# Comparative study of movement patterns of *Mastomys natalensis* in irrigated rice and fallow fields in eastern Tanzania

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## Abstract

A 2-year capture–mark–recapture study was conducted to estimate home ranges and weekly travel distance of *Mastomys natalensis* (Smith 1834) in an irrigated rice ecosystem and fallow fields. We found that adults have larger home ranges than subadults in fallow fields but not in rice fields, indicating that fallow fields are more suitable for breeding. Travel distances were larger in rice fields, especially in the transplanting stage, during which rice fields are flooded and provide less food, causing movements into neighbouring fallow fields that then temporarily experience higher population density. A decrease in travel distance was observed in rice fields during the maturity stage, which can be explained by higher food availability and a more suitable, nonflooded situation. Movement of *M. natalensis* in rice-fallow mosaic landscapes thus seems to be driven by food availability and flooding status of the rice fields, which can be attributed to land use practices.

*Key words:* fallow land, home range, land use, *Mastomys natalensis*, movement, rice field

## Résumé

Une étude de deux ans a été réalisée par capture-marquage-recapture pour estimer le domaine vital et la distance de déplacement hebdomadaire de *Mastomys natalensis* (Smith 1834) dans un écosystème de rizières irriguées et de champs en jachère. Nous avons constaté que les adultes avaient un domaine vital plus étendu que les subadultes dans les jachères mais pas dans les rizières, ce qui indique que les jachères sont plus appropriées pour la reproduction. Les distances parcourues étaient plus grandes dans les rizières, spécialement au moment du repiquage, quand les rizières sont inondées et procurent moins de nourriture, ce qui entraîne des déplacements dans les jachères proches qui connaissent temporairement une densité de population plus élevée. On observe une diminution des distances parcourues dans les rizières à maturité, ce qui peut s'expliquer par la plus grande disponibilité de nourriture et une situation non inondée plus adaptée. Les déplacements de *M. natalensis* dans des paysages en mosaïque de rizières-jachères semblent donc être déterminés par la disponibilité en nourriture et par l'état, inondé ou pas, des champs de riz, qui peuvent être attribués aux pratiques d'utilisation des terres.

## Introduction

*Mastomys natalensis* (Smith 1834) is the most important rodent pest species, which is found in large numbers in different habitats in sub-Saharan Africa (Leirs, 1994; Mulungu *et al.*, 2011). Its widespread distribution indicates a broad habitat tolerance and makes it an effective colonizer of disturbed (e.g. by agriculture) habitats (Massawe, 2003; Mulungu *et al.*, 2011). Although its spatial behaviour has been studied almost exclusively in maize or fallow habitats, recent results indicate that its spatial behaviour may be affected differently in another type of agricultural habitat (Mulungu *et al.*, 2015a). In rice fields, *M. natalensis* gener-

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ally seems to exhibit an aggregated spatio-temporal distribution (including relocations to refuges adjacent to rice fields), while in fallow fields, its distribution is less aggregated, approaching a seemingly random distribution (Borremans *et al.*, 2014; Mulungu *et al.*, 2015a).

There are several environmental factors that can affect the spatial patterns of populations and shape unique movement patterns. These factors include resource availability, predation risk, mating system and the abiotic environment. The distribution of these factors in space is usually heterogeneous and mosaic-like (Ims, 1995). Understanding the spatio-temporal scales at which organisms perceive and respond to their environment is a central issue in ecology (Wiens, 1976, 1989; Bowman, Forbes & Dilworth, 2000). Farming practices have been shown to have an impact on rodent spatial behaviour (Jacob *et al.*, 2003). In West Java, for example, rice-field rats (*Rattus argentiventer*) react to harvest-induced changes in habitat structure by relocating their home ranges on average 300–400 m to piles of rice straw on the fields and to unharvested areas, resulting in a postharvest decrease of home range size, which may indicate an immediate response to increased predation risk (Jacob *et al.*, 2003).

More specifically, numerous factors in an irrigated rice ecosystem could determine the spatial patterns of *M. natalensis*, such as the physical characteristics, the connectivity with fallow fields, the presence of bunds and the embedding of suitable habitat in an agricultural mosaic system (Kozakiewicz, 1993; Peles, Bowne & Barrett, 1999; Romanowski, Dudek & Kowalczyk, 2008). These properties may also affect population growth rate, body condition, home range compaction, foraging, parasitism, breeding and genetic variation (Patterson & Malcolm, 2010).

Home ranges of *M. natalensis* typically range from 200 to 2000 m$^2$ in grassland and bush land habitats (Hoffmann, 1999). Male and female home ranges do not seem to differ, and sexually active individuals of both sexes were found to have larger home ranges (Leirs, Verheyen & Verhagen, 1996; Borremans *et al.*, 2014). Seasonal variations in home range sizes were not found for this species (Oguge, 1995; Christensen, 1996; Leirs, Verheyen & Verhagen, 1996; Hoffmann, 1999; Borremans *et al.*, 2014).

Hoffmann (1999) reported an effect of habitat type on movement, where shorter travel distances were recorded in habitats with higher food quantity and quality, implying that *M. natalensis* movement is strongly determined by food availability. Similarly, home range size and travel distance decrease have been tentatively linked to increased food availability in an experimental study (Monadjem & Perrin, 1998).

This study aims to determine the movement and home range of *M. natalensis* in irrigated rice areas using data collected by employing capture–mark–recapture techniques, with the intention of providing useful information on the ecology of *M. natalensis*.

## Materials and methods

### Study area

This study was conducted at Hembeti village (06°16′S, 37°31′E), in Mvomero District, Morogoro, Tanzania (Fig. 1). The study area has a bimodal rainfall pattern consisting of a short rainy season from October to December and a long rainy season from March to June. Farmers in the study area produce rice crops twice per year, first from January to June and second from July to December. Farmers depend strongly on irrigation in the second rice crop production. Land preparation and rice transplanting are performed during the first month of each season (January and July for the wet and dry season, respectively). This is followed by a vegetative crop stage (February–March for the wet season and August–September for the dry season). Booting stages occur in April and October, and rice crops
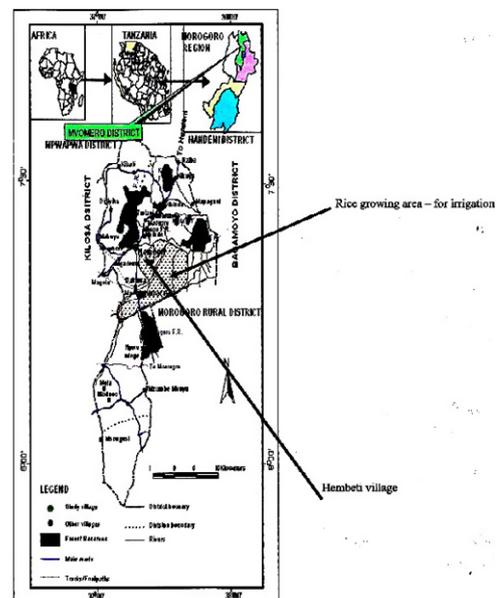


Fig 1 Map of Mvomero District, showing the location of the study area

reach physiological maturity in May and November, after which farmers harvest (June and December). Food availability to rodents is higher around and during the maturity stages, and more vegetative cover is present from the vegetative until the harvest stage. Flooding occurs during the transplanting, vegetative and booting stages.

### Rodent trapping

A capture–mark–recapture study was carried out from June 2010 to May 2012. Four 70 m × 70 m permanent trapping grids (two in rice fields and two in fallow mosaics) were established, separated by at least 300 m. This distance is more than twenty times the average home range radius of *M. natalensis* (Leirs, Verheyen & Verhagen, 1996; Borremans *et al.*, 2014) which is the major rodent pest species in the study area (Mulungu *et al.*, 2013). Each grid consisted of seven parallel lines, 10 m apart, and seven trapping stations per line, also 10 m apart (total of 49 trapping stations/grid). One Sherman LFA live trap (8 × 9 × 23 cm, H.B. Sherman Traps Inc., Tallahassee, FL, U.S.A.) was placed at each trapping station, and all were set for three consecutive nights at intervals of 4 weeks. Traps, baited with peanut butter mixed with maize bran/flour, were placed in the afternoon and inspected in the morning. During flooding of rice fields (i.e. transplanting and vegetative crop growth stages), the traps were placed on small islands made of dried grasses. The grids were located in a mosaic landscape containing a mix of rice and fallow fields.

### Rodent sampling

All captured animals were taken to the field laboratory and identified to species level (Kingdon, 1997), with >95% in both habitats (rice fields and fallow land) identified as *M. natalensis* (Mulungu *et al.*, 2013). All animals were marked by toe clipping using individual-specific number coding at the time of first capture, which has been shown not to affect *M. natalensis* movement or home range (Borremans *et al.*, 2015). Weight, trapping station, sex and reproductive status (perforated or closed vagina in females and scrotal or nonscrotal testes in males) were recorded. Animals were then released at the exact place of capture.

### Spatial patterns

For each individual, two measures of space use were estimated, a home range proxy and the weekly travel distance. The area bound by the outer capture locations was calculated using a minimum convex polygon (MCP) with an added boundary strip of 5 m (half the distance between neighbouring traps; Stickel, 1954). Although this method is an often used but rough proxy for home range, it was not possible to use more sophisticated probabilistic methods because they require a much larger number of recaptures. However, as the purpose of this study was to compare space use between different types of habitat and not to estimate absolute sizes of home ranges, the MCP method is sufficient. Following the method described in Borremans *et al.* (2014), all individuals that were captured within 12 m from the edge of the trapping grid were removed from the analyses, in order to account for edge effects on home range size estimation and to minimize the proportion of transient animals. For most of the analyses, all locations where an individual was captured were used for MCP estimation. To study the effect of breeding status on home range size, home ranges were recalculated for adults and subadults by including only those locations where an individual was trapped during its adult or subadult period.

Because home ranges span several months, it would be impossible to correlate home range estimates with monthly variables such as crop growth stages, season or population density. For this reason, we also calculated the distance between a capture location and the preceding capture location. This was performed for each time an individual was captured (except the first time) by calculating the distance between that capture location and the preceding one and dividing this distance by the interceding time period, resulting in a movement measure expressed in m week$^{-1}$.

### Density estimation

The abundance of the rodent population during each three-night trapping session 1 (during which the population was assumed to be closed) was estimated using the commonly used heterogeneity estimator M(h) in the program CAPTURE (White *et al.*, 1982). The M(h) estimator allows for variability in individual capture probabilities and appears to be quite robust (Parmenter *et al.*, 2003). This estimator has been widely used to evaluate *M. natalensis* densities from field data originating from the same trapping grids (Mulungu *et al.*, 2013) and thus permits comparison with previous study. In the study area, the population density of the *M. natalensis* varied with habitat and months and is not correlated with rainfall (Mulungu *et al.*, 2013) as previously thought in mosaic and maize dominated crop fields (Leirs,

Verhagen & Verheyen, 1993, 1994). Fallow land in rice irrigated ecosystem had a more abundant population than rice fields. The highest population peak was observed during the dry season from July to October.

### Statistical testing

Effects of breeding status (adult or subadult), body weight, sex, rice growth stage, population density, and habitat type (rice or fallow) and season (wet or dry) were analysed using ANOVA of linear mixed regression models with individuals included as random effects. Because home range size is positively correlated with the number of recaptures, this variable was included in the models. Statistical significance was assumed when $P < 0.05$. Data manipulation, home range and movement estimation and statistical analyses were performed using R 3.0.1 (R Core Team, 2013) using packages lme4 (Bates, Maechler & Bolker, 2013), adehabitat (Calenge, 2006), gpclib (Peng *et al.*, 2013), maptools (Bivand & Lewin-Koh, 2013) and Matrix (Bates & Maechler, 2013). All results are shown with standard error.

## Results

### Home range

An overview of home range sizes in rice and fallow fields is shown in Table 1. Home range sizes did not differ

**Table 1** Home range sizes (mean ± standard error) of sexes and breeding status in rice and fallow fields

|  | Habitat | |
|---|---|---|
| Category | Rice | Fallow |
| Male | 445 ± 44 m² (N = 49) | 477 ± 30 m² (N = 102) |
| Female | 483 ± 53 m² (N = 50) | 427 ± 28 m² (N = 140) |
| Adult | 280 ± 29 m² (N = 60) | 360 ± 22 m² (N = 160) |
| Subadult | 351 ± 43 m² (N = 67) | 270 ± 21 m² (N = 157) |
| Female adult | 234 ± 37 m² (N = 29) | 321 ± 28 m² (N = 89) |
| Male adult | 324 ± 44 m² (N = 31) | 409 ± 36 m² (N = 71) |
| Female subadult | 349 ± 54 m² (N = 40) | 276 ± 31 m² (N = 98) |
| Male subadult | 353 ± 72 m² (N = 27) | 259 ± 24 m² (N = 59) |

N denotes sample size.

significantly between sexes (M = 467 ± 25 m² versus F = 442 ± 25 m²; $F_{1,336} = 0.621$, $P = 0.431$) or habitats (rice: 464 ± 34 m², fallow: 448 ± 21 m²; $F_{1,335} = 0.172$, $P = 0.678$). Breeding status did not significantly affect home range size (adult = 338 ± 18 m², subadult = 294 ± 20 m²; $F_{1,438} = 2.732$, $P = 0.099$), but there was a significant interaction between breeding status and habitat ($F_{1,438} = 7.969$, $P = 0.005$), where in fallow land, home ranges of adults were larger than those of subadults ($F_{1,314} = 9.729$, $P = 0.002$), while this difference was not significant in rice fields ($F_{1,124} = 1.797$, $P = 0.183$).

### Movement

Movement since the last capture event, measured as m week⁻¹, differed between sexes (M = 4.2 ± 0.2 m week⁻¹, F = 3.6 ± 0.1 m week⁻¹; $\chi^2 = 5.323$, df = 1, $P = 0.021$), but did not correlate with breeding status (adult = 2.7 ± 0.2 m week⁻¹, subadult = 2.7 ± 0.2m week⁻¹; $\chi^2 = 0.162$, df = 1, $P = 0.687$). Body weights in rice fields (43.7 ± 0.9 g) were lower than those in fallow fields (48.5 ± 0.5 g; $\chi^2 = 4.123$, df = 1, $P = 0.042$), but travel distance did not correlate with body weight ($\chi^2 = 0.011$, df = 1, $P = 0.916$). In rice fields, movements were on average larger than in fallow fields (Fig. 2; $\chi^2 = 6.815$, df = 1, $P = 0.009$), but there was a significant three-way interaction between habitat, season and growth stage ($\chi^2 = 28.699$, df = 10, $P = 0.001$), where, in rice fields, the travel distance was significantly lower in the dry season during the maturity stage, while in fallow fields, it was only significantly lower in the wet season during the transplanting stage. No significant overall travel difference was observed between seasons ($\chi^2 = 0.033$, df = 1, $P = 0.855$). There was a significant interaction between habitat and population density ($\chi^2 = 14.552$, df = 1, $P < 0.001$), where increasing densities correlated with decreasing travel distances in fallow fields (effect estimate = 0.018 ± 0.006), while the opposite was true in rice fields (effect estimate = 0.012 ± 0.006). The number of times an individual was recaptured correlated negatively with travel distance ($\chi^2 = 141.6$, df = 1, $P < 0.001$) and was lower in rice fields than in fallow fields (3.9 ± 0.1 versus 5.0 ± 0.1 times recaptured; $\chi^2 = 10.135$, df = 1, $P = 0.002$).
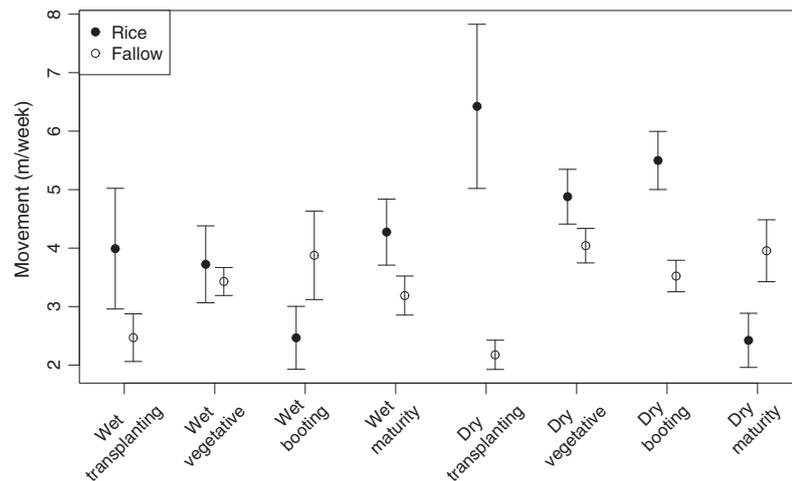
**Fig 2** Movement (mean ± standard error) for the dry and wet season (for all animals) and for the different rice crop growth stages in rice and fallow fields. In rice fields, food availability is higher around and during the maturity stages, and more vegetative cover is present from the vegetative until the harvest stage. Flooding occurs during the transplanting, vegetative and booting stages

## Discussion

### Home range

The aim of this study was to investigate space use patterns of *M. natalensis* in rice fields and whether they differ from those in fallow fields. Home range sizes in our study were consistent with those found in previous studies on *M. natalensis* (Leirs, Verheyen & Verhagen, 1996; Monadjem & Perrin, 1998; Borremans *et al.*, 2014) and were not significantly different between rice and fallow fields, suggesting that *M. natalensis* is resident in both types of habitat. While there was no significant home range size difference between rice and fallow fields, we did observe an interesting interaction between breeding status and field type, where home ranges of adults were larger than those of subadults in fallow fields, but not in rice fields. This may be because of high density in fallow land as compared to rice fields as reported by Mulungu *et al.* (2013) in the same study site leading to intense intraspecific competition hence larger home range for resource and foraging space (Mulungu *et al.*, 2015b).

Home ranges were not significantly different between sexes. This finding is consistent with previous observations (Leirs, Verheyen & Verhagen, 1996; Hoffmann, 1999; Borremans *et al.*, 2014). Also, season did not seem to significantly affect home range size, indicating that resources are sufficiently available throughout the year

in the study area (Mulungu *et al.*, 2014). Similar results were reported by Oguge (1995), Christensen (1996), Leirs, Verheyen & Verhagen (1996) and Hoffmann (1999).

### Movement

Knowledge of travel distance within and movement between different elements of the habitat mosaic are important for developing an understanding of how the environment is utilized and perceived by the rodent. In the current study, significant differences in short-term movement (i.e. within home ranges) were found between sexes, where males moved longer distances than females. This was also found by Leirs, Verheyen & Verhagen (1996). Considering that breeding occurs throughout the year (Mulungu *et al.*, 2013), this movement difference may indicate that *M. natalensis* males use a scramble competition (SC) strategy, as previously suggested by Kennis *et al.* (2008), where males move around more to increase chances of encountering receptive females. While Borremans *et al.* (2014) found that, as in our study, home ranges of males and females did not differ and concluded that this lack of difference indicated that a dominance hierarchy may be more likely than SC, we now observe that higher movement rates seem to occur within home ranges, supporting the SC hypothesis. However, our results did not show a significant difference between adult and subadult movement, which would not be in line with the SC hypothesis. This could,

however, be due to the much lower sample size in the analyses that include breeding status, as the data set had to be subdivided into adult and subadult categories. Indeed, even the significant effect of sex disappears in the regression analysis using the subdivided data set, suggesting that the statistical power may be too low to detect movement differences between adults and subadults.

The current study shows that *M. natalensis* individuals move longer distances in rice fields than in fallow land, especially during rice transplanting, similarly reported by Leirs, Verheyen & Verhagen (1996), where mouse movements were larger in maize fields than in fallow fields. We also observed a lower number of recaptures in rice fields, suggesting that the larger travel distances in rice fields are correlated with more frequent movements outside the trapping grid, perhaps to neighbouring fallow fields. This pattern is strongest during the transplanting stage, which is a period during which rice fields are flooded thus providing little food. The adjacent fallow land therefore seems to provide a stable habitat into which mice can retreat during periods when rice fields are less suitable. This is further supported by the fact that population densities in rice and fallow fields are very similar throughout the year except during the transplanting stage, when densities are, remarkably, twice as high in fallow than in rice fields ($73.5 \pm 1.2$ versus $33.0 \pm 2.0$ individuals per ha).

In this study, travel distance was observed to be smaller in rice fields during crop maturity, indicating that food quality and quantity may be a determinant of mouse movement. Indeed, Mulungu *et al.* (2014) found that seeds/grains of rice and weeds predominated, both in frequency and volume, in stomachs of *M. natalensis* rats trapped in both rice fields and fallow land.

To conclude, the larger home ranges of adults in fallow fields and the temporary movements from rice into fallow fields during transplanting suggest that fallow fields provide a stable breeding habitat for *M. natalensis* and that movements in this rice-fallow mosaic landscape are mainly driven by food availability and perhaps the flooding status of the rice fields.

## Acknowledgements

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