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Impact of crop cycle on movement patterns of pest rodent species between fields and houses in Africa

Ara Monadjem[A,G], *Themb'a A. Mahlaba*[A], *Nomfundo Dlamini*[A], *Seth J. Eiseb*[B], *Steven R. Belmain*[C], *Loth S. Mulungu*[D], *Apia W. Massawe*[D], *Rhodes H. Makundi*[D], *Katrine Mohr*[E] and *Peter J. Taylor*[F]

[A]Department of Biological Sciences, University of Swaziland, Private Bag 4, Kwaluseni, Swaziland.
[B]National Museum of Namibia, PO Box 1203, Windhoek, Namibia.
[C]Natural Resources Institute, University of Greenwich, Central Avenue, Chatham Maritime, Kent ME4 4TB, United Kingdom.
[D]Pest Management Centre, Sokoine University of Agriculture, PO Box 3110, Chuo Kikuu, Morogoro, Tanzania.
[E]Natural History Museum of Denmark, Zoological Department, Universitetsparken 15, 2100 Copenhagen Ø, Denmark.
[F]Department of Ecology and Resource Management, University of Venda, Private Bag X5050, Thohoyandou 0950, South Africa.
[G]Corresponding author. Email: ara@uniswa.sz

Abstract

Context. Rodent pests can have severe impacts on crop production in sub-Saharan Africa. In particular, the multimammate mouse *Mastomys natalensis* severely damages agricultural crops in southern and eastern Africa, leading to significant losses. Both its population ecology and breeding biology have been studied in agricultural and natural habitats. Population numbers erupt depending on the timing and amount of rainfall and may reach plague proportions, especially in agricultural settings, where it may become a serious pest. However, the ecology of this species, in particular its interactions with other species within the context of human settlement, is poorly understood. It may occasionally enter houses, but the degree to which it does so and the factors influencing this movement are not known.

Aims. We investigated the relationship between *Rattus* spp. and *M. natalensis* entering buildings in an agro-ecological setting. We predicted that *M. natalensis* would enter houses more readily when food availability was lowest in the surrounding fields, and when the larger *Rattus* spp. were absent.

Methods. We followed 40 individuals of *M. natalensis* in Swaziland and Namibia by radio-telemetry. Mice were captured in maize fields within 50 m of a homestead and fitted with radio-transmitters at three different times corresponding to different stages of crop development: pre-harvest, post-harvest and pre-planting. To corroborate the findings of the telemetry study, a non-toxic marker, rhodamine B, was mixed with standard bait and left at bait stations inside houses in 10 homesteads in Swaziland and Tanzania.

Key results. Mice remained in the fields during the entire period of study in Swaziland, but entered buildings in Namibia during the post-harvest stage, which may represent a period of food shortage for these mice in the field. Rodents captured after baiting with rhodamine B demonstrated that *Rattus* spp. predominated within the houses. A small number of rhodamine B-marked *M. natalensis* were captured outside the houses, the proportion declining with distance away from the houses.

Conclusions. These results suggest that in a typical rural African setting dominated by subsistence agriculture, *Rattus* spp. (when present) competitively exclude the smaller *M. natalensis* from entering houses.

Implications. Interactions between rodent pest species may be important in determining which rodent species enter houses in rural African landscapes. Consideration of such interactions may play an important role when developing pest management strategies.

Additional keywords: agricultural fields, houses, movement patterns.

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Introduction

Rodent pests may have severe impacts on crop production in many agro-ecosystems around the world (Singleton *et al*. 1999). In south-east Asia, such losses can amount to 5–10% of rice yield per annum (Singleton *et al*. 2008), with more than 50% crop loss in specific years or situations (Cuaterno 2008). Losses of crop yield due to rodent pests in other parts of the world are typically less, but are still significant. In east Africa, for example, several studies have shown final crop losses to be around 10% (Makundi *et al*. 1999), but potentially far greater in years of rodent outbreaks (Taylor 1968). Rodents are also of considerable importance for human health (Taylor *et al*. 2008) as carriers of a variety of potentially deadly diseases such as bubonic plague, hantaviruses, Lassa fever and typhus (Gratz 1997; Gloriani-Barzaga and Yanagihara 2008; Kernéis *et al*. 2009; Meerburg *et al*. 2009; Neerinckx *et al*. 2010).

In Africa, at least 25 species of rodent impact directly on agriculture and public health, with the most important genera being *Rattus*, *Mastomys*, *Arvicanthis* and *Rhabdomys* (Makundi *et al*. 1999). Species of *Mastomys* may damage crops and stored grain (Makundi *et al*. 1999), and are reservoirs of bubonic plague (Isaäcson *et al*. 1981) and vectors of Lassa fever (Fichet-Calvet *et al*. 2007, 2008). Furthermore, *Mastomys* species tend to occur at highest densities in disturbed habitats, such as agricultural fields, declining to relatively low densities in natural habitats, and entering houses infrequently (Leirs and Verheyen 1995; Monadjem 1997, 1999; Monadjem and Perrin 2003; Massawe *et al*. 2007; Mohr *et al*. 2007). Avenant (2000, 2003), Avenant and Cavallini (2007), and Avery (1992) all describe *Mastomys* as a generalist and good indicator species whose numbers dominate small mammal communities during and just after disturbance. *Rattus* species, on the other hand, are highly commensal with humans in Africa and are therefore rarely captured away from buildings and houses (Skinner and Chimimba 2005; Mohr *et al.* 2007). This is unlike the situation in Asia where *Rattus* species occur in substantial numbers both in houses and fields (Miller *et al*. 2008; Stuart *et al*. 2008).

Mastomys populations in southern Africa tend to increase through the wet season (November–February), peaking in the early dry season (March–June) (Monadjem and Perrin 2003; Avenant and Cavallini 2007; Avenant *et al*. 2008). In Tanzania, which has different rainfall patterns, *Mastomys* populations also undergo seasonal population fluctuations that peak in the dry season, mostly August–November (Leirs and Verheyen 1995; Makundi *et al*. 2005).

The ecology of rodent pests in agro-ecosystems has been studied in many parts of Africa (Leirs and Verheyen 1995; Monadjem 1998; Massawe *et al*. 2008; Makundi *et al*. 2010), and an elaborate model forecasting *Mastomys* outbreaks in Tanzania has been developed (Leirs *et al*. 1996*a*). All these studies, however, have focused on rodents either in crop fields or in edge habitat between fields and natural vegetation. In stark contrast, little is known about the ecology of rodents inhabiting houses and other buildings, and how they interact with rodents inhabiting the surrounding fields (Mohr *et al*. 2007). In south-eastern Africa *Rattus rattus* is known to reside in human habitation, whereas *M. natalensis* is generally considered more problematic in crop and fallow fields (Kingdon 1974; De Graaff 1981). The interactions between these two pest species are currently unknown and form the central question of this paper.

In this study we investigated the relationship between *Rattus* spp. and *M. natalensis* entering buildings in an agro-ecological setting, and predicted that *M. natalensis* would enter houses more readily when food availability was lowest in the surrounding fields. We also predicted that if the larger and possibly more aggressive *Rattus* spp. were excluding the smaller *M. natalensis* from the inside of houses, then *M. natalensis* would enter buildings where *Rattus* spp. were absent.

Materials and methods

Study area

This study was conducted at three widely separated sites in three African countries, Swaziland, Namibia and Tanzania. The Swazi site was situated at Lobamba, Hhohho District (26°28′S, 31°13′E, 690 m above sea level), the Namibian site at Diyogha Village, Kavango Region (18°05′S, 21°27′E, 1050 m above sea level), and the Tanzanian site at Berega Village, Morogoro Region (06°11′S, 37°08′E, 900 m above sea level) (Fig. 1). The Swazi and Namibian sites experience a single hot, wet summer (October–March) and a cooler, drier winter (April–September) each year, with annual rainfall of 700–850 mm, and 500–700 mm, respectively. The Tanzanian site also has a unimodal rainfall pattern, with a wet season (December–May) and a dry season (July–October), with annual rainfall of 800–1000 mm. The natural vegetation in the three areas was originally savanna, but all have been transformed into a matrix of small-scale subsistence farmland interspersed with farmers' homesteads with very little natural vegetation remaining. The main crops grown at the study sites are maize in Swaziland, millet in Namibia, and maize and sorghum in Tanzania.

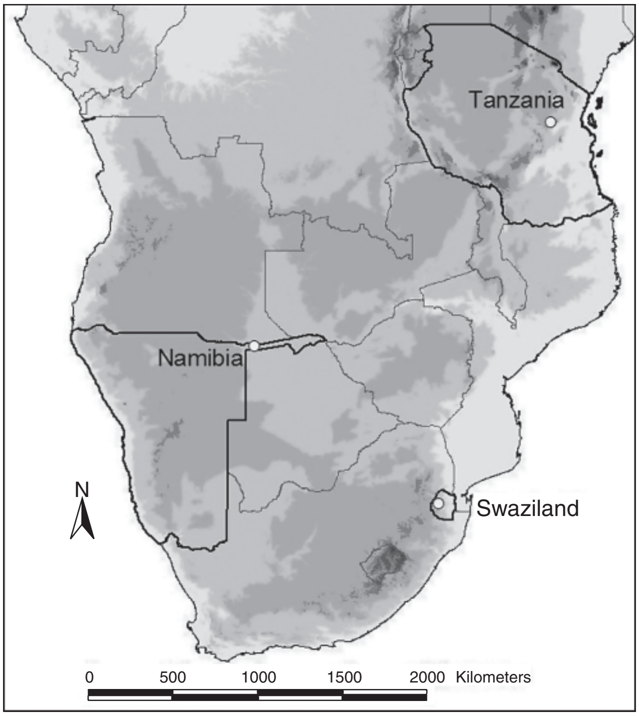

Fig. 1. Map of the southern half of Africa showing the distribution of the three study sites in Swaziland, Namibia and Tanzania. The sites are overlaid on a digital elevation map to show that all three are situated at similar altitudes (700–1000 m above sea level).

Data collection

This study was divided into three components. First, a survey was conducted to determine the rodent species composition in and around homesteads at each site. Second, we followed the movements of *M. natalensis* and *R. rattus* by radio-tracking. Third, we used bait marked with rhodamine B (RB) to assess how far rodents move from houses into surrounding fields.

Rodent species composition

We trapped rodents in and around homesteads within agro-ecosystems in Swaziland, Namibia and Tanzania using a combination of Sherman live traps (HB Sherman Traps Inc., Tallahasee, Florida, USA) and break back snap traps (Supa-kill, South Africa). We set 100 traps for three nights per month for 12 months at each of the three sites. All trapped rodents were sexed, weighed and measured according to standard museum protocol. A total of 1067 rodents were trapped in Swaziland, Namibia and Tanzania and deposited in the collections (skins, skulls and tissues) of the Durban Natural Science Museum and the National Museum of Namibia. Identification was based on a combination of morphological and molecular criteria. Morphological identification used existing keys for southern Africa (Skinner and Chimimba 2005) and Tanzania (www.fieldmuseum.org/tanzania/) based on skins and skulls. Molecular identification involved analysing complete Cytochrome-*b* sequences from 102 specimens with ambiguous or incomplete morphological identifications. DNA sequencing was conducted in the School of Biological and Conservation Sciences at the University of KwaZulu-Natal. The details of this study will be published elsewhere.

Telemetry

Rodents were captured with Sherman live traps in and around homesteads (typically within 10 m of a building, but up to 50 m away in surrounding maize fields). The traps were checked at sunrise the following morning and captured rodents were fitted with a radio-transmitter (Biotrack PIP2, Biotrack, Dorset, UK) that was fastened around the neck with a cable tie. The radio-collar (transmitter and cable tie) had a mass of 1.55 g (±0.06) representing 4% of the body mass of the smallest *M. natalensis* tracked and < 2% of the mass of *R. rattus*. In both Swaziland and Namibia, 20 individual *M. natalensis* were fitted with radio-collars, whereas 20 individuals of *R. rattus* were fitted with radio-collars in Tanzania.

Radio-collared rodents were kept in standard rodent cages during the day and released at the exact point of capture at sunset, and then followed for three consecutive nights using a radio-receiver (Biotrack Sika, Biotrack, Dorset, UK) and yagi antenna. The location (latitude and longitude using a Global Positioning System), direction of signal and signal strength of each rodent was obtained every 15 minutes. Signal strength of the transmitter was calibrated at each study site by measuring signal strength at varying distances away from the receiver. In uncluttered and open terrain, full signal strength was obtained when the receiver was 5 m away. We attempted to obtain full signal strength for each fix, especially when the rodent was in or around buildings. Rodents were tracked throughout the night from sunset to sunrise, and we attempted to get a minimum of 50 fixes per individual.

For *M. natalensis*, individuals were tracked in three different seasons related to the development of crops: pre-harvest 2008 (2–4 weeks before the crop was harvested); post-harvest 2008 (3 months after the crop was harvested); and pre-planting 2008 (2–4 weeks before the next crop was planted). In Swaziland, these three periods were in March, July and November 2008, respectively, whereas in Namibia, they were in April, August and December 2008. In Swaziland, six individuals were tracked in March and in July, and eight individuals in November. In Namibia, six individuals were tracked in April, and seven individuals in December and in August.

For *R. rattus*, all 20 individuals were tracked from late October to early November, corresponding with the post-harvest period. None of the transmitters were recovered.

Fixes were mapped using ArcView 3.2 (ESRI, New York). The locations of all fixes were corrected using the extension 'Bearing and Distance 1.1'. Subsequently, using the extension 'Home Range' (Rogers and Carr 1998), the home-range area of each rodent was calculated by the minimum convex polygon (MCP).

Rhodamine B

Rhodamine B is a non-toxic dye that has been used as a bait marker around the world (Aplin *et al*. 2003; Mohr *et al*. 2007). Rhodamine B is typically mixed into bait and left out for rodents to consume. Once it has been ingested by the rat, it becomes detectable in the whiskers under UV light for up to several weeks (Jacob *et al*. 2002).

We used a concentration of 0.2% RB (Sigma-Aldrich, product no. R6626) mixed into conventional bait (e.g. peanut butter and oats), which was the equivalent of 2 g RB in 1kg of bait. Bait mixed with RB was placed in 10 homesteads at Lobamba, Swaziland and at Berega, Tanzania. A 50 g unit of bait was placed in each building within a homestead, where rats were most likely to come into contact with it. Baiting was continued for four consecutive nights.

We trapped rodents five nights after the commencement of baiting. Rodents were trapped at incremental distances from the buildings where the RB bait was placed as follows: 0 m, 20 m, 50 m, 100 m and 200 m. Twenty-five traps were placed at 0 m, 20 m and 50 m, whereas 50 traps were placed at 100 m and 200 m. At the Swazi site, no trapping was conducted at 0 m (i.e. within the buildings), and in Tanzania no trapping was conducted at 200 m. Trapping was continued for three consecutive nights.

Six whiskers, including the follicle, were removed with tweezers from both sides of the snout from all captured rodents. These whiskers were stored separately for each individual in an Eppendorf tube until further analysis. Each whisker was placed on a glass slide in a drop of water and covered with a cover slide. The whisker was then examined under a fluorescent microscope (UV light at 530–585 nm) and in low magnification for any signs of fluorescence.

All the procedures described in this study that deal with living animals followed the Animal Ethics guidelines as laid out by the University of Swaziland.

Data analysis

A one-way ANOVA was used to test for differences in home-range area of *M. natalensis* between the three seasons, separately in Swaziland and Namibia, and a *t*-test was used to test home-range area between these two countries.

Results

Species richness and composition of rodents inhabiting agro-ecosystems differed between the three sites (Table 1). Five species were captured in Swaziland where the community was dominated by *Mastomys natalensis* and *Rattus tanezumi*. Eight species were captured in Namibia, where *M. natalensis* was numerically dominant and no *Rattus* species were present. Twelve species were captured in Tanzania with *M. natalensis* and *R. rattus* accounting for almost half of the specimens.

In Swaziland, mean home-range area (± s.e.) of *M. natalensis* was 4152 (± 892) m^2 (Fig. 2). Mean home-range areas differed between the seasons ($F = 4.56$, df = 2, 14, $P = 0.03$), with post-harvest areas significantly larger than either pre-harvest or pre-planting areas (Tukey test, $P = 0.025$). In Namibia, mean home-range area (± s.e.) of *M. natalensis* was 4407 m^2 (± 839) (Fig. 2), and did not differ between the seasons ($F = 0.6$, df = 2, 13, $P = 0.563$). There was no difference in the mean home-range areas of *M. natalensis* between Swaziland and Namibia ($t = 0.21$, df = 30, $P = 0.837$).

Radio-tracked *M. natalensis* in Swaziland stayed predominantly in the fields. Just one of the tracked mice entered a house or building, and even for this individual less than a quarter of the fixes were from within a house. In contrast, mice regularly entered buildings in Namibia, but only in the post-harvest season where six of the seven tracked individuals were found within buildings. Three of these six individuals spent the entire time that they were tracked in buildings, with two more individuals spending at least half their time in buildings. However, no mice entered houses or buildings in Namibia in the pre-harvest or pre-planting season.

Radio-tracked *R. rattus* in Tanzania were predominantly (72% of fixes) located in houses or buildings, rarely leaving the house in which they were initially captured and fitted with radio-collars (Fig. 3). Within the houses or buildings, rats were located in the roof (37% of fixes), in the bedroom (35%), kitchen (14%) and in walls and windows (14%). Rats rarely ventured outside houses (Fig. 3), but when they did, they were either located in the firewood pile (50%) or in a neighbouring building (50%).

In Tanzania, *R. rattus* ($n = 23$) was only captured within houses, whereas *M. natalensis* ($n = 22$) occurred at various distances away from the buildings (Fig. 4*a*). In Swaziland, *M. natalensis* ($n = 117$) was practically the only species captured outside of houses (Fig. 4*b*). In Tanzania, 20 out of 24 individuals that had taken RB bait were either *R. rattus* or *M. natalensis*, whereas in Swaziland all 11 RB-positive

Table 1. Species composition of small mammals inhabiting agro-ecosystems in three widely separated sites in southern and eastern Africa
Values in brackets are percentages of the country total

Order and species	Swaziland	Namibia	Tanzania
Rodentia			
Mastomys natalensis	164 (54.1)	314 (79.9)	78 (21.0)
Rattus rattus			92 (24.8)
Rattus tanezumi	122 (40.3)		
Mus spp.	1 (0.3)	14 (3.6)	4 (1.1)
Lemniscomys rosalia	15 (5.0)		9 (2.4)
Dendromus mystacalis	1 (0.3)		
Aethomys spp.		11 (2.8)	5 (1.3)
Saccostomus campestris		12 (3.1)	
Gerbilliscus leucogaster		23 (5.9)	
Thallomys nigricauda		9 (2.3)	
Steatomys pratensis		7 (1.8)	
Paraxerus cepapi		3 (0.8)	
Acomys spinosissimus			6 (1.6)
Arvicanthus neumanni			65 (17.5)
Graphiurus cf. murinus			4 (1.1)
Lemniscomys zebra			5 (1.3)
Gerbilliscus vicinus			58 (15.6)
Grammomys sp.			3 (0.8)
Soricomorpha			
Crocidura hirta			42 (11.3)
Total species (specimens)	**5 (303)**	**8 (393)**	**12 (371)**

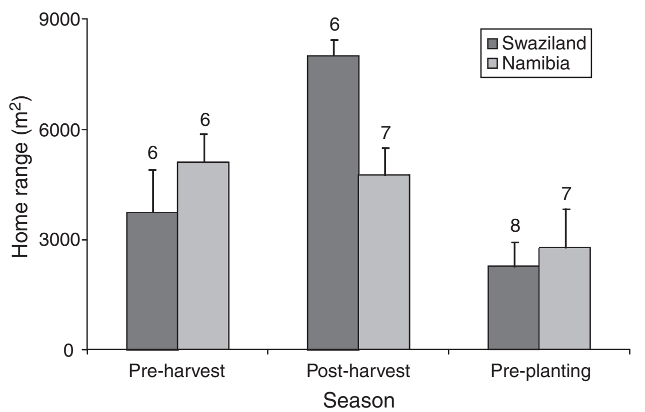

Fig. 2. Graph showing home-range areas ± s.e. (m^2) of *Mastomys natalensis* in Swaziland and Namibia in three different cropping seasons: pre-harvest, post-harvest and pre-planting. Values above bars represent sample sizes.

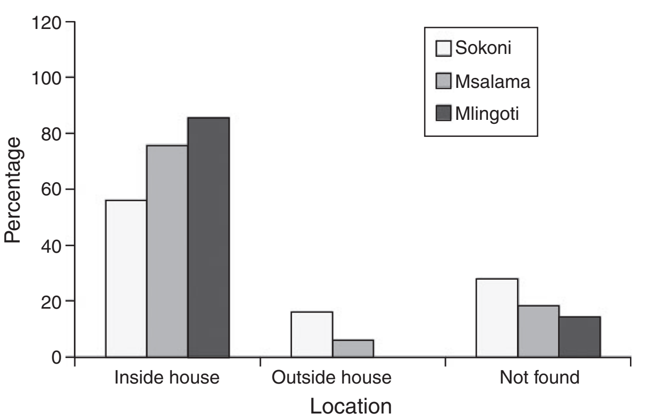

Fig. 3. Graph showing the percentage of fixes from radio-tracked *Rattus rattus* located inside and outside houses and buildings at the hamlets of Sokoni ($n = 6$), Msalama ($n = 7$) and Mlingoti ($n = 7$) in Berega, Tanzania.

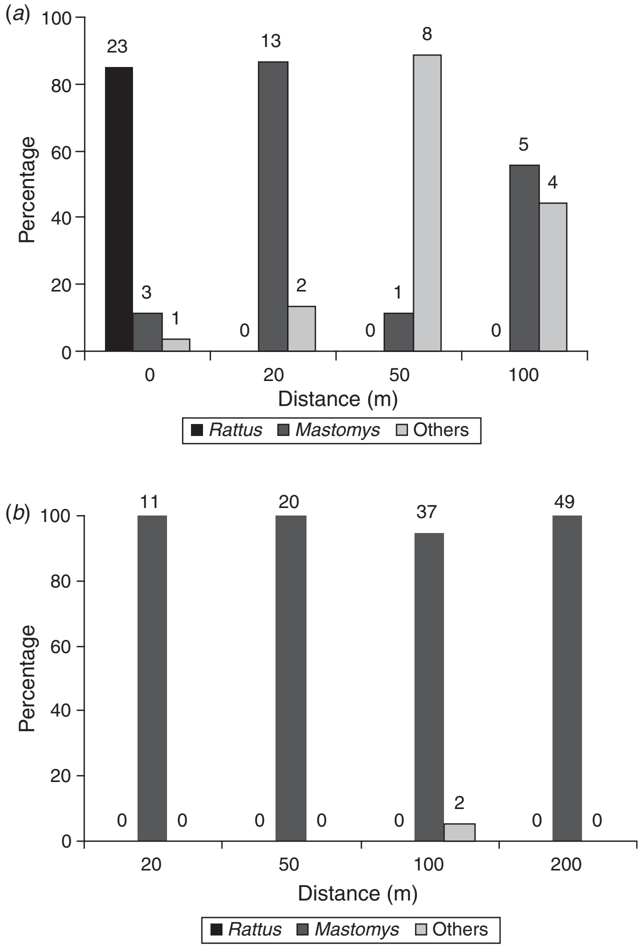

Fig. 4. Graph showing composition of rodents at different distances from the location of rhodamine B bait stations placed within houses (as a percentage of the total number of rodents captured at each distance category) for (*a*) Tanzania and (*b*) Swaziland.

rodents were *M. natalensis*. In both Tanzania and Swaziland, the percentage of RB-positive animals decreased with distance from buildings. In Tanzania, 14 of 23 *R. rattus* trapped within buildings were RB positive, whereas none of the *R. rattus* trapped outside of buildings were RB positive. For *M. natalensis*, the number of RB positive individuals was two, three, zero and one for 0 m, 20 m, 50 m and 100 m away from buildings, respectively. In Swaziland, the number of RB positive individuals of *M. natalensis* was four, four, three and zero for 20 m, 50 m, 100 m and 200 m away from buildings, respectively.

Discussion

Species richness of rodents in our three study sites varied from five to twelve, and appeared to be inversely correlated with latitude. Species richness was highest in the Tanzanian study site (6°S), lowest in the Swazi site (26°S), and intermediate in the Namibian site (19°S). This trend in species richness decreasing away from the equator is not surprising as it has been shown for a variety of mammal groups in Africa (Turpie and Crowe 1982; Eeley and Foley 1999; Burgess *et al*. 2000), but has not been discussed in relation to African agro-ecosystems. The reasons for this trend may be related to a decline in the pool of species available to colonise agro-ecosystems with increasing distance from the equator. For example, 11 species of small mammal were previously captured in a protected area (Mlilwane Wildlife Sanctuary) neighbouring the Swazi study site (Monadjem 1999), whereas species richness in the surrounding natural habitats in Tanzania may be much higher (e.g. Stanley and Hutterer 2007; Mulungu *et al*. 2008). However, other factors may also be important in affecting rodent species richness in agro-ecosystems, these include: the farming system, climate, distance to natural habitats, and degree of human conversion, which are all important factors for species richness of other taxonomic groups (Varchola and Dunn 1999; Weibull *et al*. 2003). To the best of our knowledge, this has not been investigated in an African setting.

In this study, two different species of *Rattus* were identified, based on Cytochrome-*b* sequences, with *R. tanezumi* in Swaziland and *R. rattus* in Tanzania. However, no species of *Rattus* were present at the Namibian site, which may be explained by the remoteness of this site. All *Rattus* species are alien to Africa (Skinner and Chimimba 2005), having colonised it by various routes over the past few hundred years (e.g. Tollenaere *et al*. 2010). We would argue that *Rattus* species have not yet had the chance to colonise the remote Namibian site. *Rattus tanezumi*, closely related to *R. rattus* (Robins *et al*. 2007, 2008), has only recently been discovered in sub-Saharan Africa (Taylor *et al*. 2008). The two species are morphologically very similar (Aplin *et al*. 2003), and their interactions with indigenous murids are assumed to be the same.

Home ranges of *M. natalensis* in Swaziland and Namibia presented here are similar to those previously reported from telemetry studies in natural vegetation in Uganda (Hoffmann and Klingel 2001), but between three and eight times larger than those reported from agricultural fields in Tanzania (Leirs *et al*. 1996*b*).

Interestingly, *M. natalensis* regularly entered houses in Namibia where *Rattus* species were absent. Furthermore, *M. natalensis* did not occupy houses evenly throughout the year, but only entered in the post-harvest period (corresponding to the dry season in Namibia). Rodent numbers in southern Africa typically peak during this season (Monadjem and Perrin 2003; Hoffmann and Zeller 2005; Avenant and Cavallini 2007). As a result, the post-harvest period may represent a critical period for *M. natalensis*, as the population is at its highest, yet food supply may be dwindling as a direct consequence of the harvesting of the maize crop. Furthermore, the post-harvest period typically falls during the austral winter when natural food supplies, such as insects (Lack 1986), are also in decline. Hence, food supply from both natural and agricultural sources are declining at the same time, compounding the severity of the shortage. *Mastomys natalensis*, however, only rarely entered houses in Swaziland or Tanzania. In contrast, *Rattus* spp. at both these sites rarely left the houses and associated buildings of the small-scale farmers. We suggest that *M. natalensis* is prevented from entering houses by the larger and possibly more aggressive *Rattus* spp. At the Swazi site, the mean (± s.d.) mass of *R. tanezumi* (83.1 ± 45.19 g; $n = 97$) was more than double that of *M. natalensis* (40.0 ± 17.21 g; $n = 135$), lending further support to this suggestion.

Although *R. rattus* rarely ventured beyond the houses and *M. natalensis* only entered houses infrequently, this observation was not absolute. Radio-tracked *R. rattus* occasionally left the buildings in which they were originally captured, and the RB study clearly showed that *M. natalensis* individuals were entering houses and retreating far into the surrounding fields, up to 100 m from the nearest buildings. Hence, *R. rattus* and *M. natalensis* may overlap in their use of resources, but the ecological and behavioural interactions between these two species are currently unknown and would make an interesting future study.

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