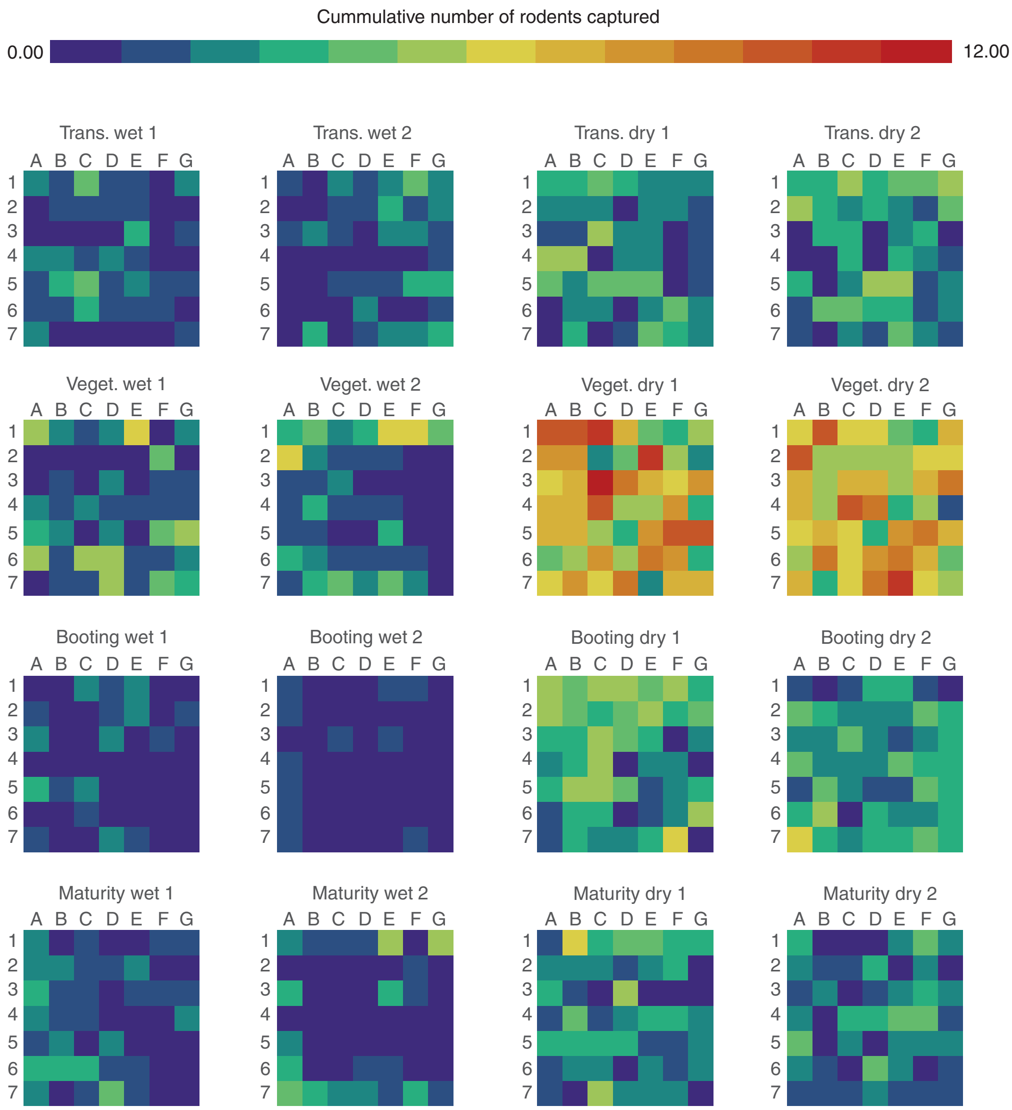

Figure 3 Heat maps showing the total number of rodents captured per trap grid location for the two fallow field grids at different crop growth stages. Wet season crops were grown from January to June and dry season crops were grown from July to December, i.e., two cropping sessions per wet and dry seasons.

Clustered patterns of distribution are reported as the most commonly observed pattern in nature (Pielou 1977, Odum 1986, Krebs 1999). According to Matteucci and Colma (1982), the main reasons leading to a clustered pattern in a population are the behavioural characteristics of the species and intra- and inter-specific relationships. Krebs (1999) argued that the most important features of animal dispersion are the causal mechanisms and factors that promote and maintain the pattern. In the present study, it is arguable that the observed aggregation is partly attributed to increased harbourage opportunities around the edge of fields due the presence of field bunds that promote nesting and family group living and foraging relatively nearby the burrow (Brown et al. 2001). Reports from other researchers show that members of group-living species may be more spatially aggregated but densities may not differ from those of solitary species if social groups are widely scattered across the habitat (Pielou 1977). However, in the present study area, population densities in the fallow land were significantly higher than those in the rice fields and that such densities were higher during dry than during wet seasons. Despite these seasonal and habitat variations in population densities, aggregated and random dispersion were found across all crop stages.

Our research provides strong evidence that *Mastomys natalensis* is the most abundant and important rodent pest species for rice production in Tanzania, evidence that widely concurs with that of other researchers in southeastern Africa investigating rodent pests in staple crop production (Leirs et al. 1996a,b, Makundi and Massawe 2011). The clustered pattern of rodent dispersion in rice fields observed in our study also concurs with the findings of studies in other parts of the world, such as in southeastern Asia, where different rodent species also tend to aggregate during rice field cropping (Brown et al. 2001, 2006). Continuous rice production through the use of irrigation can promote rodent pests, potentially stretching farmer resources too thinly to deal with the problem adequately. Outcomes from our study can help farmers by helping them to focus management actions where rodents tend to aggregate. For example, reducing bund size can limit rodent burrowing and nesting opportunities, and baiting with rodenticide within rodent burrows or trapping nearby can help farmers target their limited resources more effectively.

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