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

3

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15 **Abstract**

16 An understanding of the dispersion patterns of a pest is an important pre-requisite for developing an
17 effective management programme for the pest. In this study, rodents were trapped in two rice fields
18 and two fallow fields for three consecutive nights each month from June 2010 to May 2012.
19 *Mastomys natalensis* was found to be the most abundant rodent pest species in the study area,
20 accounting for >95% of the trapped rodent community. *Rattus rattus*, *Dasymys incomtus*, *Acomys*
21 *spinosissimus* and *Grammomys dolichurus* comprised relatively small proportions of the trapped
22 community. Morisita's index of dispersion was used for measuring the relative dispersal pattern
23 (aggregate, random, uniform) of individuals across each trapping grid as a means of comparing

24 rodent distribution in rice and fallow fields over time. This analysis revealed that the rodents in rice
25 fields generally exhibited an aggregated spatio-temporal distribution. However, rodents in fallow
26 fields were generally less aggregated, approaching a random distribution in some habitats and
27 seasons. Heat maps of trapping grids visually confirmed these dispersal patterns, indicating the
28 clumped or random nature of captured rodents. Analysis of variance showed that the parameters of
29 habitat (rice, fallow) crop stage (transplanting, vegetative, booting, maturity) and cropping season
30 (wet, dry) all significantly impacted on the number of rodents captured, with the vegetative dry
31 season fallow habitat having the highest number of rodents, and the transplanting wet season rice
32 habitat with the least number of rodents. It was concluded that such spatio-temporal patterns could
33 serve as a tool for developing stratified biodiversity sampling plans for small mammals and decision
34 making for rodent pest management strategies.

35

36 **Keywords:** aggregate distribution, dispersion, small mammals, irrigated rice, pest management,

37

38 **Introduction**

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

47

48 The study of how animals are distributed within habitats has inspired many ecologists to understand
49 and predict species distribution (Dungan et al. 2002; McGeoch & Gaston 2002; Perry et al. 2002).
50 Seeking food, shelter and mating opportunities are considered to be the primary factors controlling
51 the distribution of species (Leirs et al. 1997). Distribution of individuals and their relative aggregation
52 changes over time, where dispersal is determined by a combination of species biology, behaviour,
53 abundance and environmental heterogeneity (Dungan et al. 2002; Perry et al. 2002). Indeed,
54 distribution reflects the inherent variation in the distribution patterns of individuals across space and
55 time (He et al. 2002).

56

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

65

66 Through understanding the population structure of a species, important insights into ecological
67 relationships can be elucidated. For example, decision-making on ecologically based rodent
68 management strategies is based on information about pest population density and the distribution
69 pattern of their population (Pedigo and Buntin 1994). Analysis of distribution is considered to be an
70 essential procedure for pest population studies and it provides basic information for designing
71 efficient and cost-effective sampling plans for population estimation and pest management
72 (Southwood and Henderson 2000; Esfandiari and Mossadegh 2007). Prior to recommending

73 appropriate strategies for rodent management in a particular ecosystem, there is a need to analyse
74 the distribution patterns of the target pests. Thus, the aim of this study was to investigate spatio-
75 temporal distribution patterns of *M. natalensis* in rice and fallow land habitats in Tanzania in order
76 to inform appropriate management strategies.

77

78 **Materials and Methods**

79 **Study area**

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

88

89 **Trapping of rodents**

90 A capture-mark-recapture (CMR) study was carried out from June 2010 to May 2012. Four 70 x 70 m
91 trapping grids (two in rice fields and two in fallow land) were established, where the field edges
92 defined by raised field bunds coincided with the size of each grid. Rice fields had ongoing rice crop
93 cultivation throughout the study period while fallow fields had no cultivation during and for at least
94 one year prior to the study. The distance from one experimental field to another was >100 m. Each
95 grid consisted of seven parallel lines, 10 m apart, and seven trapping stations per line, also 10 m
96 apart making a total of 49 stations/grid. Evidence from several studies (Christensen 1996; Leirs et al.
97 1996a&b; Hoffmann and Klingel 2001; Monadjem et al. 2011) in southeastern Africa has indicated

98 that this grid size (3,600 m²) is adequate to account for the home range sizes of *Mastomys*
99 *natalensis*, where the majority of a population (80%) typically does not move more than 50 m from
100 their burrows, with average home range sizes of 200 to 4000 m². Agricultural fields typically have
101 home ranges at the lower end of this spectrum (Leirs et al. 1996a&b). One Sherman LFA live trap (8 x
102 9 x 23 cm, H.B. Sherman Traps Inc., Tallahassee, FL, U.S.A.) was placed at each trapping station and
103 all were set for three consecutive nights at intervals of four weeks. Traps were baited with peanut
104 butter mixed with maize bran/maize flour, set in the afternoon, and inspected in the morning.
105 During flooding, the traps were placed on top of dried grass mounds at the same grid locations.

106

107 **Processing of captured rodents**

108 All the captured animals were taken to the field laboratory and identified to species level according
109 to Kingdon (1984). On the first day of capture, all the captured animals were individually marked by
110 toe clipping. The animals were then released at the same station of capture. New animals captured
111 on subsequent days and during subsequent rounds of trapping were similarly marked, recorded and
112 released.

113

114 **Data collection and analysis**

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

$$119 \quad I_d = n \left[\frac{\sum x^2 - \sum x}{(\sum x)^2 - \sum x} \right]$$

120 where I_d = Morisita's index of dispersion

121 n = Sample size

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

127

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

131
$$\chi^2 = \frac{n \sum X^2}{N} - N$$

132 where χ^2 = chi-square distribution

133 n = total number of plots

134 X = number of individuals in a single plot

135 ΣX^2 = sum of all values of X^2

136 N = total number of individuals in all plots

137

138 Monthly trapping data of *M. natalensis* from each grid were used to produce a mean dispersion
139 index according to habitat (rice, fallow), season (wet, dry) and crop stage (transplanting, vegetative,
140 booting, maturity). In order to visualize the potential variation in dispersion, heat maps were
141 produced (Tableau 8.1, <http://www.tableausoftware.com/>) for each trapping grid using the total
142 number of *M. natalensis* captured per trap station and according to the same three parameters of
143 habitat, season and crop stage. Statistical analysis using ANOVA with Fisher LSD was performed in
144 XLSTAT version 2010.5.02 to compare the effects of habitat, season and crop stage using Morisita's
145 Dispersion Index as well as the mean number of *M. natalensis* captured per trapping station per
146 cropping session (Jul-10 to Dec-10, Jan-11 to Jun-11, Jul-11 to Dec-11 and Jan-12 to Jun-12).

147

148 **Results**

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

157

158 For *M. natalensis*, Morisita's Dispersion Index showed there were differences in dispersion patterns,
159 particularly between rice and fallow field habitats (Figure 1). Dispersion values of 1, or close to 1,
160 were calculated for the fallow land habitat, indicating rodents were generally randomly distributed.
161 Relatively higher dispersion values were calculated for the rice field habitat showing that rodents
162 were more aggregated, with the highest aggregation occurring when rice crops were at maturity
163 (Figure 1). A chi-square analysis to evaluate whether the Morisita values significantly departed from
164 random was interpreted on the basis of a critical value of 65.17 for $P = 0.05$ for $n - 1$ (48) degrees of
165 freedom. All chi-square values above 65.17, therefore, indicated the Morisita index was significantly
166 different from 1.0, where 1.0 equals a random distribution. All Morisita dispersion values above 1.5
167 were shown to be significantly different, thus indicating aggregated dispersion. Significant values
168 were more predominant in the rice habitat (55%, 27 out of 49 values), with few significant values in
169 fallow fields (16%, 8 out of 49 values). Mature rice crops were observed to have the highest Morisita
170 values (1.3 - 9.3), closely aligning with observations in Figure 1. Statistical analysis (ANOVA with
171 Fisher LSD) of dispersion index values showed that all three parameters of season, habitat and crop

172 stage had some limited but significant effects on rodent dispersion patterns (ANOVA $df = 15$, $F = 1.9$,
173 $P = 0.035$; Table 2), confirming that rodents in rice crops were relatively more aggregated than in
174 fallow fields, particularly at the time of maturity.

175

176 Heat maps showing the total number of *M. natalensis* captured at each trap station for each
177 monthly cropping session visually indicated the aggregated nature of rodent presence in rice fields at
178 different crop stages (Figure 2). Heat maps for fallow habitats (Figure 3) suggest more random
179 dispersion/limited aggregation with relatively higher numbers of rodents compared to the rice
180 habitat. However, both habitats generally follow the same patterns of rodent abundance according
181 to crop stage, with the vegetative stage showing the highest number of rodents in both habitats.
182 Generally, it can be observed in the heat maps that rodents were often aggregated around the field
183 edges, a factor that can be attributed to common geographic features of rice fields where raised
184 bunds provide harbourage and nesting sites for rodents, as was the case in our study design where
185 each grid was surrounded by a raised bund (Brown et al. 2001, 2006). Observations from these heat
186 maps are supported by statistical analysis (ANOVA with Fisher LSD) performed on the number of
187 rodents caught at each trap station over each of the four cropping cycles (Jul-10 to Dec-10, Jan-11 to
188 Jun-11, Jul-11 to Dec-11 and Jan-12 to Jun-12) which showed that there were significant effects in
189 the distribution of *M. natalensis* among crop stage, habitat and season (ANOVA $df = 15$, $F = 103.3$, P
190 < 0.0001 ; Table 2). The data show a particularly strong interaction between the vegetative stage and
191 dry season where the highest number of rodents was observed.

192

193 **Discussion**

194 The data collected within the present study revealed that two species of rodents were found in rice
195 fields whilst five species were captured in fallow land habitats relatively nearby (100 - 500 m).
196 *Mastomys natalensis* was clearly the most abundant species in both habitats. These findings are

197 consistent with those reported by Sluydts et al. (2009) in monoculture agriculture habitats and in
198 maize fields (Massawe et al. 2005). *Mastomys natalensis* has been recorded in high densities in
199 disturbed landscapes and agricultural fields throughout East African countries (Leirs et al. 1996a &
200 b). Under natural conditions its ecological requirements are essentially grasslands, but it is also
201 found in different kinds of habitats including savannahs, woodland, secondary growth, forest
202 clearings, houses and cultivated fields (Granjon et al. 2008). Due to its wide distribution across sub-
203 Saharan Africa, the species has broad habitat tolerances; a fact that makes it a pioneer species in the
204 colonization of disturbed habitats (Ferreira and Van Aarde 1996).

205

206 The aggregated distribution pattern of rodents in rice fields in the current study is consistent with
207 those presented by Leirs (1994) who reported that aggregated distribution patterns were a
208 characteristic of rodent communities, whilst uniform distribution patterns were rare and mainly
209 found in populations where there was strong competition among individuals. The more random
210 distribution of rodents in fallow land may be attributed to relatively larger home ranges (Leirs 1996a;
211 Monadjem et al. 2011), more weeds and generally higher plant diversity providing differential
212 coverage and food resources. Clustered patterns of distribution are reported as the most commonly
213 observed pattern in nature (Pielou 1977, Odum 1986 and Krebs 1999). According to Matteucci and
214 Colma (1982) the main reasons leading to a clustered pattern in a population are the behavioural
215 characteristics of the species and intra- and inter-specific relationships. Krebs (1999) argued that the
216 most important features of animal dispersion are the causal mechanisms and factors that promote
217 and maintain the pattern. In the present study it is arguable that the observed aggregation is partly
218 attributed to increased harbourage opportunities around the edge of fields due the presence of field
219 bunds that promote nesting and family group living and foraging relatively nearby the burrow
220 (Brown et al. 2001). Reports from other researchers show that members of group-living species may
221 be more spatially aggregated but densities may not differ from those of solitary species if social

222 groups are widely scattered across the habitat (Pielou 1977). However, in the present study area,
223 population densities in fallow land were significantly higher than those in rice fields and that such
224 densities were higher during dry than during wet seasons. Despite these seasonal and habitat
225 variations in population densities, aggregated and random dispersion were found across all crop
226 stages.

227

228 Our research provides strong evidence that *M. natalensis* is the most abundant and important
229 rodent pest species for rice production in Tanzania, evidence that widely concurs with other
230 researchers in southeastern Africa investigating rodent pests in staple crop production (Leirs et al.
231 1996a&b; Makundi and Massawe 2011). The clustered pattern of rodent dispersion in rice fields
232 observed in our study also concurs with studies in other parts of the world, such as southeastern
233 Asia, where different rodent species also tend to aggregate during rice field cropping (Brown et al.
234 2001, 2006). Continuous rice production through the use of irrigation can promote rodent pests,
235 potentially stretching farmer resources too thinly to adequately deal with the problem. Outcomes
236 from our study can help farmers by helping them to focus management actions where rodents tend
237 to aggregate. For example, reducing bund size can limit rodent burrowing and nesting opportunities,
238 and baiting with rodenticide within rodent burrows or trapping nearby can help farmers target their
239 limited resources more effectively.

240

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248

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332

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

Species	Rice fields, N (%)	Fallow land, N (%)	Total, N (%)	
<i>Mastomys natalensis</i>	1302 (99.85%)	2064 (99.33%)	3366 (99.53%)	335
<i>Rattus rattus</i>	2 (0.15%)	6 (0.29%)	8 (0.24%)	336
<i>Dasymys incomtus</i>	-	6 (0.29%)	6 (0.18%)	337
<i>Acomys spinosissimus</i>	-	1 (0.05%)	1 (0.03%)	338
<i>Grammomys dolichurus</i>	-	1 (0.05%)	1 (0.03%)	339
Total	1304 (100%)	2078 (100%)	3382 (100%)	340
Trap nights	7056	7056	14112	341
Trap success (%)	18.48	29.45	23.97	342
				343

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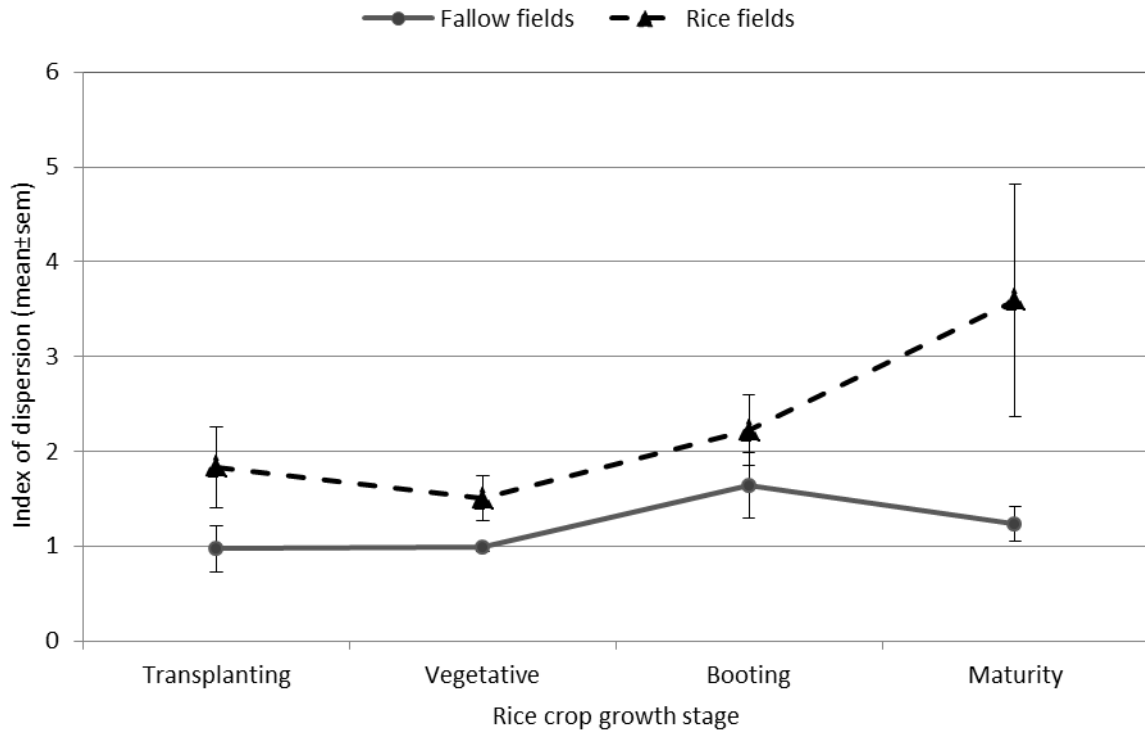
345
 346 Table 2: Analysis of Variance (ANOVA) using Morisita's Dispersion Index and the number of rodents
 347 captured per trapping grid according to parameters of habitat (rice, fallow), season (wet, dry) and
 348 crop stage (transplanting, vegetative, booting, maturity).

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}

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

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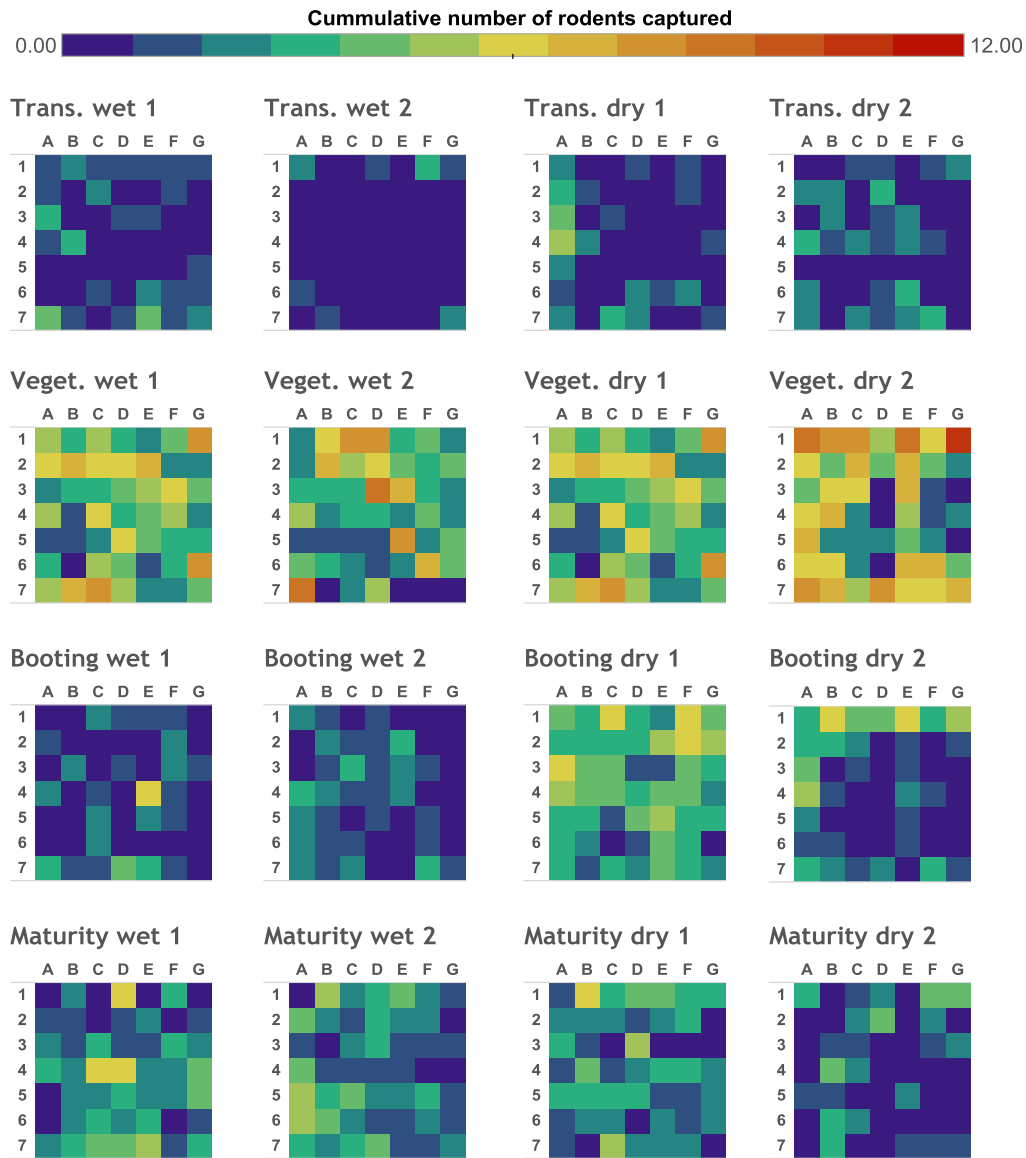
352 Figure 1. Morisita's index of dispersion where $Y = 1$ indicates a random dispersion, $Y < 1$ indicates a
353 uniform dispersion and $Y > 1$ indicates an aggregated dispersion. Data from wet and dry cropping
354 seasons are combined ($n = 4$).



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

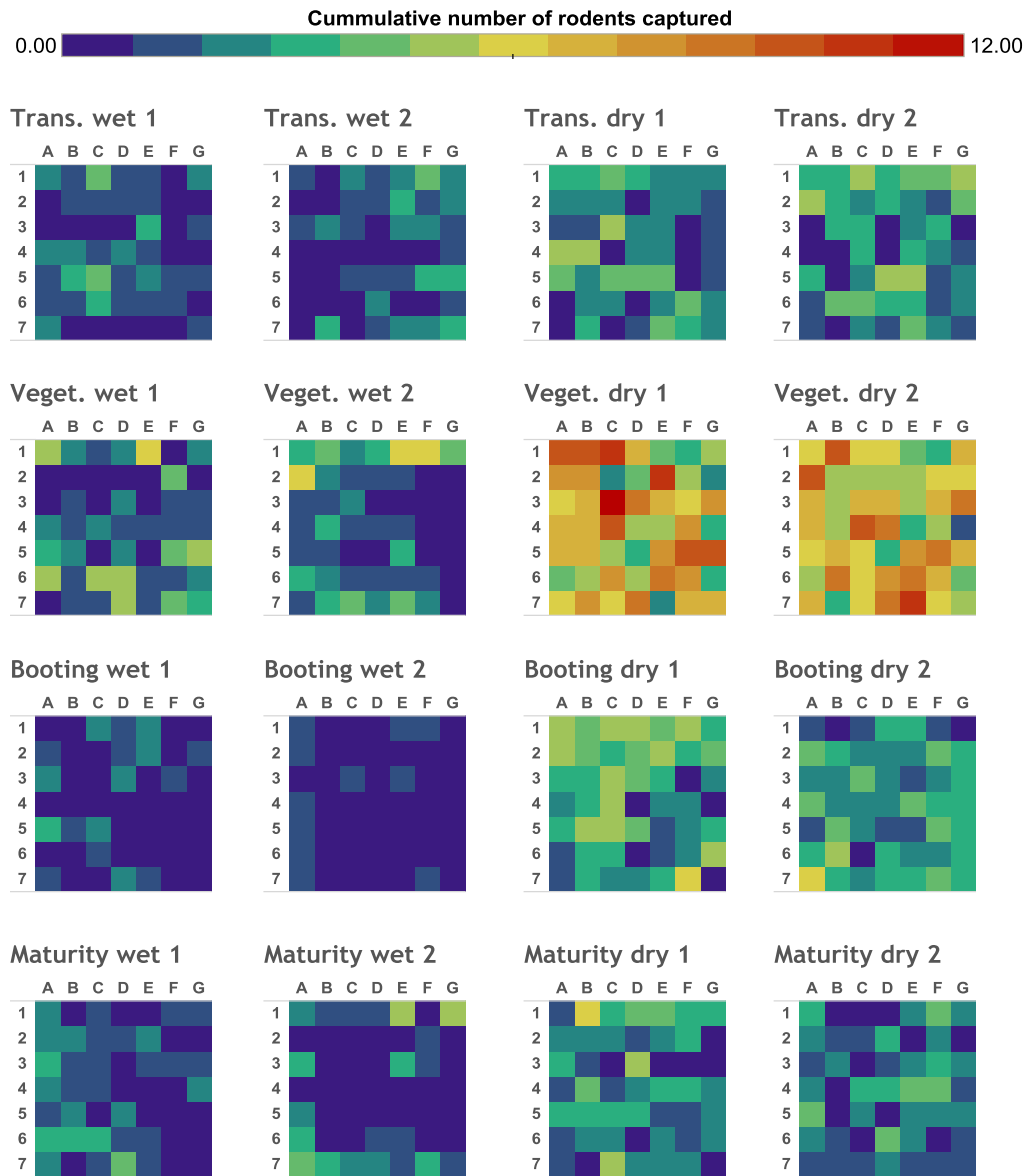


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364 Figure 3. Heat maps showing the total number of rodents captured per trap grid location for the two
365 fallow field grids at different crop growth stages. Wet season crops were grown from January to
366 June and dry season crops were grown from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



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