Population and breeding patterns of the pest rodent : mastomys natalensis in a maize dominated agroecosystem in Lake Victoria crescent zone, Eastern Uganda

Reference:

Mayamba Alex, Byamungu Robert Modest, Leirs Herwig, Moses Isabirye, Makundi Rhodes H., Kimaro Didas N., Massawe Apia W., Kifumba David, Nakiyemba Alice, Mdangi Mshaka E., ...- Population and breeding patterns of the pest rodent : mastomys natalensis in a maize dominated agroecosystem in Lake Victoria crescent zone, Eastern Uganda
African zoology / Zoological Society of Southern Africa - ISSN 1562-7020 - 56:1(2021), p. 76-84
Full text (Publisher's DOI): https://doi.org/10.1080/15627020.2021.1879675
To cite this reference: https://hdl.handle.net/10067/1777600151162165141

Population and breeding patterns of the pest rodent: *Mastomys natalensis* in a maize dominated agroecosystem in Lake Victoria crescent zone, Eastern Uganda

Alex Mayamba[1,2]*, Robert Modest Byamungu[2], Herwig Leirs[3], Isabirye Moses[1], Rhodes H Makundi[4], Didas N Kimaro[5], Apia W Massawe[4], David Kifumba[1], Alice Nakiyemba[1], Mshaka E Mdangi[6], Brian E Isabirye[7] and Loth S Mulungu[4]

[1] *DEPARTMENT, Busitema University, Tororo, Uganda*
[2] *Department of Wildlife Management, Sokoine University of Agriculture, Morogoro, Tanzania*
[3] *Evolutionary Ecology Group, Universiteit Antwerpen, Antwerpen, Belgium*
[4] *Pest Management Centre, Sokoine University of Agriculture, Morogoro, Tanzania*
[5] *Department of Engineering Sciences and Technology, Sokoine University of Agriculture, Morogoro, Tanzania*
[6] *Ministry of Agriculture Training Institute (MATI) Ilonga, Kilosa, Tanzania*
[7] *International Center of Insect Physiology and Ecology (ICIPE), Kasarani, Nairobi, Kenya *Correspondence: alexmayamba@gmail.com*

Multimammate mice (*Mastomys natalensis*) are a key rodent pest species to cereal crop production in Sub-Saharan Africa. This study aimed at generating information on the population fluctuation and breeding patterns of *M. natalensis* in a maize dominated agro-ecosystem in the Mayuge district, Eastern Uganda. The area is characterised by a bimodal rainfall pattern with rains in the periods March to May and August to November. A Capture–Mark–Recapture study was established in cultivated and fallow field habitats with, in each habitat, two plots of 60 m by 60 m with 49 evenly spaced trapping points. Trapping was conducted monthly for three consecutive nights, and the study extended from January 2016 to June 2018. A Generalised Linear Mixed Model analysis showed higher population density in fallow land compared to cultivated fields, with densities highest in the second wet season and lowest in first dry season <please include stats like next sentence>. The percentage breeding females differed significantly across months ($\chi^2 = 27.05$, df = 11, $p = 0.003$) and seasons ($\chi^2 = 17.64$, $p = 0.0003$). Breeding females occurred throughout all the months of trapping, but with significantly higher percentages in the months of March to July (i.e. first wet season extending to second dry season) and generally lowest in the first dry months (i.e. January and February in 2017, and February 2018). The results of this study have important consequences for the timing of control efforts, and recommends that control should be initiated during the dry seasons prior to wet seasons to counteract potential damaging population build up in later wet seasons when crop planting is expected.

Keywords: habitat type, multimammate mouse, population abundance, seasons, sexual activity

Introduction

Rodents of the family Muridae are gaining importance as agricultural pests due to the conversion of wild areas into intensive agricultural land (Makundi et al. 2007; Swanepoel et al. 2017; Mlyashimbi et al. 2018). In Uganda, several small rodent species including *Mus triton, Aethomys hindei*, *Lemniscomys zebra*, *Lophuromys sikapusi* and *Graphiurus murinus* among others, are documented in and around crop fields and forests (Basuta and Kasene 1987; Amatre et al. 2009). *Mastomys natalensis* (Smith, 1834) is, however, the dominant species associated with agricultural areas (Mayamba et al. 2019). Elsewhere in the region, this species has been observed to dominate agricultural fields, and has received considerable research attention (Leirs 1992; Mulungu et al. 2013; Makundi et al. 2015) due to its economic importance. It is described as one of the key rodent pest species of significant agricultural importance and also a vector of endemic diseases such as plague (Mulungu et al. 2011a; Bonwitt et al. 2017). *Mastomys natalensis* is characterised by high reproductive rates, active movement patterns and the ability to easily colonise new areas (Leirs 1992; Makundi et al. 2006, Massawe et al. 2006). *Mastomys natalensis* has also been found to inhabit different kinds of habitats (Mulungu et al. 2011b), including savannahs, woodland, secondary growth, forest clearings, houses and cultivated fields (Kingdon 1974, Happold 2013, Monadjem et al. 2015). Accordingly, it is a pioneer species in the colonization of disturbed (e.g. agriculture) habitats (Massawe et al. 2003). In many Sub-Saharan Africa localities the presence of this species may cause substantial crop damage (Fiedler 1988), and occasional outbreaks may result in significant harvest losses, leading to food insecurity (Leirs 1992; Leirs et al. 1996; Mwanjabe and Leirs 1997; Mulungu 2003). The amount and duration of rainfall have been linked to this species' population dynamics, with the primary productivity of nutritious seeds and vegetation cover influencing abundance (Delany 1975; Leirs et al. 1994).

Limited information exists on the basic ecology of the above-mentioned species in Uganda and thus management efforts cannot be appropriately planned (Mayamba et al. 2019; Makundi et al. 2007). While considerable information exists on the ecology of *M. natalensis* in neighbouring Tanzania, several ecological factors are effectively different between these two countries, including the farming systems and weather patterns; attributes that have been shown to significantly influence the population and breeding patterns of this pest species (Massawe et al. 2006; Mulungu et al. 2015). Understanding the relationship between rainfall patterns and habitats, and rodent population abundance and breeding cycles in a Ugandan agroecosystem will aid selection and timing of appropriate management strategies for more effective rodent control in a given locality (Mulungu et al. 2013). This study therefore set out to generate information on how *M. natalensis* population density and breeding patterns fluctuate over the year, with rainfall seasons and across maize/fallow habitats in a typical Ugandan agroecosystem characterised by a bimodal rainfall pattern.

Materials and methods

Description of study area

This study was conducted at Kigulu village (6°16′ S, 37°31′ E) in the Kigandalo subcounty, Mayuge district, Eastern Uganda (Figure 1). Rains are received from March to end-May (first wet season) and August to end-November (second wet season). Farmers in the study area produce maize and other annual crops twice per year. The first cropping season is from March to June, and the second is from September to December. Land preparation is done in the dry months of January/February and July/August. The crops are in the vegetative stage in April and October, and reach physiological maturity in May and November. Farmers harvest in June/July and December/January for the first and second cropping season respectively.

Rodent field trapping procedure

A Capture–Mark–Recapture study was done from January 2016 to June 2018. Four 60 × 60 m permanent trapping plots (two cultivated fields initially with a maize crop, and two fallow fields) were selected (based on availability and willingness of the landowner to allow this study in that AFRICA Uganda *Lake Victoria* Mayuge district Kigula parish Kigula parish Kigandalo subcounty Kigandalo subcounty Mayuge district Mayuge district U G A N D A 0 5 10 km See enlarged area 0°18′ N 33°30′ E **Figure 1:** Map showing the location of the study site, Kigandalo subcounty, Mayuge district Eastern Uganda *African Zoology* 2021: 1–9 3 particular area). The fallow fields selected were previously under annual crop production, but were left uncultivated for more than two years without a crop. They mostly comprised of annual grassy weeds and approximately 30% tick berry (*Lantana camara*). Both cultivated fields and fallow fields were characterised by a diversity of plant species. The four trapping areas (two replicates of each kind of field) were separated by a minimum distance of 500 m, to limit rodent movements from one grid to another (Borremans et al. 2014). Due to witch weed (*Striga* sp.) invasion in the area, farmers practice crop rotation and thus in the second year of the study cassava was introduced in the cultivated fields and intercropped with maize and common beans. Each field consisted of seven parallel lines, 10 m apart, and seven trapping stations per line, also 10 m apart (giving a total of 49 trapping stations per field). One Sherman LFA live trap (8 × 9 × 23 cm; HB Sherman Traps Inc., Tallahassee, USA) was placed at each trapping station, and all were set for three consecutive nights per month at intervals of four weeks. These live traps were baited with peanut butter mixed with maize bran/maize flour, and were opened in the afternoon and inspected / closed in the morning.

Examination of captured animals

All the captured animals were field examined and identified to species level. On the first day of capture, all the captured animals were individually marked by toe clipping and wounds sterilised with alcohol. Their body weight, trapping station, sex and reproductive status were recorded. For the reproductive conditions, we noted for females either a perforated or closed vagina, whether nipples were swollen (= lactating), or whether pregnant; for males, whether the testes had a scrotal or non-scrotal position. The animals were then released at the same point of capture. In subsequent trappings, newly trapped animals were toe clipped, while the already toe clipped animals (recaptures) were examined for weight and reproductive status.

Data analysis

Species composition
The relative abundance for each of the species captured was calculated by dividing the number of captured individuals of each species by the total number of all the captured animals in a particular habitat, and multiplying by 100.

Population dynamics
Abundance of *Mastomys natalensis* was estimated each month in the program CAPTURE, for a closed population (White et al. 1982). Throughout, we used the M(h) jackknife estimator, which allows for individual heterogeneity in trapping probability, since this has proven to be an overall robust estimator and was also used in earlier studies of this rodent species (Leirs et al. 1997<a or b?>; Davis et al. 2003). Population abundance data were subjected to a Generalised Linear Mixed Model with the Penalised Quasi Likelihood (PQL) method, package 'glmmPQL' (Karim and Zeger 1992; Knudson 2018) using R software (R Core Team 2013), in order to assess changes in *M. natalensis* population abundance across habitat and season. We applied a Poisson distribution family abundance, with seasons (first dry season, second dry season, first wet season, second wet season), habitats (cultivated and fallow), months of trapping, and years as fixed effects factors. Descriptive bar graphs

were plotted showing the trends in population abundance variation across the months in the different years of trapping. A linear regression was performed using annual seasonal data for years 1 and 2 only to establish the relationship between mean annual rainfall and mean annual population abundance of *M. natalensis* as earlier studies have shown its significance in regulating rodent abundance (Leirs et al. 1996).

Sex ratio
The sex ratio of *M. natalensis* was computed as the percentage of males out of the total trapped animals. The percentage data were arcsine transformed to normalise their distribution before they were subjected to repeated measures analysis of variance.

Sexual activity
Mastomys natalensis breeding patterns were determined by establishing the monthly proportion of reproductively active and non-active female mice in both habitats. The definition of sexual activity followed that of Leirs (1995) who defined sexual activity as a physiological condition and not as a typical behaviour. Thus, females were considered to be sexually active when the vagina was perforated, when their nipples were swollen on account of lactation, or when they were pregnant. A Kruskal-Wallis test with a Chi-square distribution fit for percentage distribution data was done to establish the effect of years, months, habitat and seasons on percentage of sexually active females of *M. natalensis* as the response variable. The *post hoc* median separation was done with a Mann–Whitney test.

Recruitment
Mastomys natalensis recruitment per trapping session was counted as the number of new animals trapped for the first time relative to the total number of trapped individuals in that session. We used a Kruskal–Wallis test for the non-normally distributed data, with a Chi-square test appropriate for percentage data. Months, years, seasons and habitats were treated as the explanatory variables and the percentage of recruitment as the response variables.

Results

Species composition

A total of 14 112 trap nights were undertaken, with an overall 17.1% trap success. This yielded eleven identified small rodent species, with *Mastomys natalensis* the most dominant species with 65 % of all captures. Other species were *Mus triton* (17.3%), *Aethomys hindei* (7.2%), *Lemniscomys zebra* (5.2%), *Lophuromys sikapusi* (3.2%), *Arvicanthis cf. niloticus* (1.2%), *Gerbilliscus* sp. (0.7%), *Graphiurus murinus* (0.04%), *Steatomys parvus* (0.04%), *Dasymys incomtus* (0.04%) and *Grammomys dolichurus* (0.04%). *Mastomys natalensis* comprised of 550 and 607 individuals in cultivated and fallow fields, respectively; the details on relative numbers of other species are reported elsewhere (Mayamba et al. 2019).

Population dynamics

GLM models showed the relative importance of the different variables considered on *M. natalensis* population abundance. In terms of studied seasons/years of trapping, *M. natalensis* abundance was significantly higher in the first half of 2018 compared to 2016 and 2017 (Table 1). There was also a significantly low population abundance in year 2017. Model estimates for months also varied with a significant negative estimate for January, estimating lower population abundance as shown by the negative coefficient ($\beta = -0.79$, $p = 0.019$; Table 1, Figure 2), followed by December ($\beta = -0.75$), though not significant. March showed the highest population abundance, with a significant model estimate and a positive coefficient ($\beta = 0.53$, $p = 0.016$; Table 1, Figure 2). In terms of habitats, model estimations showed significantly higher population abundance estimates for fallow fields than for cultivated habitat ($\beta = 0.69$, $p < 0.0001$, Table 1). Significantly higher abundance was also found in the first wet season ($\beta = 0.75$, $p = 0.006$; Table 1, Figure 2). Rainfall and mean annual population density were significantly positively correlated ($R^2 = 0.84$, $p = 0.001$, Figure 3).

Breeding patterns

Sexual activity
There was no difference in *M. natalensis* breeding performance between habitats, therefore data from the two habitats were combined. The between seasons percentage of actively breeding females differed significantly ($\chi^2 = 17.64$, $p = 0.0003$) with the highest percentage of actively breeding females occurring at the end of the first wet, and start of the second dry seasons of 2016 (Figure 4). Further analysis on the effect of months showed a highly significant difference ($\chi^2 = 27.05$, $p = 0.003$) with the month of June showing the highest percentage of breeding females (>90%) in both 2016 and 2018 (Figure 4). The lowest percentage of actively breeding females were found during the first dry season of 2017, in the months of January and February (less than 15% of females breeding) and similarly low breeding in February 2018 (= first dry season) (Figure 4).

Recruitment
Data on newly trapped *M. natalensis* individuals in the Capture–Mark–Recapture trappable population were computed as a percentage of newly trapped animals against overall captured animals (Mulungu et al. 2013; Mlyashimbi et al. 2019). This percentage of recruitment in the trappable population did not significantly differ between habitats ($\chi^2 = 0.010$, $p = 0.918$). Thus, further analysis combined data from the two habitats. The effect of seasons ($\chi^2 = 14.5$, $p = 0.0001$) and months ($\chi^2 = 23.16$, $p = 0.0122$) on recruitment was significant. Highest recruitment occurred in the second dry season (June to August) of 2016 (Figure 5). In 2017, the highest recruitment was observed in the months of March (first wet season), June–July (second dry season) and October (second wet season). In the 2018 half-year study period recruitment was highest in March (Figure 5).

Sex ratio
There was no significant sex ratio difference on the effect of habitat ($F = 0.076$, df = 1, $p = 0.784$) and season ($F = 2.980$, df = 1, $p = 0.116$) calculated over the whole study period, with the ratio of females to males at parity.

Discussion

Population dynamics
In the present study we explored aspects of the population ecology of *M. natalensis* in an agricultural setting, following a Capture–Mark–Recapture trapping program in fallow and cultivated field habitats. Earlier studies conducted in agricultural systems in different parts of eastern and southern Africa mentioned this particular species as the most important small rodent pest species, with its population noted to exhibit irregular fluctuations depending on the geographic locality, habitat and climate (Leirs 1995, 1996; Makundi et al. 2007; Addisu and Bekele 2013; Mulungu et al. 2013). We therefore hypothesised that the population dynamics in terms of population density, breeding pattern and recruitment would significantly vary with habitat type and season. In terms of population abundance, habitat characteristics (habitat type) indeed played a significant role, with higher population abundance in fallow habitat than in cultivated habitat. These results could be attributed to the characteristic relative stability of fallow habitats, which are less disturbed by human activities while offering better ground cover for protection from potential predators. This same explanation was suggested by several other authors who reported higher population densities of *M. natalensi*s in fallow habitats compared to other habitats (Makundi et al. 2009; Addisu and Bekele 2013; Mulungu et al. 2013). Our findings are in agreement with earlier theories that suggest that biological species differ in their distributions across space, as some habitats offer a wider range of resources for species to persist than others (Brown 1984; Brown et al. 1996; Gyllenberg and Hanski 1997; Mulungu et al. 2013). The current study also confirmed that, although the studied species is regarded as a good coloniser of disturbed habitats/agricultural farmlands (Afework and Leirs 1997; Magige and Senzota 2006; Massawe et al. 2006), its population density can be impacted by the levels of human activity in those habitats (Leirs et al. 1997 <<a or b?>>). Our results also partly support those of Tadesse and Afework (2008) who concluded that bushy habitats, like fallow land, tend to offer more food and adequate cover, thus supporting higher numbers of rodents. The influences of months and seasons on population abundance of *M. natalensis* were also important model parameters, with highest abundances found at the start of the first wet season, with abundance in the second wet season at times almost as high as in the first wet season. Higher rodent abundances in the second wet season were observed in a study on rodents in Kafta-Sheraro National park in Ethiopia (Assefa and Chelmela 2019). The observation of higher abundances of *M. natalensis* in wet periods was possibly a result of increased availability of vegetation, which serves both as a source of food and cover (Iyawe 1988; Leirs 1995, 1996; Makundi et al. 2007; Mulungu et al. 2013). Our study also partly attributes the high population in the second wet season to the higher percentage of actively breeding females in the months of April, May, June and July, which resulted in population build up. In general our results agree with several other studies on *M. natalensis* which demonstrated seasonal population changes in relation to factors driven by rainfall patterns, viz. food supply and vegetation cover (Leirs 1995; Leirs et al. 1997a; Linzey and Kesner 1997; Makundi et al. 2007; Sheyo and Kilonzo 2012; Massawe et al. 2012; Makundi et al. 2015; Mulungu 2017; Chidodo 2017; Mlyashimbi et al. 2018). Particularly, higher trap success of *M. natalensis* was recorded in the wet season in northern Ethiopia and the Western Usambara Mountains in Tanzania (Makundi et al. 2007; Chekol et al. 2012). These studies concluded that rainfall was the main driver of population changes, as it triggers more primary productivity, yielding more food and ground cover. Yihune and Bekele (2012) also reported that rodents exhibit variations in numbers following on seasonal variation in vegetation structure, ground cover and other related environmental factors. Our study indeed showed a strong positive linear relationship between the amount of rainfall and *M. natalensis* population density, a finding which conforms to Leirs et al.'s (1996) study, which identified rainfall as the determining factor for *M. natalensis* population growth.

Breeding patterns of M. natalensis

Sexual activity
Previous studies (e.g. Mulungu 2017) have demonstrated that breeding females are key in regulating population changes. Our results showed that actively breeding females were present both in the wet and dry seasons, and almost across all months, but with significantly higher percentages in the period March to July (i.e. first wet

season extending to the second dry season). Lower percentages were generally found in the first dry months (i.e. January and February 2017, and February 2018). This result can most probably be linked to the availability of abundant food for rodents from growing vegetation, as a result of the first wet season major planting extending through to the short second dry season when there are residual seeds on the ground, left over from harvesting. These conditions may have triggered more females into active breeding. Rodents generally show synchronised seasonal reproductive patterns aligning with the most favourable periods of the year, a strategy to maximise reproductive success (Bronson 1985; Gittleman and Thompson 1988). Similarly, a number of studies on African rodent species indicate a synchronization of reproduction with occurrence of rainfall events and plant productivity, as a mechanism to maximise growth and survival of newly born individuals under conditions of high-quality food availability and suitable environmental conditions (Neal 1986; Leirs et al. 1994, 1997b; Bekele and Leirs 1997; Makundi et al. 2007). The results of this study therefore concur with these findings since significantly higher percentages of actively breeding *M. natalensis* occurred towards the end of the first wet season, when abundant drying cereal crops and other food crops were also plentiful in the gardens. Granjon et al. (2005) also reported higher actively breeding females of *M. hurbeti* in the late rainy season, extending through the dry season. On the other hand, habitat types had no significant effect on actively breeding females, a result that indicated that habitat alone does not regulate breeding patterns in *M. natalensis*. These results confirm earlier reports that showed that breeding patterns of small rodents in general are more influenced by weather conditions (Leirs 1992; Makundi et al. 2007; Meheretu et al. 2015) than the habitat type.

Sex ratio

The male to female sex ratio of the trapped animals was observed to be balanced in this study, regardless of the habitat or season. Other related studies on rodent sex ratios demonstrated a male-biased higher capture probabilities, and attributed it to intersexual differences in home-range size, where males tend to exhibit higher mobility as they search for mates which increases their chances of being trapped in a given habitat and season (Christensen 1996). Our findings, however, are in support of Mulungu et al. (2013) where they found equal proportions of males to females in a study conducted in irrigated rice and fallow habitats.

Recruitment

The percentage of newly trapped individuals in the trappable population was significantly higher in the months of June and July (second dry season), extending through to August. This is expected to be as a culmination of increased breeding with the start of the rainy season, in March. The offspring of the actively breeding animals that were observed in the previous months, therefore resulted in this influx of new individuals in the trappable population. Similar explanations for higher proportions of new individuals can be attributed to the favourable conditions in terms of enhanced vegetation due to rainfall, which offers increased food availability. Both quality and quantity of food has been shown to be a key exogenous factor for regulating rodent population abundance and the breeding cycle (Revitali et al. 2009; Mulungu et al. 2013, 2014). Likewise, Leirs et al. (1994) reported that rodents tend to respond quickly to changes in weather after a long dry spell, which normally results in an influx of high numbers of new individuals in the trappable population.

Conclusions

From the present study, it is evident that *M. natalensis* can equally occupy cultivated fields and fallow lands in agro ecosystems, with relatively higher population abundances in fallow habitats, a state that could be attributed to the limited human activities, compared with cultivated fields. This observation thus justifies the inclusion of fallow fields in management plans that aim for effective control of agriculture rodent pest species.< but if the abundance is higher in fallows, why would this justify inclusion in mgmt plans - if the concern is to regulate pest populations? Reword to address> Secondly the study revealed that *M. natalensis* in the study area exhibit seasonal population changes associated with weather conditions, particularly rainfall patterns where increased rainfall results in increased population growth, presumably enhanced by the increased vegetation growth that provides abundant food and shelter to the animals. The study also revealed that active breeding in *M. natalensis* females is almost continuous throughout the year in the studied area, though with higher percentages in the months April and May (first wet season), extending to June and July (second dry season). These results suggest that food production cycles may also play a major role in *M. natalensis* breeding. We therefore recommend that control efforts should be continuous, but with increased emphasis in the first months of the first rainy season (March and April), to counter future breeding generations. Lastly, the study has shown that the ratio of male to female *M. natalensis* in the studied area was at parity. Control efforts should therefore target both sexes to prevent population growth from attaining damaging levels.

Acknowledgments — We are extremely grateful to the Ecologically Based Management of Rodent Pests in Maize and Rice in East Africa to Sokoine University of agriculture project (Grant No. OPP1112579). We are also grateful for the tireless project field work efforts rendered by Kisakye Alex, Ouma Namulochi and Ramadhani Kigunguli from Busitema University, Namasagali campus, Uganda and Pest Management Centre, Sokoine University of Agriculture, Morogoro, Tanzania respectively.

Funding — We thank the Bill and Melinda Gates Foundation that funded Alex Mayamba's PhD studies, of which this paper is part.

Ethical considerations — This research was carried after thorough review by Sokoine University of Agriculture, Wild life department, Tanzania. Further research approval was obtained from the Uganda Wild life Authority for conducting research on live animals in Uganda.

References Addisu A, Bekele A. 2013. Habitat preferences, seasonal abundance and diets of rodents in Alage, Southern Ethiopia. *African Journal of Ecology* 52: 284–291. https://doi.org/10.1111/ aje.12115. Afework B, Leirs H. 1997. Population ecology of rodents of maize fields and grassland in central Ethiopia. *Belgian Journal of Zoology* 127: 39–48. Amatre G, Babi N, Russell E, Ogen-Odoi A, Atiku LA, Akol A, Gage KL, Eisen RJ. 2009. Flea diversity and infestation prevalence on rodents in a plague-endemic region of Uganda. *The Journal of Tropical Medicine and Hygiene* 81: 718–724. https://doi. org/10.4269/ajtmh.2009.09-0104 Assefa A, Chelmela S. 2019. Comparison of rodent community between natural and modified habitats in Kafta-Sheraro Natural Park and its adjoining villages, Ethiopia; implication for conservation. *Journal of Basic and Applied Zoology* 80: 59(2019). https://doi.org/10.1186/s41936-019-0128-9. Basuta G, Kasene JM. 1987. Small rodent populations in selectively felled and mature tracks of Kibale forest, Uganda. *Biotropica* 193: 260–266. https://doi.org/10.2307/2388345. Bekele A, Leirs H. 1997. Population ecology of rodents of maize fields and grassland in central Ethiopia. *Belgian Journal of Zoology* 127: 39–48. Bonwitt J, Sáez AM, Lamin J, Ansumana R, Dawson M, Buanie J, Lamin J, Sondufu D, Borchert M, Sahr F, et al. 2017. At home with *Mastomys* and *Rattus*: human-rodent interactions and potential for primary transmission of Lassa virus in domestic spaces. *The Journal of Tropical Medicine and Hygiene* 96: 935–943. https://doi.org/10.4269/ajtmh.16-0675. Borremans B, Hughes NK, Reijniers J, Sluydts V, Katakweba AAS, Mulungu LS, Sabuni CA, Makundi RH, Leirs H. 2014. Happily together forever: temporal variation in spatial patterns and complete lack of territoriality in a promiscuous rodent. *Population Ecology* 56: 109–118. https://doi.org/10.1007/ s10144-013-0393-2. Bronson FH. 1985. Mammalian reproduction: an ecological perspective. *Biology of Reproduction* 32: 1–26. https://doi. org/10.1095/biolreprod32.1.1. Brown JH, Stevens GC, Kaufman DM. 1996. The geographic range: Size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* 27: 597–623. https://doi. org/10.1146/annurev.ecolsys.27.1.597. Brown JH. 1984. On the relationship between abundance and distribution of species. *American Naturalist* 124: 255–279. https://doi.org/10.1086/284267. Chekol T, Bekele A, Balakrishnan M. 2012. Population density, biomass and habitat association of rodents and insectivores in Pawe area, northwestern Ethiopia. *Tropical Ecology* 53: 15–24. Chidodo DJ. 2017. Evaluation of Normalized Difference Vegetation Index of common vegetation habitats for monitoring rodent population and outbreaks in Ismani, Tanzania. MSc Thesis. Sokoine University of Agriculture, Tanzania. Christensen JT. 1996. Home range and abundance of *Mastomys natalensis* (Smith, 1834) in habitats affected by cultivation. *African Journal of Ecology* 34: 298–311. https://doi. org/10.1111/j.1365-2028.1996.tb00624.x. Davis SA, Akison LK, Farroway LN, Singleton GR, Leslie KE. 2003. Abundance estimators and truth: accounting for individual heterogeneity in wild house mice. *Journal of Wildlife Management* 67: 634–645. https://doi.org/10.2307/3802720. Delany MJ. 1975. *The Rodents of Uganda*. Kettering: The George Press. Fiedler LA. 1988. Rodent pest problems in East Africa. Rodent pest management. In: Prakash I (Ed.). *Rodent pest Management*. Boca Raton: CRC Press. pp 35–65. Gittleman JL, Thompson SD. 1988. Energy allocation in mammalian reproduction. *American Zoologist* 28: 863–875. https://doi.org/10.1093/icb/28.3.863. Granjon L, Cosson J, Quesseveur E, Sicard B. 2005. Population dynamics of the Multimammate rat *Mastomys huberti* in an annually flooded agricultural region of central Mali. *Journal of Mammalogy* 86997–1008. https://doi. org/10.1644/1545-1542(2005)86[997:PDOTMR]2.0.CO;2. Gyllenberg M, Hanski I. 1997. Habitat deterioration, habitat destruction, and metapopulation persistence in a heterogenous landscape. *Theoretical Population Biology* 52 198–215. https:// doi.org/10.1006/tpbi.1997.1333. Happold DCD. 2013. Mammals of Africa. Volume III: *Rodents, hares and rabbits*. London: Bloomsbury Publishing. Iyawe JG. 1988. Distribution of small rodents and shrews in a low land rain forest zone of Nigeria, with observations on their reproductive biology. *African Journal of Ecology* 26: 189–195. https://doi.org/10.1111/j.1365-2028.1988.tb00970.x. Karim M, Zeger S. 1992. Generalized Linear Models with random effects; salamander mating revisited. *Biometrics* 48: 631–644. https://doi.org/10.2307/2532317. Kingdon J. 1974. East Africa mammals: an atlas of evolution in Africa. Volume II Part B *Hares and Rodents*. London: Academic Press. Knudson C. 2018. An introduction to mode-fitting with the R-package glmm. https://cran.r-project.org/. Leirs H, Stenseth NC, Nichols JD, Hines JE, Verhagen R, Verheyen W. 1997a. Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. *Nature* 389: 176–180. https://cran.r-project. org/10.1038/38271. Leirs H, Verhagen RON, Sabuni CA, Mwanjabe P, Verheyen NW. 1997b. Spatial dynamics of *Mastomys natalensis* in a field-fallow mosaic in Tanzania. *Belgian Journal of Zoology* 127: 29–38. Liers H 1992. Population ecology of *Mastomys natalensis* (Smith, 1934) multimammate rat: possible implications for rodent control in Africa. PhD thesis. University of Antwerp, Belgium. Leirs H. 1995. Population ecology of *Mastomys natalensis* (Smith, 1834): implications for rodent control in Africa. A report from the Tanzania–Belgium Joint Rodent Research Project (1986–1989). Agricultural Edition No. 35. Belgian Administration for Development Cooperation, Brussels. Leirs H, Verhagen R, Verheyen W. 1994. The basis of reproductive seasonality in *Mastomys* rat (Rodentia: Muridea). *Journal of Tropical Ecology* 10: 55–66. https://doi.org/10.1017/ S0266467400007719. Leirs H, Verhagen R, Verheyen W, Mwanjabe P, Mbise T. 1996. Forecasting rodent outbreaks in Africa: an ecological basis for *Mastomys* control in Tanzania. *Journal of Applied Ecology* 33: 937–943. https://doi.org/10.2307/2404675. Linzey AV, Kesner MH. 1997. Small mammals of a woodlandsavannah ecosystem in Zimbabwe. I. Density and habitat occupancy patterns. *Journal of Zoology* 243: 137–152. https:// doi.org/10.1111/j.1469-7998.1997.tb05760.x. Magige F, Senzota R. 2006. Abundance and diversity of rodents at the human-wildlife interface in Western Serengeti, Tanzania. African Journal of Ecology 44: 371–378. . doi:10.1111/j.1365-2028.2006.00641.x. *African Zoology* 2021: 1–9 9 Makundi RH, Massawe AW, Borremans B, Laudisoit A, Katakweba A. 2015. We are connected: flea–host association networks in the plague outbreak focus in the Rift Valley, northern Tanzania. *Wildlife Research* 42: 196. https://doi.org/10.1071/WR14254. Makundi RH, Massawe AW, Mulungu LS, Katakweba A. 2009. Species diversity and population dynamics of rodents in a farm-fallow field mosaic system in Central Tanzania. *African Journal of Ecology* 48: 313–320. https://doi. org/10.1111/j.1365-2028.2009.01109.x. Makundi RH, Massawe AW, Mulungu L. 2007. Reproduction and population dynamics of *Mastomys natalensis* Smith, 1834 in an agricultural landscape in the Western Usambara Mountains, Tanzania. *Integrative Zoology* 2: 233–238. https://doi. org/10.1111/j.1749-4877.2007.00063.x. Massawe AW, Leirs H, Rwamugira WP, Makundi RH. 2003. Effect of land preparation methods on spatial distribution of rodents in crop fields. In: Singleton GR,. Hinds LA, Krebs CJ, Spratt DM (Eds), *Rats, Mice and People: Rodent Biology and Management*. Canberra: Australian Centre for International Agricultural Research. Massawe AW, Rwamugira W, Leirs H, Makundi RH, Mulungu LS. 2006. Do farming practices influence population dynamics of rodents? A case study of the multimammate field rats, *Mastomys natalensis*, in Tanzania. *African Journal of Ecology* 45: 293–301. https://doi.org/10.1111/j.1365-2028.2006.00709.x. Massawe AW, Apia W, Makund, RH, Mulungu LS, Katakweba A, Shayo TN. 2012. Breeding dynamics of rodent species inhabiting farm—fallow mosaic fields in central Tanzania. *African Zoology* 47: 128–137. https://doi.org/10.1080/15627020.2012.11407531 Mayamba A, Byamungu RM, Makundi RH, Kimaro DN, Isabirye M, Massawe AW, Kifumba D, Nakiyemba A, Leirs H, Mdangi ME, et al. 2019. Species composition and community structure of small pest rodents (Muridae) in cultivated and fallow fields in maize-growing areas in Mayuge district, Eastern Uganda. *Ecology and Evolution* 9: 1–12. https://doi.org/10.1002/ece3.5371. Meheretu Y, Welegerima K, Sluydts V, Bauer H, Gebrehiwot K, Deckers JF, Makundi RH, Leirs H. 2015. Reproduction and survival of rodents in crop fields: the effects of rainfall, crop stage and stone-bund density. *Wildlife Research* 42: 158–164. https://doi.org/10.1071/WR14121. Mlyashimbi EC, Mariën J, Kimaro DN, Tarimo AJ, Machang'u RS. 2019. Home ranges, sex ratio and recruitment of the multimammate rat (*Mastomys natalensis*) in semi-arid areas in Tanzania. *Mammalia* 84: 10. Mlyashimbi ECM, Mariën J, Kimaro DN, Tarimo AJP, Isabirye M, Makundi RH, Massawe AW, Mdangi ME, Kifumba D, Nakiyemba A, et al. 2018. Relationships between seasonal changes in diet of Multimammate rat (*Mastomys natalensis*) and its breeding patterns in semi-arid areas in Tanzania. *Cogent Food & Agriculture* 4: 1–13. https://doi.org/10.1080/23311932.2018.1507509. Monadjem A, Taylor J, Denys C, Cotterill PD. 2015. *Rodents of sub-Saharan Africa: a biogeographic and taxonomic synthesis*. Berlin: De Gruyter. https://doi.org/10.1515/9783110301915. Mulungu LS. 2017: Control of rodent pests in maize cultivation: the case of Africa. In: Watson D (Ed.), *Achieving sustainable maize cultivation*, vol. 2. Cambridge: Burleigh Dodds Science Publishing. pp 318–337. Mulungu LS. 2003. Assessment of maize (*Zea mays* L) damage and yield loss due to rodents in the field. PhD thesis. Sokoine University of Agriculture, Tanzania. Mulungu LS, Mahlaba TA, Massawe AW, Kennis J, Crauwels D, Eiseb S, Monadjem A, Makundi RH, Katakweba AS, Leirs H, et al. 2011a. Dietary differences of the multimammate mouse, *Mastomys natalensis* (Smith 1834), across different habitats and seasons in Tanzania and Swaziland. *Wildlife Research* 38: 640–646. https://doi.org/10.1071/WR11028. Mulungu LS. Mahlaba TA, Massawe AW, Kennis J, Crauwels D, Eiseb S, Monadjem A, Makundi RH, Katakweba AS, Leirs H, et al. 2011b. Differences in diet between two rodent species of *Mastomys natalensis* and *Gerbilliscus vicinus* in fallow land habitat of Central Tanzania. *African Zoology* 46: 387–392. https://doi.org/10.3377/004.046.0218 Mulungu LS, Ngowo V, Mdangi M, Katakweba A, Tesha P, Mrosso F, Mchomvu M, Kilonzoa BS. 2013. Population dynamics and breeding patterns of Multimammatemouse, *Mastomys natalensis* (Smith 1834), in irrigated rice fields in Eastern Tanzania. *Journal of Pest Management Science* 69: 371–377. https://doi. org/10.1002/ps.3346. Mulungu LS, Mlyshimbi ECM, Ngowo V, Mdangi M, Katakweba AS, Tesha P, Mrosso FP, Mchomvu M, Kilonzo BS, Belmain SR. 2014. Food preferences of the multimammate mouse, *Mastomys natalensis*, in irrigated rice habitats in Tanzania. *International Journal of Pest Management* 60: 1–8. https://doi.org/10.1080/09 670874.2013.871759. Mulungu LS, Sixbert V, Ngowo V, Mdangi M, Katakweba AS, Tesha P, Mrosso FP, Mchomvu M, Kilonzo BS, Belmain SR. 2015. Spatio-temporal patterns in the distribution of the multimammate mouse, *Mastomys natalensis*, in rice crop and fallow land habitats in Tanzania. *Mammalia* 79: 177–184. Mwanjabe P, Leirs H. 1997. An early warning system for IPM-based rodent control in small holder farming systems in Tanzania. *Belgian Journal of Zoology* 127: 49–58. Neal BR. 1986. Reproductive characteristics of African small mammals. *Cimbebaria Series A8*: 113–127. Revitali MANP, Ima MAL, Eserve PELM, Elt DOAK. 2009. Population dynamics of two sympatric rodents in a variable environment: rainfall, resource availability and predation. *Ecology* 90: 1996–2006. https://doi.org/10.1890/08-0405.1. R Core Team. 2013. R: A language and environment for statistical computing. R. foundation for statistical computing, Vienna, Austria. Swanepoel LH, Swanepoel CM, Brown PR, Eiseb SJ, Goodman SM, Keith M, Kirsten F, Leirs H, Mahlaba TAM, Makundi R, et al. 2017. A systematic review of rodent pest research in Afro-Malagasy small-holder farming systems: are we asking the right questions? *PLoS One* 12: e0174554. https://doi. org/10.1371/journal.pone.0174554. Tadesse H, Afework B. 2008. Habitat association of insectivores and rodents of Alatish National Park, northwestern Ethiopia. *Tropical Ecology* 49: 1–11 White GC, Anderson DR, Burnham KP, Otis DC. 1982. *Capturerecapture and removal methods for sampling closed populations* Los Alamos: Los Alamos National Laboratory. Yihune M, Bekele A. 2012. Diversity, distribution and abundance of rodent community in afro-alpine habitat of the simian mountains national park, Ethiopia. *International Journal of Zoological Research* 8: 137–149. https://doi.org/10.3923/ijzr.2012.137.149.

Manuscript received: 17 May 2019, revised: 30 November 2020, accepted: 12 December 2020 Associate Editor: N Avenant