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Soil type influences population dynamics and survival of the Multimammate rat (\*\*Mastomys natalensis\*\*) in semi-arid areas in Tanzania

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| 1  | Soil type influences population dynamics and survival of the Multimammate rat (Mastomys  |
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| 2  | natalensis) in semi-arid areas in Tanzania   |
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#### 24 Abstract

Rodent population dynamics and survival in semi-arid areas of Tanzania were investigated in 25 fallow land and maize fields (land use) and two soil types (sandy loam and black clay). Capture-26 Mark-Release (CMR) methods with four 60 m  $\times$  60 m trapping grids, (two in maize and two in 27 fallow mosaic fields) were used. Mastomys natalensis comprised >94% of the total captures, and 28 the remaining six percent comprised 11 other small mammals species. The number of M. 29 30 natalensis was higher in sandy loam (7.82) than in black clay (2.89) soils and higher in fallow 31 land (40.25) than in maize fields (26.49). Highest rodent abundance was observed during the dry season (from June to August) of each year, while the lowest abundance was recorded during the 32 33 wet seasons (February to April) in both habitats. A significantly different proportion of reproductively active female *M. natalensis* was observed in sandy loam than in black clay soils. 34 It was observed that female *M. natalensis* are found to breed almost throughout the year. 35 36 Survival of *M. natalensis* differed between dry and wet seasons and was lower in clay soils during the wet season compared to sandy soils. However, there were no significant effects with 37 respect to interactions between soil type and land use, soil type and month, land use and month 38 and soil type, land use and month. Management strategies should therefore, be aimed at 39 emphasizing the importance of targeting March-May in order to interrupt reproduction and 40 41 young rearing.

#### 42 Key words

43 Soil types, land use, population dynamics, survival, *M. natalensis*, semi-arid, pest management
44 1. Introduction

45 Rodents are among the most serious threats to food production worldwide (Stenseth et 46 al., 2003) and major pests in cereal grains, causing both qualitative and quantitative damage

47 (Mdangi et al., 2013). Damage to stored maize in developing countries can reach up to 35 % and 48 even higher in certain cropping seasons during rodent outbreaks (Mdangi et al., 2013). Rodents 49 also play a role as reservoirs of human and animal diseases such as plague in Karatu, Mbulu and 50 Lushoto districts (Kilonzo et al., 2006), leptospirosis in various areas in Tanzania (Mgode et al., 51 2015) and can act as the vector of several zoonotic diseases including lassa fever, hemorrhagic 52 fever, lymphocytic choriomeningitis, leptospirosis, scrub typhus, toxoplasmosis, murine typhus 53 and Lyme disease (Katakweba et al., 2012; Meerburg et al., 2009).

Rodent outbreaks lead to severe food shortages, affecting highly vulnerable and food-54 insecure families (Singleton et al., 2010). In Tanzania, rodent outbreaks were recorded as early 55 56 in 1912 in the Rombo district in Kilimanjaro region (Mulungu et al., 2011), with the Multimammate rat (Mastomys natalensis Smith 1834) being the most encountered species in 57 most outbreaks across the country (Mulungu et al., 2011; Mwanjabe et al., 2002). Population 58 59 irruptions of this rodent species have caused yield losses of up to 48%, and during severe outbreaks damage can be even more than 80% at sowing and seedling stages in maize (Mulungu 60 et al., 2003; Mwanjabe et al., 2002). In the Isimani division of Iringa region, serious rodent 61 outbreaks and severe damage to maize crops have been occurring in the past 20 years (Tesha, P. 62 personal communication, 2015). Farmers in these areas (practicing multiple cropping of maize, 63 sunflower, vegetables and other leguminous crops) reported rodents as among major constraints 64 in crop production. It is believed by farmers that areas with black clay soil experience more 65 severe rodent outbreaks as compared to areas with other types of soils (Kipako, S. personal 66 communication, 2017). 67

68 Most studies revealed that rodent populations can be influenced by factors such as 69 vegetation covering (Meliyo et al., 2014), food availability (Busch et al., 2000; Mlyashimbi et 70 al., 2018), topography and slope gradient (Wilschut et al., 2012), soil and microclimate 71 (Mantilla-Contreras et al., 2011). Indeed, according to Wilschut et al. (2012), soil type has a significant influence on the spread and abundance of rodents. More specifically, the soil 72 microclimate, which is a function of soil type and micro-geographical features, is an important 73 parameter influencing the distribution of rodent burrows (Massawe et al., 2008). In addition, 74 climatic variables affecting soil properties may change the suitability of an area for rodent 75 76 species (Hoover et al., 1977). Thus, factors that influence burrow structure could ultimately determine the impact a burrow has on soil processes in an area (Laundré and Reynolds, 1993). 77 Soil type, temperature, moisture and organic matter determine the distribution, abundance and 78 79 diversity of rodent species (Massawe et al., 2008) and population growth of M. natalensis in agricultural farms (Meliyo et al., 2015). For example, in the Mediterranean region one of the 80 major factors affecting rodent burrowing is soil water content since it directly influences density, 81 82 cohesiveness, and shear strength of a given soil (Lövy, 2015). According to Verheye and de la Rosa (2005) reported that clay-rich soils typically shrink and harden during the long dry seasons. 83 In this study, the aim was to generate scientific knowledge on the influence of soil types 84 on the population dynamics and survival of *M. natalensis* in semi-arid areas of Tanzania where 85

farmers claimed that the population is higher in black clay soils during rodent outbreaks as compared to other soils. The study area has been reported to damage maize seedlings in farmers' fields ranging from 30-71% (Mlyashimbi et al. accepted). Understanding which soil influences the population dynamics of rodent pest species remains a key focus that provides vital insight into breeding and survival of rodent species that lead to demographic sub-populations that can erupt into an outbreak. This knowledge could also serve as a tool for planning and development of pest management strategies for rodent pest species.

#### 93 2. Materials and Methods

94 2.1. Study Area

This study was conducted in Isimani division in Iringa region, Tanzania. The area is 95 located between 35° 16' 13" m E and 35° 56' 56" m E and 8° 8' 14" m S and 7° 13' 68" m S. 96 covering at an elevation ranging from 1073 –1356 m above sea level (Fig. 1). The study area has 97 a single rainy season (unimodal rainfall pattern) from November through May with clear dry and 98 99 wet, and the mean annual precipitation ranges from 200 to 750 mm/year. It is characterised by 100 low erratic rainfall and periodic droughts giving it a semi-arid nature where precipitation is below potential evapotranspiration. Both seasons were subdivided on the basis of the rainfall and 101 102 evapotranspiration relationship into three sub seasons (Fig. 2).

The dry season can be divided into three sub-seasons namely: start dry, mid dry and end 103 dry sub-seasons. The start dry sub season is from May to July while, mid dry is from August to 104 105 September and end dry sub-season lasts from October to November. The wet season is divided into three sub seasons namely; start wet, mid wet and end wet sub seasons. The start wet is from 106 December to January while, mid wet is in February and end wet sub-season lasts from March to 107 April. The area is dominated by mosaic of fallow lands and agricultural fields with maize as a 108 major crop. Maize crop reaches physiological maturity between May and June and is harvested 109 starting in July to August. 110

111 2.2. Soil Types and its Characteristics

In the study sites, soil characteristics, colour and types have been described and mapped as shown in Table 1. The rodent population and survival in each grid was calculated and determined based on available data of soil properties. Soil properties have different effects on the

- species of resident small mammals (Laundre and Reynolds, 1993). Rodent trapping was carriedout in four grids with soil types ranging between sandy loam and black clay (Table 1).
- 117 2.3. Rodent Trapping

Capture-Mark-Release (CMR) methods were carried out from February 2015 to January 118 2018. Four 60 m x 60 m trapping grids of which first two in maize fields (one in clay and other 119 in sandy loamy soils) and the other two in fallow land in similar soils as maize fields. Grids were 120 121 laid and set in famers' fields and separated by at least >300 m. Each grid consisted of seven parallel lines, 10 m apart, and seven trapping stations per line 10 m apart (a total of 49 trapping 122 stations/grid). One Sherman LFA live trap (8  $\times$  9  $\times$  23 cm, H. B. Sherman Traps Inc., 123 Tallahassee, FL, USA) was placed at each trapping station and for three consecutive nights at 124 intervals of four weeks. Traps were baited with peanut butter mixed with maize bran/maize flour, 125 placed in the field during afternoon and inspected early in the morning. 126

127 2.4. Data Analysis

128 2.4.1. Small mammal species composition

The percentages of each species relative to others were calculated by dividing the number of captured individuals of each species by the total number of captured animals in a particular habitat, and multiplied by 100.

132 2.4.2. Population size estimation

The population size was estimated for each three-day trapping session using the M(h) estimator of the program CAPTURE. Further analysis was done using the SAS System (1997) for two ways ANOVA (habitats and soil types) and comparison of significant differences of mean values for effect of soil type, habitat and sampling period (month) was done by means separation test using the Tukey test method.

138 2.4.3. Survival

For the CMR analysis we decided to focus only on *M. natalensis*, since this was the most dominant species. The dataset consisted of 4311 captures of 1635 unique *M. natalensis* individuals. Survival and capture probability of *M. natalensis* were estimated used multi-event capture-recapture models (Pradel, 2005 in E-SURGE; Choquet et al., 2009).

143 2.4.4. Goodness of fit

144 A goodness of fit (GOF) test was carried out with the program U-CARE to evaluate potential confounding factors such as an excess of transience animals and trap-dependence 145 (Choquet et al., 2009; Pradel et al., 2003). The GOF test showed that there was an excess of 146 147 transient individuals in this dataset (see results), which are individuals that were captured only once during one secondary capture occasion. These individuals were (most likely) not re-148 encountered because they moved outside of the trapping grid, and not because they died shortly 149 150 after release.] Since we were interested in survival and capture probability of only resident animals, we decided to remove all transient animals (N = 755) from the dataset (Sluydts et al., 151 2007). Additionally, the GOF test showed that trapped individuals were trap happy, meaning that 152 the capture probability of individuals captured in the previous session was higher than those that 153 were not captured in the previous trap session (see results). We implemented the aware-unaware 154 method, described by Pradel and Sanz-Aguilar (2012) to correct for trap awareness. 155

156 2.4.5. Modelling

157 Survival and capture probability of *M. natalensis* were estimated using multi-event 158 capture-recapture models (Pradel, 2005 in E-SURGE; Choquet et al., 2009). Multi-event models 159 are an extension to classic capture-recapture models (Lebreton and Pradel, 2002) where the 160 number of states can be greater than the number of events. This allowed incorporating detection

heterogeneity into the models (Pradel and Sanz-Aguilar, 2012). As mentioned before, trapping was done using Pollock's closed robust design, where the population is assumed to be closed (i.e. no entry or exit of individuals into the population) within each trap session and open between trapping session (Pollock, 1982). However, it was hard to fix survival probability within each trap session to one. An initial set of models were run to test whether sex impacted on survival. The best model did not show survival varying by sex (Mulungu et al., 2015), and hence all further analysis combined the sexes.

We ran 20 models (Table 4) where survival was allowed to differ between the two habitats (fallow land and maize field), soil type (sandy or clay), among all four fields or no difference at all. Survival in each of these four main models was allowed to vary between seasons (dry and wet) and sub season (start dry/wet, mid dry/wet, end dry/wet sub-seasons) and with time dependence over the three years. Since variation in survival probability is the main focus of this work, we decided to use the same capture parameters for each model.

Similarly, the capture probability was allowed to differ between; (i) trap aware 174 (individuals that were trapped in the session before) and trap unaware individuals (those that 175 were not captured in previous trap session), to account for the trap dependence, (ii) between the 176 four different fields, since initial modelling showed that these models fitted the data more closely 177 (i.e. lower AIC). Models were ranked using Akaike's information criterion (AIC) (Burnham and 178 Anderson, 2004), where the model with the lowest AICc value was the best fit for the data. 179 Where  $\triangle$ AICc (the difference in AICc between models) for any two (or more) models with < 2.0, 180 they were both deemed to be equally good. 181

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183

#### 184 **3. Results**

185 3.1. Species composition

A total of 2501 rodent individuals and 44 shrews were captured in the study area. The rodent species captured were *M. natalensis, Lemniscomys rosalia, Gerbilliscus vicinus, Arvicanthis neumani, Thallomys paedulcus, Acomys wilsoni, Grammomys dolichurus, Pelomys fallax, Lemniscomys zebra, Rattus rattus, Mus* minutoides *and Aethomys hindei* (Table 2). *Mastomys natalensis* comprised the highest proportion (>94%) of small mammal species captured in the study area (Table 2).

192 3.2. Population Dynamics

193 Since *M. natalensis* constituted the species captured in the highest proportion in both land use (maize fields and fallow land) and sampling period (months), subsequent analyses were 194 carried out based on this species. There was a significant difference ( $F_{1, 95} = 30.67$ , p = 0.0001) 195 between soil types whereby sandy loam (mean = 43.17) had a higher number of *M. natalensis* 196 compared to black clay soil (mean = 28.58). Similarly, a significant difference was observed by 197 months ( $F_{11, 95} = 3.80$ , p = 0.0002) whereby the population of *M. natalensis* was higher from 198 June to August each year and lowest in March and April. Significant differences were recorded 199 between land use ( $F_{1,95} = 0.94$ , p = 0.0001) where population in fallow land (40.25) was higher 200 than in maize fields (26.49) (Fig. 3). 201

However, there were no significant effects with respect to interactions between soil type and land use ( $F_{1,95} = 0.43$ , p = 0.52), soil type and month ( $F_{11,95} = 0.90$ , p = 0.543), land use and month ( $F_{11,95} = 0.53$ , p = 0.879) and between soil type, land use and month ( $F_{11,95} = 0.19$ , p = 0.980) over the study period.

206

207 3.3. Breeding Patterns

Significant differences were observed between soil type ( $F_{1, 95} = 16.97$ , p = 0.0001) whereby sandy loam (mean = 7.93) had a higher number of reproductively active female *M*. *natalensis* compared to black clay soil (mean = 2.97).

Significant differences were observed between land use ( $F_{1, 95} = 0.01$ , p = 0.0001) whereby fallow land (mean = 10.99) had a higher number of reproductively active female *M*. *natalensis* compared to maize fields (mean = 7.79). Similarly, a significant difference ( $F_{11, 95} =$ 0.50, p = 0.0001) was observed across month, where more reproductively active female individuals were observed from February to June and the least from September to December each year (Fig. 4).

No significant difference was observed on the interactions of soil type and month ( $F_{11, 95}$ = 2.37, p = 0.17), land use and month ( $F_{11, 95}$  = 1.95, p = 0.42), between land use ( $F_{1, 95}$  = 0.56, p = 0.4581) and among the interaction of soil type and land use ( $F_{1, 95}$  = 0.50, p = 0.48) and between soil type, land use and month ( $F_{11, 95}$  = 0.26, p = 0.99).

221 3.4. Survival of *M. natalensis* 

222 3.4.1. Goodness of fit

The GOF test showed strong deviation against the assumption on transience (TEST 3.SR one sided test for transience:  $\chi^2 = 239$ , df =105, p < 0.0001) and trap- dependence (TEST 2.CT,  $\chi^2 = 452$  df =105, p < 0.001, animals became trap-happy). There were 46% of *M. natalensis* trapped only once and were subsequently deleted from the dataset. Removing the transience individuals removed the transience effect (TEST 3.SR one sided test for transience  $\chi^2 = 239$ , df = 98, p = 1); however, the deviation against trap-dependence remained in the dataset (TEST 2.CT,  $\chi^2 = 264$  df =105, p < 0.001), i.e. animals became trap-happy after being trapped. We corrected

for this trap-dependence by creating two new states: trap aware (previously trapped) and trap
unaware (not trapped in previous session) both with a different capture probability as described
by Pradel and Sanz-Aguilar, (2012).

233 3.4.2. Modelling

From all the 20 models we ran, the four highest ranked models (with the lowest AICc) all 234 supported variance in survival probability between sub-seasons which varied over the three years 235 236 (Table 3). The next four models had the same time dependence over the two different seasons (Table 3). This suggests that survival probability differed between the seasons and between the 237 three years. The model that best fitted our data (with the lowest AICc value, Table 3) was the 238 239 model where survival probability differed between soil types (black clay and sandy loam) and varied between sub-seasons over the three years. We found no support for differences in survival 240 probability between the two land use types, or between the four fields separately. Survival 241 242 probability of *M. natalensis* in the wet season was always higher in sandy soils compared to the clay soils. 243

In the first wet season in 2015 the survival probabilities were the same pattern as in the 244 second wet season as well as in the third wet season in 2017 (Table 4). However, survival 245 probability in the last wet season was similar between the two soil types in 2017, but the standard 246 error in the clay soil was extremely high. Within the dry seasons, survival probability differed 247 between the two soil types, but there was no clear pattern as within the wet seasons. At the start 248 of the first dry season (2015) survival probability between the two soil types were similar but 249 switched during the middle and end of the first dry season (Table 4). At the start and middle of 250 the second dry season (2016) survival probability was similar for both soil types but survival 251 decreased at the end in the sandy soil. In the last dry season, survival probability in sandy soils 252

- was higher at the start than clay soils, but lower in the middle (Table 4). At the end of the last dryseason survival was similar between the fields (Table 4).
- 255 3.4.3. Recapture estimates

Each model was run with the same recapture structure. From the final model, it was found that trap aware individuals (those were caught at time -1) had a higher capture rate than trap unaware individuals, but it differed between the four fields (fallow and sandy field: aware =  $0.40 \pm 0.01$ , unaware =  $0.25 \pm 0.01$ ; maize and sandy: aware =  $0.41 \pm 0.02$ , unaware =  $0.25 \pm$ 0.01; fallow and clay: aware =  $0.51 \pm 0.01$ , unaware =  $0.34 \pm 0.01$  and maize clay: aware =  $0.36 \pm 0.02$ , unaware =  $0.21 \pm 0.02$ ).

Based on the best model, the survival of *M. natalensis* was significantly different between land use and time. However, the survival of *M. natalensis* was not significantly different between maize field (average = 0.68) and fallow land (average survival = 0.63) over time, and between sandy loam soil (average survival = 0.65) and black clay soil (average survival = 0.64).

#### 266 **4. Discussion**

In the current study area, the rodent populations captured were dominated by Mastomys 267 natalensis. This dominance is consistent with previous studies by Mulungu et al. (2014); 268 Mulungu et al. (2013) and Vibe-Petersen et al. (2006). Results in the current study revealed that 269 population density was higher in fallow land compared to maize fields, indicating that fallow 270 land encourages more rodents to reside in the relatively densely vegetation covered sites 271 (Kluever et al., 2016). Similar results had been reported by Leirs et al. (1997), who studied 272 spatial dynamics and breeding patterns of *M. natalensis* and showed higher densities in fallow 273 land compared to maize field. It was also reported that M. natalensis were most commonly found 274 in areas or sites with many bushes or tall grasses (Mulungu et al., 2013). 275

276 The results also showed that the population was higher in fallow land compared to maize fields. This is similar to the findings by Mulungu et al. (2013) in bimodal rainfall patterns in 277 irrigated rice where it was observed that population was higher in the fallow lands compared 278 with rice field. The current study area recorded extended breeding patterns of *M. natalensis* from 279 January to October with highest peaks of reproductive activity occurring in April and May. 280 During this time, rainfall seemed to play a strong influence on the reproductive activity triggered 281 282 by secondary compounds obtained from young vegetative materials when the animals have consumed. It was reported that green plant food (vegetative materials) induces breeding in M. 283 natalensis due to the presence of a secondary plant compound 6-methoxy-2-benzoxazolinone (6-284 285 MBOA) which originates in young sprouting plants or grasses with a labile precursor formed enzymatically from a glucoside when plant tissues are crushed (Klun and Robinson, 1969). 286 According to Makundi et al. (2007) reproductive activity in tropical rodents has conventionally 287 288 been related to rainfall. Other studies in Africa have also linked reproduction of rodents with rainfall (Achigan et al., 2003; Workneh, 2003). Results from the current study indicated that 289 reproductively active and inactive female *M. natalensis* were present throughout the year. This 290 was probably due to the revealed observation on Normalised Difference Vegetation Index 291 (NDVI) from the same location of the study (semi-arid areas) that reported to predict rodent 292 abundance and compares better with field measured rodent abundance than the rainfall predicted 293 abundance (Chidodo, 2017). 294

The current study indicated that the best model had soil type in it, meaning that there was a difference in survival between the soil types, but not the land use. It seems that survival in clay soil types was always lower than in sandy loam, but only in the wet season. This could be due soil cracks that inhibit rodent movement or that rain water does not flow through clay soils as

easily when compared to sandy soils that enable movement and easy burrowing for rodents. In the dry season it is unclear. Previous studies have indicated that the rates of survival and recruitment are necessary components of models that describe and explore the changes of animal population size (Mulungu et al., 2015). According to Mlyashimbi et al. (2018) observed that *M. natalensis* in semi-arid areas have a longer period of reproductive activity compared with other locations in Tanzania with bimodal rainfall patterns and single cropping season (Mulungu, 2017).

306 Our results also showed that the population of *M. natalensis* in the sandy loam was significantly higher than in black clay soils. The reason for lower population abundance of M. 307 308 natalensis in black clay soils was probably due to wide and deep cracks formed during extensive dry period that restricted movement and burrowing for this species and thus, providing plentiful 309 shelter opportunities and the potential to support high densities of native predators such as bush 310 311 cats (Leptailurus serval) and snakes which predate on rodents. Similar observation by Massawe et al. (2008) reported that rodents prefer loam-textured soils with a high percentage of sand, 312 which are probably better than clay soils for burrowing and nesting, particularly in the rainy 313 season (Massawe et al., 2008). Survival rates of M. natalensis were higher in the rice fields 314 compared with fallow land (Mulungu et al., 2013). In the other hand, Pavey at al. (2014) 315 observed that *Pseudomys australis* are favoured by clay soils when form wide and deep cracks 316 over an extensive area which provide plentiful shelter opportunities and result high densities. 317

In conclusion, *Mastomys natalensis* is the most abundant rodent pest species in the study area and its population abundance varied with soil type and season/time of the year. The highest population peak was observed during the dry season (from June to October) and lowest during the wet season (in February to April). Female *M. natalensis* were reproductively active

throughout the year, although reproduction reaches the highest level in March to May, which corresponds to the long rainfall, suggesting reproduction is highly influenced by rainfall. Survival of *M. natalensis* was higher during the wet season of each year in sandy loam soil than in black clay soil. However, no significant difference was recorded between survival rates of *M. natalensis* in land use with time. Management strategies should, therefore, be aimed at emphasizing the importance of targeting the March-May in order to interrupt reproduction and young rearing.

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ALA ALA

| Coordinates |         | Field Soil texture |            | Soil colour Soil drainage |          | Soil crack |  |
|-------------|---------|--------------------|------------|---------------------------|----------|------------|--|
| 803822      | 9157884 | Fallow 1           | Sandy loam | Brown                     | Moderate | No         |  |
| 805626      | 9157085 | Maize 1            | Sandy loam | Red                       | Well     | Yes        |  |
| 803852      | 9165911 | Fallow 2           | Black Clay | Black                     | Moderate | Yes        |  |
| 805452      | 9168620 | Maize 2            | Black Clay | Black                     | Poor     | Yes        |  |

**Table 1.** Description of the soil types and their characteristics in the trapping sites of Isimani

 division, Iringa region, Tanzania

Source: Chidodo, 2017

| Table 2. Species | composition | of sma | ll mammals | s in maiz | e fields | and | fallow | land in | the study |
|------------------|-------------|--------|------------|-----------|----------|-----|--------|---------|-----------|
|                  |             |        |            |           |          |     |        |         |           |

area

|      |                                      | Field types    |               |               |               |
|------|--------------------------------------|----------------|---------------|---------------|---------------|
| S/no | Species trapped                      | Fallow land 1  | Maize field 1 | Fallow land 2 | Maize field 2 |
|      |                                      | Number         | Number        | Number        | Number        |
| 1    | Mastomys natalensis Smith 1834       | 1 215 (94.40%) | 410 (96.93%)  | 620 (94.66%)  | 172 (95.56%)  |
| 2    | Acomys wilsoni, Thomas, 1832         | 0 (0.00%)      | 1 (0.24%)     | 0 (0.00%)     | 2 (1.11%)     |
| 3    | Arvicanthis neumanni, Matschie 1894  | 38 (2.95%)     | 3 (1.71%)     | 11 (1.68%)    | 0 (0.00%)     |
| 4    | Crocidura spp, Wagler, 1832          | 12 (0.93%)     | 6 (1.42%)     | 24 (3.66%)    | 3 (1.67%)     |
| 5    | Gerbilliscus vicinus, Peter 1878     | 9 (0.70%)      | 1 (0.24%)     | 0 (0.00%)     | 0 (0.00%)     |
| 6    | Grammomys dolichurus, Smuts, 1832    | 3 (0.23%)      | 0 (0.00%)     | 0 (0.00%)     | 0 (0.00%)     |
| 7    | Lemniscomys rosalia, Thomas, 1904    | 3 (0.23%)      | 1 (0.24%)     | 0 (0.00%)     | 2 (1.11%)     |
| 8    | Lemniscomys zebra, Trouessart, 1881  | 2 (0.16%)      | 0 (0.00%)     | 0 (0.00%)     | 0 (0.00%)     |
| 9    | Mus minutoides, A Smith, 1834        | 0 (0.00%)      | 1 (0.24%)     | 0 (0.00%)     | 0 (0.00%)     |
| 10   | Rattus rattus, Linnaeus, 1758        | 0 (0.00%)      | 0 (0.00%)     | 0 (0.00%)     | 1 (0.56%)     |
| 11   | Thallomys paedulcus, Surdevall, 1846 | 1 (0.08%)      | 0 (0.00%)     | 0 (0.00%)     | 0 (0.00%)     |
| 12   | Pelomys fallax, Peters, 1852         | 2 (0.16%)      | 0 (0.00%)     | 0 (0.00%)     | 0 (0.00%)     |
| 13   | Aethomys hindei, Thomas, 1902        | 2 (0.16%)      | 0 (0.00%)     | 0 (0.00%)     | 0 (0.00%)     |
|      | Total                                | 1 287 (100%)   | 423 (100%)    | 655 (100%)    | 180 (100%)    |

128 128

| Model | Suvival                     | Np | Deviance | AICc     | ΔAICc  |
|-------|-----------------------------|----|----------|----------|--------|
| 1     | Sub season x year x soil    | 41 | 11755.54 | 11838.54 | 0      |
| 2     | Sub season x year           | 23 | 11798.28 | 11844.6  | 6.06   |
| 3     | Sub season x year x habitat | 41 | 11767.91 | 11850.91 | 12.37  |
| 4     | Habitat                     |    |          |          |        |
|       | Sub season x year x field   | 76 | 11704.06 | 11859.49 | 20.95  |
| 5     | Season x year x soil        | 19 | 11837.98 | 11876.2  | 37.66  |
| 6     | Season x year x habitat     | 19 | 11839.26 | 11877.48 | 38.94  |
| 7     | Season x year x field       | 33 | 11811.79 | 11878.44 | 39.90  |
| 8     | Season x year               | 12 | 11857.21 | 11881.3  | 42.76  |
| 9     | Season x soil               | 9  | 11864.8  | 11882.85 | 4431   |
| 10    | Season x field              | 13 | 11857.32 | 11883.43 | 44.89  |
| 11    | Sub season x field          | 29 | 11831.07 | 11889.57 | 51.03  |
| 12    | Sub season x soil           | 17 | 11856.64 | 11890.82 | 52.28  |
| 13    | Season x Habitat            | 9  | 11878.93 | 11896.99 | 58.45  |
| 14    | Season                      | 7  | 11884.32 | 11898.36 | 59.82  |
| 15    | Sub season x habitat        | 17 | 11867.14 | 11901.32 | 62.78  |
| 16    | Sub season                  | 11 | 11879.94 | 11902.02 | 63.48  |
| 17    | Soil                        | 7  | 11973.41 | 11987.45 | 148.91 |
| 18    | Habitat                     | 7  | 11973.48 | 11987.51 | 148.97 |
| 19    | Field                       | 9  | 11970.14 | 11988.19 | 149.65 |
| 20    | Cte                         | 6  | 11976.39 | 11988.41 | 149.87 |

**Table 3.** Model selection results of the 20 models. Models are ranked on the AICc from low to

high

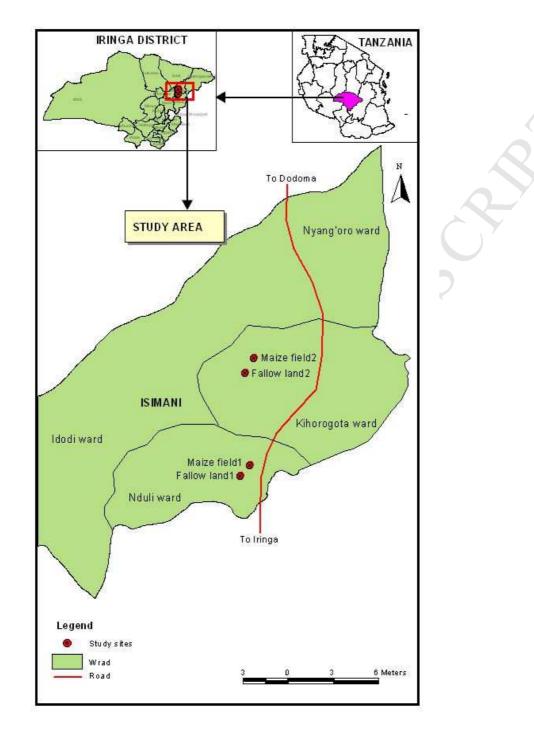
**Note:** The best model (with the lowest AICc) is shown in bold. For each model, the number of parameters (Np), deviance and AICc are given.  $\Delta$ AICc is the difference in AICc between the current model and the top ranked one. For each model, we used the same capture probability, which differed between the four fields and between trap aware and unaware individuals.

| Year | Season | Soil type       |                 |  |  |
|------|--------|-----------------|-----------------|--|--|
|      |        | Sandy soil      | Clay soil       |  |  |
| 2015 | MW     | $0.89\pm0.09$   | 0.79 ± 0.13     |  |  |
|      | MD     | $0.69\pm0.04$   | $0.81 \pm 0.05$ |  |  |
|      | EW     | $0.62\pm0.06$   | $0.42\pm0.09$   |  |  |
|      | ED     | $0.72\pm0.05$   | $0.53\pm0.06$   |  |  |
|      | SD     | 0.79 ± 0.03     | $0.83\pm0.04$   |  |  |
| 2016 | SW     | $0.56\pm0.06$   | $0.38 \pm 0.10$ |  |  |
|      | SD     | $0.79\pm0.04$   | $0.81\pm0.05$   |  |  |
|      | MW     | $0.88 \pm 0.04$ | $0.88\pm0.04$   |  |  |
|      | MD     | $0.88\pm0.04$   | $0.88\pm0.04$   |  |  |
|      | EW     | $0.78\pm0.06$   | $0.71\pm0.12$   |  |  |
|      | ED     | $0.75\pm0.04$   | $0.91\pm0.04$   |  |  |
| 2017 | SW     | $0.63\pm0.16$   | $0.69\pm0.49$   |  |  |
|      | SD     | $0.87\pm0.04$   | $0.71\pm0.09$   |  |  |
|      | MW     | $0.39\pm0.08$   | $0.36\pm0.12$   |  |  |
|      | MD     | $0.65\pm0.06$   | $0.88\pm0.10$   |  |  |
|      | EW     | $0.51\pm0.07$   | $0.26\pm0.09$   |  |  |
|      | ED     | $0.77\pm0.07$   | $0.77\pm0.16$   |  |  |

**Table 4:** Survival probabilities (mean  $\pm$  standard error) of Mastomys natalensis in differentseasons and soil types

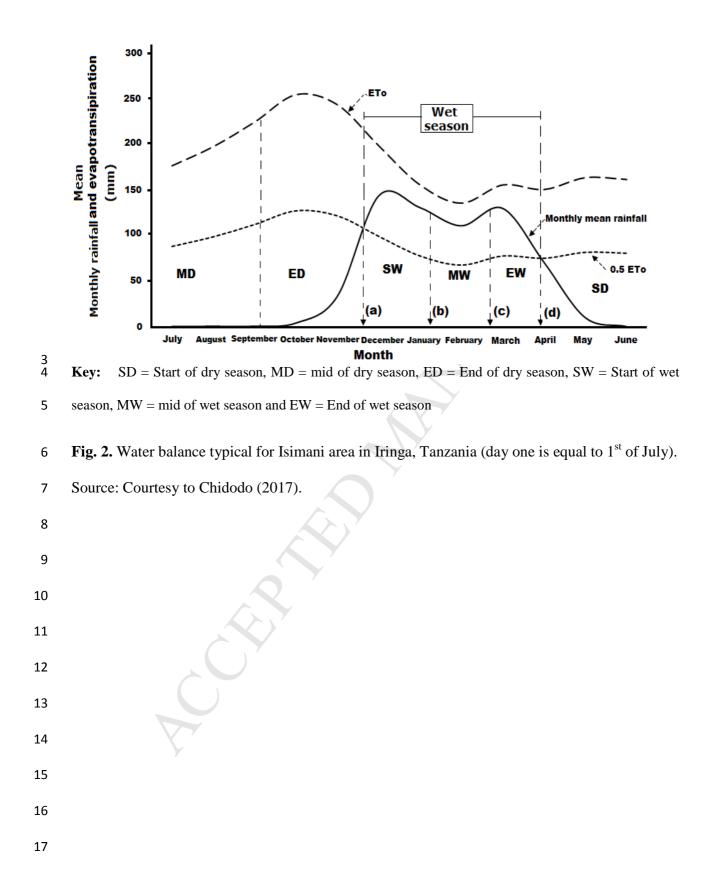
Key: SD = Start of dry season, MD = mid of dry season, ED = End of dry season, SW =

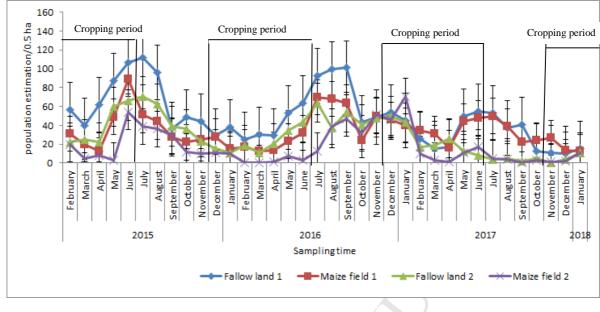
Start of wet season, MW = mid of wet season and EW = End of wet season



1

2 Fig. 1. Location of study sites in Isimani division, Iringa region Tanzania







19 Fig. 3. Population abundance/0.5ha of *M. natalensis* captured in two land uses in the study area

- 20 of Isimani division, Tanzania

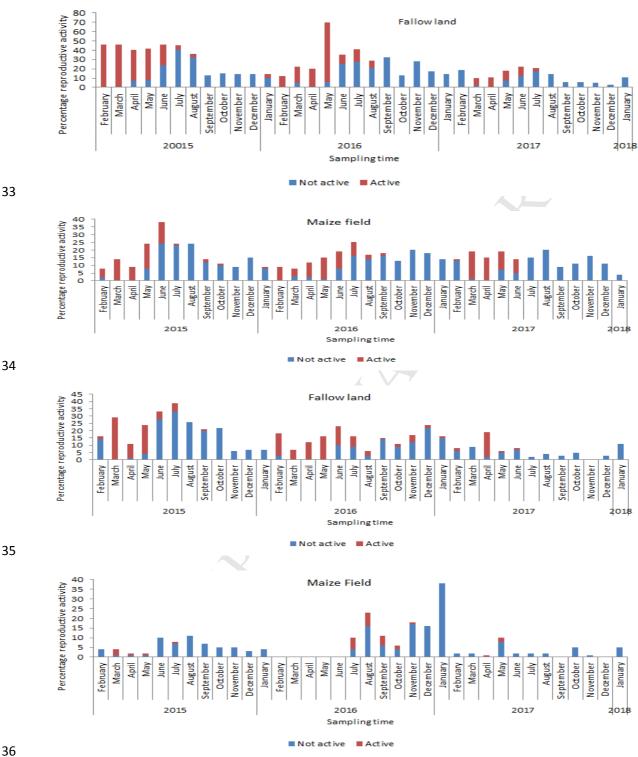


Fig. 4. Percentage reproductive activity of female M. natalensis captured in fallow land and 37 maize fields in the study area of Isimani division, Tanzania from January 2015 to January 2018. 38

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