

Experimental treatment-control studies of ecologically based rodent management in Africa: balancing conservation and pest management

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Abstract

Context. Rodent pests severely affect crop production, particularly in monocultures where one or two rodent pest species dominate. We predict higher species richness of native small mammal species in more heterogeneous mosaic (crop–fallow–bush) subsistence agro-ecosystems in Africa. Conservation and agro-ecological imperatives require that such diverse natural communities should be maintained and may benefit crop protection through limiting domination of pest species. Ecologically based rodent-management alternatives to rodenticides are urgently required and one such method (community trapping) is herein advocated.

Aims. To provide baseline information on rodent and shrew communities in agro-ecosystems in three African countries and to demonstrate efficacy of ecologically based rodent management (EBRM) in Africa (e.g. community household trapping).

Methods. Removal-trapping in a variety of agro-ecological habitats provided accurate small-mammal species lists. Intensive kill-trapping by rural agricultural communities was carried out experimentally where the efforts of communities were scientifically monitored by kill-trapping to measure impact on rodent numbers and the levels of post-harvest damage to stored grains.

Key results. Our study revealed a high diversity of endemic species in agricultural habitats in Tanzania and Namibia (but not Swaziland) and the existence of undescribed and possibly rare species, some of which may be at risk of extinction from unchecked habitat transformation for agriculture. Treatment-control studies showed that communities in three African countries could effectively reduce pest rodent populations and rodent damage by intensive trapping on a daily basis in and around the community.

Conclusions. Community trapping reduced pest rodent populations and damage to stored grains. Unlike the use of indiscriminate rodenticide, this practice is expected to have a negligible effect on beneficial non-target rodent and shrew species.

Implications. Ecologically based rodent management approaches such as community trapping will conserve beneficial non-pest rodent communities and ultimately improve crop protection.

Additional keywords: Africa, DNA bar-coding, EBRM, ecology, management, rodents, taxonomy.

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Introduction

Worldwide, a few significant pest species of rodents negatively affect crop production (Singleton *et al.* 1999, 2003, 2008) and

public health (Taylor *et al.* 2008; Meerburg *et al.* 2009). In Africa, rodents constitute a persistent pest problem in small-holder farms (Makundi *et al.* 1999). Population densities of rodents, such as

multimammate mice, *Mastomys natalensis*, can be very high in agricultural and fallow fields (>1400 rats ha⁻¹ during outbreaks in Tanzania).

For at least a decade, ecologically based rodent management (EBRM) has been advocated as best practice, although studies have focussed on south-eastern Asia and Australia (Singleton *et al.* 1999, 2003, 2007, 2008; Stenseth *et al.* 2003; Brown *et al.* 2006; Sluydts *et al.* 2009; Jacob *et al.* 2010), with relatively few studies in Africa (Makundi *et al.* 1999; Leirs *et al.* 1996; Leirs 2003). EBRM addresses the need for a balanced approach that optimises both nature conservation and crop production and protection. Agricultural expansion may result in conservation threats to native small mammals from habitat alteration, introduction of niches better suited to introduced pest species, negative impacts of introduced species and negative consequences of rodent-control measures such as indiscriminate rodenticide use. A good understanding of small-mammal community dynamics and habitat-use patterns in agro-ecosystems is critical to finding a balance between the often conflicting imperatives of conservation and pest management (Aplin and Singleton 2003).

Habitat characteristics are important determinants of rodent species diversity; in more homogeneous habitats, the diversity of rodents is usually low (Monadjem 1997, 1999), although certain species tend to be abundant because of higher resource availability (Monadjem and Perrin 1998). In contrast, habitat heterogeneity allows more species to coexist because of availability of more niches (Aplin and Singleton 2003). In savannah regions of Africa, agricultural landscapes comprise a mosaic of agricultural fields, fallow land, pasture, indigenous savannah and woodland, which can harbour diverse communities of endemic rodents and shrews (Corti *et al.* 2005; Kirsten and von Maltitz 2005).

Because of taxonomic instability, species richness of African rodents remains vastly underestimated (see Corti *et al.* 2005, for a useful review for east Africa; also Barome *et al.* 2001; Fadda *et al.* 2001; Castiglia *et al.* 2003, 2006; Veyrunes *et al.* 2005; Carleton and Byrne 2006; Carleton *et al.* 2006; Taylor *et al.* 2009; Denys *et al.* 2011). In the past 20 years from 1988 to 2008, 45 new African rodent species have been described (Hoffmann *et al.* 2009) and the number of evolutionary lineages awaiting formal description remains high (Corti *et al.* 2005). Species diversity is also highly underestimated in African shrews (e.g. Dubey *et al.* 2007). Taxonomic instability and cryptic diversity is also true in the case of introduced rodents, such as those belonging to the genus *Rattus* (Aplin *et al.* 2003; Bastos *et al.* 2011). In our study, we used a combination of molecular and morphological methods to obtain accurate species lists for each study area and to try to flag undescribed or potentially range-restricted taxa that may merit conservation action.

From January 2007 to December 2009, the ECORAT project (www.nri.org/ecorat, accessed 1 November 2011) carried out research on rodent taxonomy, ecology and rodent–human interactions in rural communities in Tanzania, Namibia and Swaziland. The current paper presents the results from the ecological and taxonomic components of this research as well as the results of a treatment-control study to demonstrate the efficacy of intensive community trapping in terms of reduced rodent populations and reduced damage to storage grain. Other

aspects such as population dynamics, diseases and parasites, knowledge, awareness and practice surveys and rodent movement patterns are being reported separately (Monadjem *et al.* 2011; Mulungu *et al.* 2011).

On the basis of previous studies that have demonstrated a high diversity of rodent species in agricultural landscapes in southern (Kirsten and von Maltitz 2005) and eastern Africa (Corti *et al.* 2005), we expected to find high species richness of rodents and shrews and we predicted that species richness would be positively correlated with habitat heterogeneity and the extent of natural habitat persisting in the landscape matrix. We predicted that just a few commensal pest species would predominate in peri-domestic situations and that intensive household trapping should be equally effective in reducing rodent numbers and damage to stored grains.

Materials and methods

Study areas

The present study was conducted at three widely separated sites in three different African countries, Swaziland, Namibia and Tanzania, as a means to provide comparison across different contexts found within southern African savannah agro-ecosystems. 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 (and nearby villages of Kake and Andara), 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). 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 once savannah, but all have been transformed into a matrix of small-scale subsistence farmland and farmers' homesteads, with very little natural vegetation remaining, particularly in Swaziland. The main crops grown at the study sites are maize in Swaziland, millet in Namibia and maize and sorghum in Tanzania.

Habitat use trapping

Collecting of rodents in Tanzania, Namibia and Swaziland was undertaken with the approval of institutional ethics committees and existing arrangements between respective government agencies and the Sokoine University of Agriculture, National Museum of Namibia and University of Swaziland, respectively. Collecting permits were not required in any country for trapping of rodents in communal farming areas; however, in each country, permission to conduct the research was obtained from local communities after extensive preliminary discussions. Trapping, handling and euthanasia of rodents followed closely the Guidelines of the American Society of Mammalogists (Gannon and Sikes 2007); in particular voucher specimens of all sacrificed animals were deposited either in the Durban Natural Science Museum or the National Museum of Namibia. Veterinary import permits from the South African Department of Agriculture were obtained to import preserved rodents from

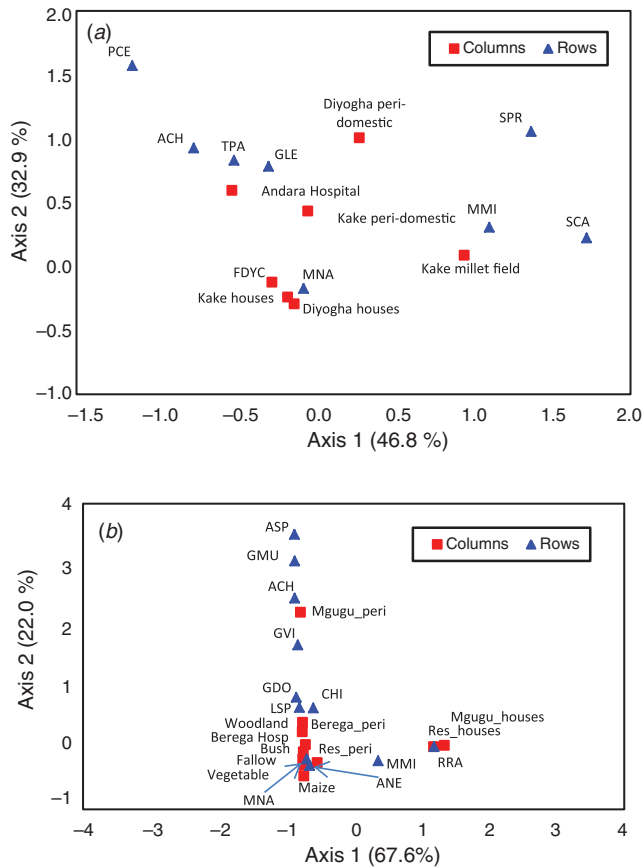


Fig. 1. Correspondence analysis plots, showing associations of trapping sites and species abundance (number of trapped individuals) for (a) Namibia and (b) Tanzania. Species codes are as follows: ASP=*Acomys* cf. *spinossissimus*, ACH=*Aethomys* cf. *chrysophilus*, ANE=*Arvicanthis neumanni*, CHI=*Crociodura hirta*, GLE=*Gerbilliscus leucogaster*, GVI=*Gerbilliscus vicinus*, GDO=*Grammomys* cf. *dolichurus*, GMU=*Graphiurus* cf. *murinus*, LSP=*Lemniscomys* spp., MNA=*Mastomys natalensis*, MMI=*Mus* cf. *minutoides*, RRA=*Rattus rattus*, SCA=*Saccostomus campestris*, TPA=*Thallomys paeudulus*, UNK = unknown.

Tanzania to South Africa (Permit numbers 13/1/1/30/1-195 and 13/1/1/30/9/8-46 for the two consignments).

Traps were baited with peanut butter and maize bran; they were set in the afternoon and checked early in the morning. Traps were operated for three consecutive nights. In Tanzania, the following two trapping regimes were followed:

- (1) Trapping was conducted in houses, peri-domestic areas and community places at intervals of 3 months between March, 2007 and February 2008. We placed three box and five Sherman traps at corners in houses and in their surroundings. The combination of trap types was used (both here and elsewhere) to avoid bias resulting from differential trap preferences of different species and to maximise the chance of comprehensively sampling rodent communities. For community places (schools, hospitals, markets), 35 traps (10 box and 25 Shermans) were set per site.

- (2) Trapping was conducted in different agro-ecological habitats (cultivated plots, fallow, bush and woodland) from March 2008 to February 2009. Each month, 25 snap and 25 Sherman traps were placed in each of the different habitats, totalling 50 traps per habitat in a 5 × 5 arrangement, with 10-m spacing between traps; the traps were operated for three consecutive nights for a total of 150 trap-nights per habitat per trapping session.

In Namibia, similar protocols were followed in which trapping was carried out in millet farms, areas inside and outside ('peri-domestic') of houses at Kake Village, Diyogha Village, Andara Hospital (surroundings) and a hostel (Frans Dimbare Youth Centre). In Swaziland, similar protocols were followed in which trapping was conducted in maize fields, adjacent fallow lands and grazing lands at Lobamba.

Community trapping

Intensive kill-trapping in communities with user-friendly break-back traps (SupaKill, Johannesburg, South Africa, www.supakill.com/), coincided with harvesting of staple crops in the three countries in 2008, namely in April 2008 in Swaziland, June 2008 in the Kavango, Namibia (June 2008), and in July 2008 in Berega, Tanzania. Rodent trapping for the purpose of monitoring of rodent populations was carried out continuously over a period of 12 months. Four communities (hamlets within villages) in each of the countries were selected to participate in the field activities of the project. Communities either conducted daily intensive kill-trapping (intervention) or continued with their indigenous rodent-control practices, including the use of cheap household rodenticides (non-intervention). Intervention and non-intervention villages/hamlets were located at least 1 km apart to ensure that the treatment (intervention trapping) did not affect results from non-intervention villages (a parallel study by Monadjem *et al.* (2011) of rodent movements at the same study sites, using radio-tracking and Rhodamine B baiting indicated that rodents rarely moved more than 200 m). Two intervention communities were each divided into quadrats, with an intensive trapping regime carried out in each quarter, moving cyclically through the community. Trapping was carried out nightly within the same households for a week before traps were relocated to the next quadrat, thereby rotating through all the households in the village on a monthly basis. Each community comprised ~200 households, meaning that ~50 households were trapping each week in each community, with two traps per household, i.e. 100 trap-nights per day per community. The non-intervention communities, two communities nearby (1 km from the intervention sites) that were similar in size and in habitat, served as the control. Meetings with the respective communities and their leaders were held in advance to organise the project activities. Designation of intervention and non-intervention communities for the intensive trapping regime formed the basis of the experimental design to compare changes in rodent populations and damage.

Post-harvest damage estimation

In Swaziland, the maize harvest is traditionally stored in 'rodent-proof' metal tanks. For this reason, we do not present data on rodent damage to stored maize in Swaziland. In Namibia and in

Tanzania, farmers store millet and maize, respectively, in sacks inside their homes, often in sleeping areas on the ground or on raised platforms. Rodent damage is known to occur throughout the storage period by farmers, who note the presence of faecal contamination and partially eaten grains. Because of the different traditional storage methods of each country and the type of crop stored, the trials in the two countries had different procedures. In all cases, sampling was carried out consecutively each month, during which the grain was inspected for evidence of rodent contamination (droppings and hairs) and weighed. Also, farmers' houses were randomly selected in the intervention and in non-intervention communities.

In Namibia, the trial consisted of two bags of millet, each 5 kg. One sack was enclosed in a small wire-mesh (rodent proof) and the second sack contained a larger-sized wire-mesh to prevent domestic animals from gaining access to the grain while still being accessible to rodents. The sacks of millet were admixed with an insecticide (permethrin/pirimiphos-methyl dust ('Actellic Super', Syngenta, South Africa) applied at 1% w/w) to enable losses to be assigned to rodents rather than insects, following the pack instructions and placed in the houses of 10 participating farmers per village, for a total of 40 houses for intervention and non-intervention communities. The insecticide used was tasteless and non-lethal to rodents, so was not expected to result in rodent avoidance of the grain. Because it is difficult to identify rodent damage to the individual millet kernel, the sacks were weighed only monthly to determine grain loss. A 300-g subsample of grain was taken from each sack every month after mixing, and the number of rodent droppings and rodent hairs was counted. The subsample was returned to each respective sack afterwards. The trial was monitored from January to July 2009.

In Tanzania, two types of storage structures were compared. Two households from each of five communities were randomly selected. The four treatments were as follows: sacks – open or closed and enclosed with wire-mesh in one household; and cribs or baskets – open or closed (and sealed with clay) in the second household. Each structure was replicated five times. Storage structures contained 90 kg of maize admixed with an insecticide (Actellic Super Dust) following pack instructions. Sampling was carried out by scooping four 250-g subsamples for a total of 1 kg per container. The maize kernels were separated into two groups, namely damaged and undamaged seeds. Kernels in each group were counted and weighed, and the percentages of damage and weight loss were calculated. A scale of rodent faecal contamination with five classes was developed as follows: 1 = no contamination (0 droppings per kg); 2 = slight contamination (1–10 droppings per kg); 3 = moderate contamination (11–20 droppings per kg); 4 = High contamination (21–50 droppings per kg); and 5 = severe contamination (>50 droppings per kg). The subsamples of maize kernels were returned to their respective sacks and mixed. The trial was repeated during the next crop-storage season with six households from five communities, from August 2008 to June 2009.

Taxonomy and identification

Sacrificed rodents were preserved in the field either by freezing (Swaziland), or by storage in formalin or 70% ethanol (Namibia,

Tanzania), after first dissecting soft tissue for preservation in 90% ethanol in 'Eppendorf' tubes for later molecular analysis. In all, 1069 specimens were deposited in the mammal collections of the Durban Natural Science Museum or the National Museum of Namibia. All tissue samples were sent to Durban where a subset was analysed at the School of Biological and Conservation Sciences, University of KwaZulu-Natal. Tentative identifications made in the field (from keys in Kingdon 1974, 1997; Skinner and Chimimba 2005; and the Tanzanian Online Mammal Key at www.fieldmuseum.org/tanzania/, accessed 1 June 2011) were confirmed where possible by careful measurement and inspection of cleaned skulls and alcohol skins. Standard mammal keys such as Misonne (1974) and Skinner and Chimimba (2005) were often inadequate for accurate species identification. Holden (2005), Musser and Carleton (2005), Corti *et al.* (2005) and recent generic taxonomic studies (*Acomys*: Barome *et al.* 2001; Verheyen *et al.* 2011; *Aethomys*: Castiglia *et al.* 2003; Russo *et al.* 2006; *Arvicanthis*: Castiglia *et al.* 2006; *Gerbilliscus*: Colangelo *et al.* 2007; *Grammomys*: Kryštufek 2008; Kryštufek *et al.* 2008; *Graphiurus*: Kryštufek *et al.* 2004; Holden 2005; *Lemniscomys*: Carleton and Van der Straeten 1997; *Mus* (*Nannomys*): Veyrunes *et al.* 2005) were consulted for the current genus and species nomenclature and taxonomy. Most of these studies (*op cit.*) included molecular analyses, most frequently entailing DNA sequencing of the Cytochrome-*b* gene, and thus providing a reference library of sequences available on the NCBI GenBank online database for DNA bar-coding of our rodent sequences as described in detail in Appendix A1, available as Supplementary material on the web.

Statistical analyses of trapping data

Statistical analyses were conducted in R2.11.1 (R Development Core Team, Vienna, available at <http://www.r-project.org>, accessed 22 August 2011). For both the rodent-trapping and grain-contamination and loss data, we built four models that allowed us to evaluate the effect of date (month of the year) and intensive trapping on the capture success of rodents within households in Swaziland, Namibia and Tanzania. The four models were (1) date, (2) intervention (trapping), (3) date and intervention, and (4) date, intervention and their interaction. Akaike's information criterion was calculated and used to select the best model.

To analyse patterns of association between habitats and rodent species, we conducted a correspondence analysis using the statistical package XLSTAT 2008.2.03 (Addinsoft 2008).

Results

Habitat use

In Swaziland, 309 individuals were captured in crop field, fallow and grazing-land habitats. The original woodland and savannah habitats, which would have prevailed in the study area, have been completely removed, leaving a relatively homogeneous open 'grassland' landscape dominated by cultivation. Except for 15 individuals of *Lemniscomys rosalia* and single individuals of *Mus cf. minutoides* and *Dendromus mystacalis*, all the other captures were *M. natalensis* individuals. No *Rattus tanezumi* was reported in crop, fallow or grazing habitats in Swaziland, although this

species was dominant in houses, as shown by the community-trapping results (below).

In Namibia, 393 individuals were captured during habitat surveys, of which *Mastomys natalensis* contributed ~80%. Other species included *Gerbilliscus leucogaster*, *Saccostomus campestris*, *Thallomys paedulus*, *Aethomys* cf. *chrysophilus*, *Mus* cf. *minutoides* and *Steatomys pratensis*. Six species were recorded in houses, i.e. they were commensal (Table 1). As indicated by correspondence analysis of the data from Table 1 (Fig. 1a), rodent communities differed among millet fields, houses (including Frans Dimbare Youth Centre) and peri-domestic areas (including Andara Hospital). At each of the seven trapping sites, *M. natalensis* outnumbered all other species combined (Table 1) and was clearly a generalist found in all habitats (as shown by its position near the origin of the plot in Fig. 1a). *M.* cf. *minutoides*, *S. pratensis* and *S. campestris* were associated with millet fields, and *T. paedulus*, *G. leucogaster* and *A.* cf. *chrysophilus* with peri-domestic areas and Andara Hospital (Fig. 1a).

At Berega in Tanzania, the relative abundance of rodents inside houses and peri-domestic areas is shown in Table 2, whereas that of agro-ecological habitats is shown in Table 2.

Our results suggest that *Mastomys natalensis*, *Rattus rattus*, *Arvicanthis neumanni* and *Crocidura hirta* were commensal (Table 2). In total, 1337 individuals belonging to 12 species of rodents and shrews were captured, of which *M. natalensis* contributed ~50% (Table 3). Whereas *M. natalensis* was dominant (80% of captures) in agro-ecological habitats (Table 2), it was less dominant (34% of captures) in houses and peri-domestic areas where *R. rattus* predominated (50% of captures; Table 2). As indicated by correspondence analysis, small-mammal community composition is surprisingly similar across a wide range of diverse habitats sampled, including cultivated (maize and vegetable), fallow, bush and woodland habitats, peri-domestic habitats and houses (Fig. 1b).

Community trapping

Mastomys natalensis was the dominant commensal rodent represented in community-trapping samples in Namibia, whereas two *Rattus* species were the dominant commensal species in Tanzania (*R. rattus*) and Swaziland (*R. tanezumi*). No *Rattus* was found in Namibian communities, although a larger variety of rodent species was trapped in Namibian households

Table 1. Number of rodents captured during the ‘habitat trapping’ program in houses, peri-domestic areas and millet fields at Kake and Diyogha villages, Kavango Province, Namibia, from June 2007 to May 2008

No invasive species of *Rattus* and *Mus* were captured, although the endemic *M. natalensis* is regarded as a major agricultural pest

Species	Kake millet field	Kake houses	Kake peri-domestic	Diyogha houses	Diyogha peri-domestic	FDYC	Andara hospital
<i>Mastomys natalensis</i>	42	82	13	127	6	7	37
<i>Gerbilliscus leucogaster</i>	1	6	2	3	4	0	7
<i>Saccostomus campestris</i>	10	0	1	1	0	0	0
<i>Mus</i> cf. <i>minutoides</i>	7	1	0	2	1	0	1
<i>Steatomys pratensis</i>	4	0	1	0	2	0	0
<i>Aethomys</i> cf. <i>chrysophilus</i>	0	1	2	2	0	0	7
<i>Thallomys paedulus</i>	0	0	1	2	1	1	3
<i>Paraxerus cepapi</i>	0	0	0	0	0	0	3
Unknown	0	0	0	1	0	0	1

Table 2. Number of rodents captured during ‘habitat-trapping’ program in peri-domestic areas, inside houses and public places and in fields, fallow land and woodland at Berega Village, Tanzania, from March 2007 to February 2008

Species	Residential		Public places				Agricultural and natural habitats					Total
	Peri-domestic	Inside house	Mgugu Secondary School		Berega hospital		Woodland	Bush	Maize	Vegetable	Fallow	
			Peri-domestic	Inside house	Peri-domestic	Inside house						
<i>Mastomys natalensis</i>	259	28	10	0	23	2	59	14	134	35	78	642
<i>Rattus rattus</i>	35	433	1	8	0	0	0	0	0	0	0	477
<i>Arvicanthis neumanni</i>	37	0	2	0	3	0	3	4	4	1	3	57
<i>Crocidura hirta</i>	32	7	14	0	4	1	19	4	2	4	3	90
<i>Gerbilliscus vicinus</i>	8	0	19	0	4	0	12	0	1	1	7	52
<i>Mus</i> cf. <i>minutoides</i>	1	1	0	0	0	0	0	0	0	0	0	2
<i>Lemniscomys</i> spp.	1	0	1	0	0	0	0	2	0	0	1	5
<i>Acomys</i> cf. <i>spinosissimus</i>	0	0	3	0	0	0	1	0	0	0	0	4
<i>Aethomys</i> cf. <i>chrysophilus</i>	0	0	1	0	1	0	0	0	0	0	0	2
<i>Graphiurus</i> cf. <i>murinus</i>	0	0	3	0	0	0	0	0	1	0	0	4
<i>Grammomys</i> cf. <i>dolichurus</i>	0	0	0	0	0	0	2	0	0	0	0	2
Total	373	469	54	8	35	3	96	24	142	41	92	1337

Table 3. Rodent species composition from intensive community trapping ('intervention villages') in the three countries

Species	Swaziland	Namibia	Tanzania
<i>Rattus</i> spp.	633	0	893
<i>Mastomys natalensis</i>	16	1010	53
<i>Mus</i> cf. <i>minutopides</i>	0	15	0
<i>Saccostomus campestris</i>	0	23	0
<i>Gerbillus</i> spp.	0	101	0
<i>Thallomys paedulus</i>	0	41	0
Other (not identified)	358	0	1

than in households of the other two countries (Table 3). Trapping results presented in terms of trap success showed that intensive trapping worked in reducing rodent populations in all countries (Fig. 2a–c). The AIC values for the effect of date and intervention in Swaziland, Namibia and Tanzania are shown in Table 4. In each country, the best model (with the lowest AIC value) was the interaction of date and intervention. Hence, the time of year, the trapping effort and their interaction are statistically related to rodents captured. Despite temporal fluctuations in relative abundance, communities with intensive trapping regimes (intervention) experienced a reduction in rodent populations in most months, compared with villages without community trapping (non-intervention). In general, intervention communities in the two countries where both intervention and non-intervention monitoring was conducted (Tanzania conducted only non-intervention monitoring and intensive-trapping) experienced a relative rodent population reduction of 48% (Swaziland) to 63% (Namibia) in comparison to non-intervention communities (data from Fig. 2a, b).

Post-harvest damage estimation

Millet in Namibia

Contamination and loss of grain was lower in the intervention than in the non-intervention villages (Fig. 3a). When contamination (number of droppings) was averaged across all households and sample sessions, non-intervention households recorded a mean of 18.1 droppings per sack, whereas intervention households recorded 7.6 droppings per sack. However, given the enormous fluctuations observed in our measurements of rodent droppings (presumably because of localised opportunistic, massive rodent-infestation or measurement errors), we treated these data with caution and did not attempt further statistical analysis. When percentage loss was averaged

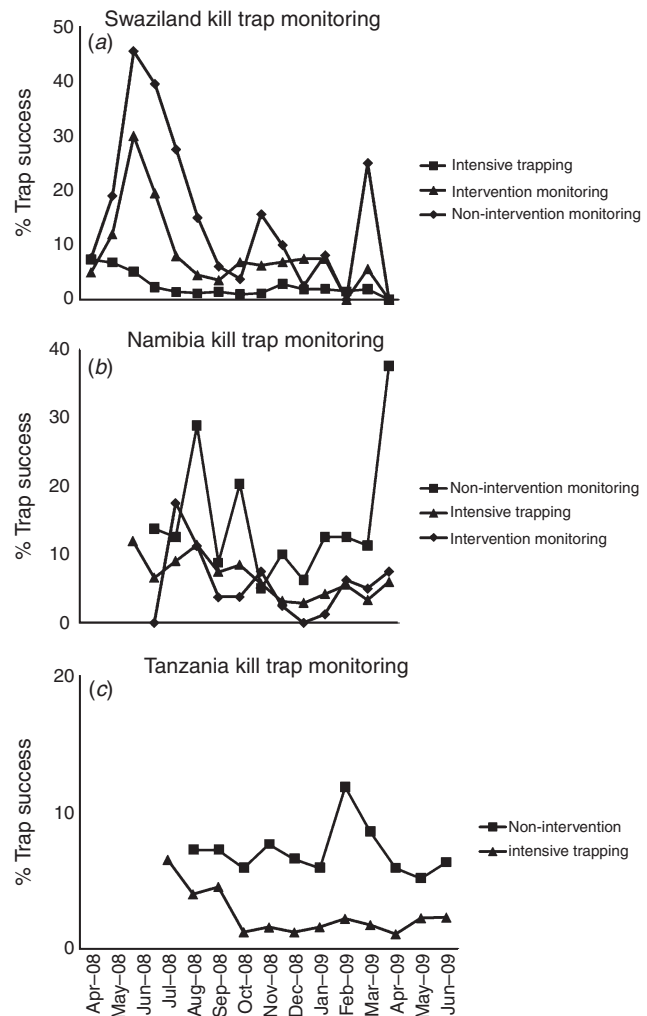


Fig. 2. Results of monitoring of intensive trapping with kill-traps in intervention and in non-intervention villages in the three countries (no monitoring with kill traps was conducted in intervention villages in Tanzania).

across all households and sample sessions, the difference between intervention (mean 12.2% grain loss, $n=95$) and non-intervention (mean 15.1% grain loss, $n=53$) was non-significant ($F_{1,147}=0.701$, $P>0.05$) and the linear model involving Treatment (intervention) alone showed the highest AIC value, whereas the model involving Date and Treatment independently (without interaction) had the lowest AIC value,

Table 4. Akaike's information criterion (AIC) values for four models fitted to explain changes in rodent numbers trapped in households in Swaziland, Namibia and Tanzania, and changes in damage to maize (as percentage and mass of damaged kernels) caused by rodents in households in Tanzania

The best model (with the lowest AIC value) is shown in bold

Model	Rodent numbers			% Damaged Tanzania	Mass damaged Tanzania
	Swaziland	Namibia	Tanzania		
Date	1761	431.2	379.7	2508.5	3025.8
Treatment	1105	445.6	413.4	2431.5	3033.3
Date + Treatment	777.6	358.1	294.2	2500.9	3022.0
Date × Treatment	769.7	343.7	283.8	2509.8	3026.2

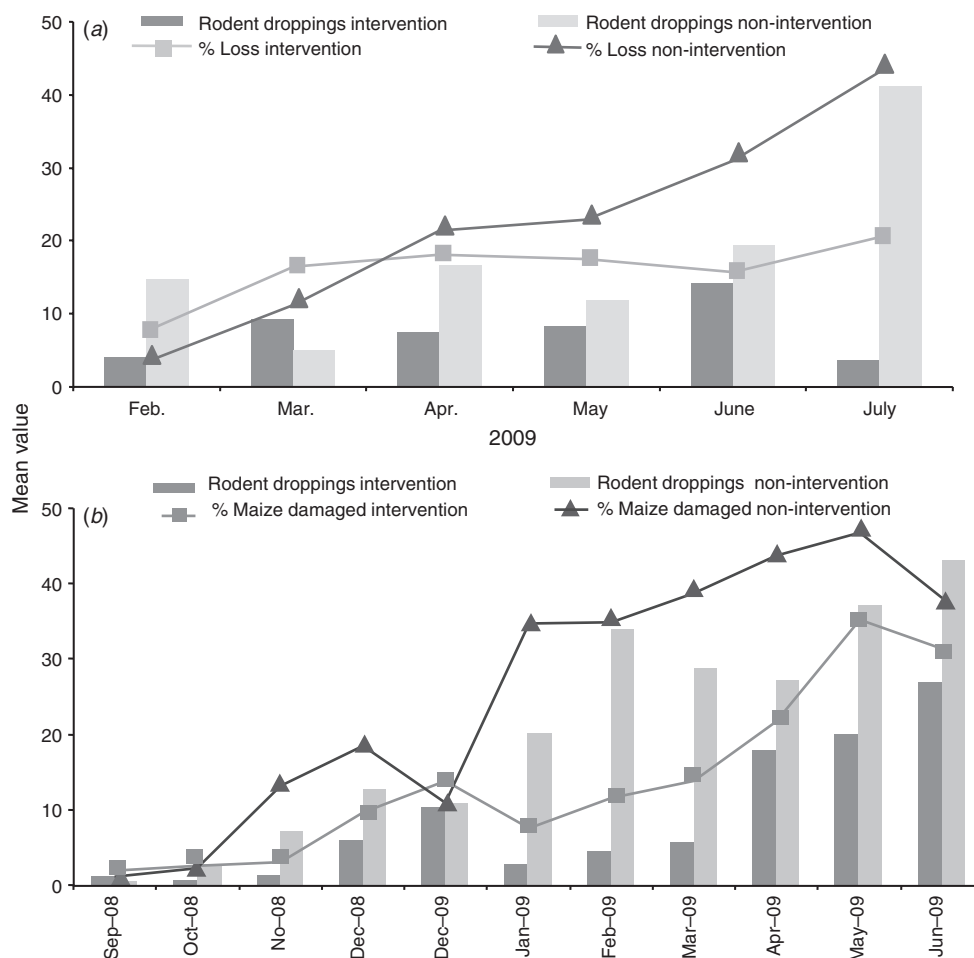


Fig. 3. Mean monthly rates of loss (percentage) and contamination (number of rodent droppings) caused by rodents (a) to bags of millet placed in farmers' stores in Kavanga Province of Namibia during 2009, and (b) to bags of maize placed in farmers' stores in Berega, Tanzania, over a period of 9 months in 2008/09.

although this was only marginally lower than the model for Date alone. Unavoidable biases in data collection, such as theft of millet from sacks by chickens, goats and children, losses in control sacks because of holes made by rodents and difficulty in accessing all households by field workers probably contributed to the non-significant results for the community-trapping intervention in Namibia.

Maize in Tanzania

Loss of maize as a result of rodent activity, as a percentage and mass of damaged kernels, was higher in the communities where no trapping (non-intervention) was carried out, compared with the intervention communities with continuous trapping (percentage of damaged kernels of 13.8% and 25.8% for intervention and non-intervention, respectively; mean mass of damaged maize of 33.8 g and 57.3 g for intervention and non-intervention, respectively; Fig. 3b). There was also an association with the level of rodent contamination (numbers of rodent droppings) which was higher in the non-intervention communities (mean of 8.8 and 20.4 droppings per sample for intervention and non-intervention, respectively; Fig. 3b). On the basis of AIC values,

the model that best explained variation in damage (for percentage damage and mass of damaged kernels) was Date + Treatment (without interaction) (Table 4). These variables together explained 19.9% and 12.9% of variation in percentage damage and mass of damaged kernels respectively ($F_{11,252} = 5.69$ and 3.40, respectively; $P < 0.001$).

Taxonomy and identification

Twenty-three terrestrial small-mammal species were collected from villages and surrounding agricultural lands in the three countries, comprising one shrew species (*Crocidura hirta*) and 22 rodent species. Twelve species were recorded from Berega in Tanzania, nine from Diyogha, Kake and Andara in Namibia and five from Lobamba in Swaziland (Table 5). Identifications were based on morphological, combined morphological and molecular or molecular data (Table 5).

In some genera, sequences obtained from sampled individuals did not closely match any known species, suggesting (1) very high intra-specific Cytochrome-*b* divergence values, (2) absence of sequences on GenBank of candidate species or (3) the existence of cryptic species within a species-complex.

Table 5. Identification (using morphological and, in some cases, molecular criteria) of rodent and shrew species from 16 genera on the basis of 1069 specimens collected between 2007 and 2009 in villages in three African countries included in the Ecorat Project (specimens currently housed in the Durban Natural Science Museum and National Museums of Namibia)

Species identified solely on morphological grounds are indicated in *italic* font; those identified solely on molecular grounds in ***bold italic*** font, and those identified by concordant molecular and morphological characters in ***bold italic and underlined***. Asterisks designate instances where molecular identification contradicted morphological identifications. Species names with 'cf.' indicate instances where the closest DNA match on GenBank exceeded 5% Cytochrome-*b* divergence; in cases where two or more divergent clades were identified within a monophyletic species complex; these are indicated as sp. 1, sp. 2, . . . sp. *x*

Taxon	Species		
	Tanzania	Namibia	Swaziland
Order Rodentia			
Family Sciuridae			
<i>Paraxerus</i>	<i>x</i>	<i>cepapi</i>	<i>x</i>
Family Gliridae			
<i>Graphiurus</i>	cf. <i>murinus</i>	<i>x</i>	<i>x</i>
Family Muridae: subfamily Gerbillinae			
<i>Gerbilliscus</i>	<i>vicinus</i> *	<i>leucogaster</i>	<i>x</i>
Subfamily Dendreominae			
<i>Dendromus</i>	<i>x</i>	<i>x</i>	<i>mystacalis</i>
<i>Steatomys</i>	<i>x</i>	<i>pratensis</i>	<i>x</i>
Subfamily Cricetomyinae			
<i>Saccostomus</i>	<i>x</i>	<i>campestris</i>	<i>x</i>
Subfamily Deomyinae			
<i>Acomys</i>	cf. <i>spinosissimus</i>	<i>x</i>	<i>x</i>
Subfamily Murinae			
<i>Aethomys</i>	cf. <i>chrysophilus</i> sp. 1	cf. <i>chrysophilus</i> sp. 2	<i>x</i>
<i>Arvicanthis</i>	<i>neumanni</i>	<i>x</i>	<i>x</i>
<i>Grammomys</i>	cf. <i>dolichurus</i>	<i>x</i>	<i>x</i>
<i>Lemniscomys</i>	<i>rosalia</i> , <i>zebra</i>	<i>x</i>	<i>rosalia</i>
<i>Mus</i>	cf. <i>minutoides</i> sp. 1	cf. <i>minutoides</i> sp. 2 and sp. 3	cf. <i>minutoides</i> sp. 4
<i>Mastomys</i>	<i>natalensis</i>	<i>natalensis</i>	<i>natalensis</i>
<i>Rattus</i>	<i>rattus</i>	<i>x</i>	<i>tanezumi</i> *
<i>Thallomys</i>	<i>x</i>	<i>paedulus</i> *	<i>x</i>
Order Soricomorpha: family Soridae			
<i>Crocidura</i>	<i>hirta</i>	<i>x</i>	<i>x</i>

Discussion

As shown by the results of our study and previous studies (Corti *et al.* 2005; Kirsten and von Maltitz 2005), EBRM efforts in Africa should be cognisant of the high diversity (both described and undescribed species) of endemic species found in some African agro-ecosystems. Species and genus richness seem both to increase from south to north towards the equator in southern Africa and also tend to be higher in heterogeneous bush–fallow–crop mosaic landscapes where a significant proportion of the savannah woodland matrix persists, such as e.g. Berega in Tanzania. Future EBRM efforts should address the importance of retaining natural islands and corridors of natural vegetation in agro-ecosystems because these clearly promote biodiverse small-mammal communities. Apart from the obvious conservation value of such a strategy, as advocated by the emerging field of agro-ecology (Gliessman 2007), the persistence of diverse small-mammal communities in heterogeneous natural habitats may benefit crop protection by competing with potentially invasive pest species of *Mastomys*, *Rattus* and *Mus* and by providing food sources and habitat for beneficial predators such as raptors and small mammalian carnivores. Insectivores such as shrews may play a positive role in controlling insects that are potential crop pests. Our study demonstrated the potential benefits of enhanced small-

mammal biodiversity in Tanzania and Namibia in terms of lower proportions of captures of the highly fecund pest species, *M. natalensis*, compared with the situation in Swaziland where highly transformed agro-ecosystems resulted in almost complete domination by *M. natalensis* in crop fields and *R. tanezumi* in houses.

Non-selective rodenticides that affect both pest and beneficial wildlife species are usually inappropriate and ineffective in small-scale subsistence agriculture. Despite this, acute and often illegal rodenticides were found to be in routine use at the sites included in the present study (Dlamini *et al.* 2008; Belmain 2010). Notwithstanding difficulties in conducting scientific experiments based in rural communities, the present study has shown that simple, environmentally sustainable methods, such as improved design of grain-storage structures and community-based trapping in houses and peri-domestic habitats are effective in reducing both rodent numbers and post-harvest crop damage while avoiding the environmental costs of rodenticides. Because they focus on trapping rodents in and around households that are dominated by invasive commensals, there is relatively little impact on sylvatic or endangered rodent species which are usually not situated close to or inside houses. Our data (Table 3) confirmed that intensive household trapping targeted only pest species (*Rattus* spp. and *M. natalensis*) in Tanzania and

Swaziland, and in Namibia it overwhelmingly targeted pest species (*M. natalensis* and *G. leucogaster*), with native species captures (*M. minutoides*, *T. paedulcus* and *S. campestris*) comprising only 7% of the total. Our study did not include the possible role of intensive trapping in reducing pre-harvest losses in the field and such studies are urgently required.

We acknowledge that our data were limited to a single year and rodent abundance and crop damage levels may vary from year to year. Population fluctuations of *M. natalensis* vary among seasons, years and localities, largely influenced by the amount and duration of rainfall (Leirs *et al.* 1989; Makundi *et al.* 2005). In years with abundant rainfall, food resources build up, increasing the survival of individuals within the population and leading to high densities of *M. natalensis*, with subsequent increase in crop damage (Leirs and Verheyen 1995; Makundi *et al.* 2010). In all countries included in the study, rainfall levels and rodent populations were considered to be 'normal' as neither drought or flooding occurred during the course of the study. EBRM techniques such as community trapping would be expected to be less effective than reported here during years with rodent irruptions and to be more effective than reported here during drought years with low rodent populations.

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