Spatial and temporal population dynamics of rodents in three geographically different regions in Africa: Implication for ecologically-based rodent management[†]

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As part of a three-year study to develop ecologically-based rodent management (EBRM) in southern Africa, a capture–mark–recapture study was carried out in Tanzania, Namibia and Swaziland to establish the demographic patterns and population dynamics of rodents. Two study grids were established in each country. In Tanzania, ten species of rodents and one shrew (*Crocidura* sp.) were identified in the study area. The rodent species consisted of *Mastomys natalensis, Aethomys chrysophilus, Arvicanthis neumanni, Gerbilliscus vicina, Acomys spinosissimus, Lemniscomys griselda, Lemniscomys zebra, Rattus rattus, Graphiurus* sp. and *Mus minutoides. Mastomys natalensis* was dominant and contributed more than 70% of the captures. In Namibia, five species were captured, namely *Mastomys natalensis, Gerbilliscus leucogaster, Saccostomus campestris, Mus minutoides* and *Steatomys pratensis. Mastomys natalensis* contributed about 50% of the captures. In Swaziland, only *M. natalensis* was captured in the study grids. There was a clear pattern in the population dynamics, with breeding confined to the wet seasons in the three countries. *Mastomys natalensis* was the dominant pest species, for which EBRM should focus on. The highest population density of *M. natalensis* occurred during and after the rains, which coincided with the most susceptible phenological stage of crops. The breeding seasonality and density fluctuations observed in the three countries conform with observations made elsewhere in Africa, which support the hypothesis that rainfall events promote primary productivity on which murid rodents depend. Development of EBRM in these countries will be determined by the local conditions and how they influence the demographic processes of the rodent populations. EBRM should make use of the available ecological knowledge of the local rodent pest species and the focus should be on (ecological) management practices applicable at the community level including community based intensive trapping, field hygiene, removing cover and sources of food for rodents.

Key words: **Tanzania, Swaziland, Namibia, recruitment, survival, capture–mark–recapture, pest management, *Mastomys, Aethomys, Arvicanthis, Gerbilliscus, Acomys, Lemniscomys, Rattus, Graphiurus, Mus, Saccostomus, Steatomys*.**

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INTRODUCTION

Rodent species show spatial and temporal fluctuations in numbers, which are ascribed to ecological and environmental factors. The underlying causes of density fluctuations are important considerations for developing ecologically-based rodent management (EBRM) systems around the world, particularly in Africa, where conventional management practices are most often not effective enough to reduce the damage and losses of crops (Makundi & Massawe 2010). Understanding the phenomenon that brings about marked fluctuations of rodent numbers both temporally and spatially has ecological, economic, epidemiological and management implications (D'Andrea 2007). Landscapes show heterogeneity geographically and in time; the variations have significant impact on the rodent assemblage (Utrera *et al.* 2000). An understanding of the spatial and temporal scale of population dynamics can provide us with insight into the processes that contribute to the dynamics (Steen *et al.* 1996). For example, populations can fluctuate in abundance synchronously over large regions, a phenomenon considered to be a response to some region-wide processes (Ranta *et al.* 1995). Conversely, some populations' exhibit fine-scale variability in demographic parameters, a phenomenon that suggests the contribution of local rather than regional processes (Krohne & Burgin 1990; Bowman *et al.* 2000). Various studies on rodents within the southern African region have been carried out to address the question of when, where and how crop damage occurs in order to propose ideas both for forecasting and for limiting their impact to agriculture by taking appropriate action at the right place and time (Leirs 1995; Mwanjabe & Leirs 1997; Makundi *et* al. 1999; Makundi *et al.* 2005; Makundi *et al.* 2009). Some of these findings, such as early warning systems for impending rodent outbreaks (Mwanjabe & Leirs 1997), have been incorporated in rodent control programmes in Tanzania. In sub-Saharan Africa, rodents are widely distributed in savanna, woodlands, secondary growth, forest clearings and cultivated fields (Kingdon 1974). Some of these species may invade cultivated fields, resulting in widespread crop damage particularly when the cropping cycle coincides with high population peaks. In rural farm settings in southern Africa, small plots of agricultural fields are often surrounded by bush and fallow land, making them prone to rodent infestation both at crop-sowing and the seedling stage during which the crops, particularly cereals are most susceptible to damage (Leirs *et al.* 1996; Mwanjabe & Leirs 1997; Mulungu *et al.* 2005; Odhiambo *et al.* 2005). Several studies have indicated that there is a strong climatic influence, particularly rainfall, on breeding and population dynamics of rodent species (Taylor & Green 1976; Leirs *et al.* 1989; Leirs 1992; Leirs *et al.* 1996). Outbreaks of some rodent species have been reported in many localities in sub-Saharan Africa (Taylor 1968; Leirs 1995; Leirs *et al.* 1996; Leirs 2003; Leirs *et al.* 2010). Leirs (1999) reviewed the different models that have been put forward by different authors (Sheppe 1972; Taylor & Green 1976; Hubert & Adam 1985; Leirs *et al.* 1996; Granjon *et al.* 2005) to provide an explanation for rodent outbreaks in different locations in Africa. Studies in Tanzania and elsewhere in eastern Africa suggest that large litter size (average 11–13 young/litter), several litters per season, increased survival and quick maturation are some of the demographic factors that favour high population turnover of *M. natalensis* within a short period (Telford 1989; Leirs 1992). Rainfall promotes abundant primary productivity of particularly nutritious seeds and vegetation cover, which enable natural habitats to maintain large numbers of the species (Delany 1972; Leirs 1992). Therefore, it is widely accepted that rainfall plays an indirect role in the ecology of *M. natalensis* by determining when, where and how much food will be available. Understanding the diversity, breeding patterns and density fluctuations of rodents in rural farming communities could be an important step towards using this knowledge for sustainable EBRM programmes. Therefore, the objective of the current study was to establish the species diversity, breeding patterns and density changes of rodents in areas neighbouring rural farming communities in Tanzania, Namibia and Swaziland. We hypothesized that the breeding patterns and high rodent densities will synchronize with rainfall in the study areas in Tanzania, Swaziland and Namibia.

MATERIALS & METHODS

Two permanent grids in field/fallow mosaics near rural communities were laid out in Tanzania, Namibia and Swaziland for capture–mark–recapture (CMR) trapping. In the three countries, permanent trapping grids could not be established in farmers' fields due to on-going agricultural activities and therefore they were set in neighbouring fallow land. In all the study areas, the cropping calendar depended on the timing of rainfall, with sowing of crops taking place immediately after it started raining. The major aim of the CMR trapping was to provide information about the population ecology of rodents in the study site. Therefore it was necessary for the CMR trapping to be carried out in permanent grids, which are not subject to disturbances such as those due to agriculture, grazing, etc. In Tanzania, the study was carried out in Berega village, Gairo Division (Kilosa District) at 06°10′S, 37°08′E, 830 m above sea level. The two permanent grids, abbreviated as TBA (Tanzania Berega A) and TBB (Tanzania Berega B) were 100 × 100 m each. Berega has a unimodal rainfall pattern in which December to May is the wet season, while July–October is the dry season. Tanzania Berega A (TBA) was initially under maize cultivation but was left fallow two years before the study. The vegetation in this grid was dominated by both annual and perennial grasses of several species. The grid was surrounded by crop fields planted with maize, beans, sweet potatoes and pigeon peas during the wet season. Grid TBB was set at a distance of 1000 m from grid TBA. The grid was permanently fallow, set in an area with thorny shrubs and scattered trees, and was also surrounded by fields of maize, beans and pigeon peas. In Namibia, the study was carried out in Kake village in the Kavango region in two grids, measuring 70 × 70 m, abbreviated as NKA (Namibia Kavango A) and NKB (Namibia Kavango B). The study area has a unimodal rainfall pattern, which extends from November to April, with an average of ±600 mm. The dry season in the Kavango region is from May to October. The Namibia Kavango A (NKA) study area was located at 18°05′20.7″S, 21°29′49.8″E at an elevation of 1026 m above sea level. The grid was located in fallow land often grazed by domestic animals. The grid had a mixture of clay and sandy soils. The vegetation cover included grass species: *Heteropogon contortus, Eragrostis trichophora, E. viscose, E. nindensis, E. superba, Schmidtia pappaphoroides, Aristida adscensionis* and *Urochloa oligotricha.* The commonest trees around the study site were *Acacia nigrescens, A. karoo, A. erioloba, Ximenia caffra, X. americana, Gymnosporia senegalensis, Terminalia prunoides, T. serricea, Strychnos cocculoides, Dichrostachys cinerea, Grewia bicolour* and *G. flavescens.* The study area, NKB, was located at 18°05′33.5″S, 21 30′10.5″E at an elevation of 1019 m above sea level and was fallow land. Compared to NKA, NKB had more intensive grazing and therefore had less vegetation cover and diversity. The NKB study area had a mixture of clay and sandy soils. The commonest trees surrounding the study site were *Acacia nigrescens, A. karoo, A. erioloba, Gymnosporia senegalensis, Terminalia prunoides, T. serricea, Strychnos cocculoides, Dichrostachys cinerea, Grewia bicolour* and *G. flavescens.* Identified grass species were the *Aristida congesta, A. adsecensionis, Stipagrostis uniplumis, Tragus berteronianus, Eragrostis trichophora E. nindensis, E. superba* and *Aristida adscensionis.* In Swaziland, the study was conducted in two 70 × 70 m grids, abbreviated as SLA (Swaziland Lombada A) and SLB (Swaziland Lombada B), in the Lobamba region. Swaziland Lombada A (SLA) was located at 26°48′83.5″S, 31°21′47.0″E at an elevation of 434 m above sea level in pristine land. Swaziland Lombada B (SLB) was fallow land located at 26°46′82.7″S, 31°22′08.3″E at an elevation of 413 m above sea level.

The Swaziland and Namibian sites experience a single hot wet summer (October–March) and a cooler, drier winter (April–September), with annual rainfall of 700–850 mm and 500–700 mm, respectively. The main crops grown at the study sites are maize in Swaziland, millet in Namibia.

Trapping was conducted from January 2007 to September 2009 in Tanzania, May 2007 – May 2009 in Namibia and January 2008 – August 2009 in Swaziland. Sherman live traps (H.B. Sherman Traps Inc., Tallahassee, FL, U.S.A.) were used at all sites and set for three consecutive nights at intervals of four weeks. A single trap was placed at each trapping station (49 traps per grid in Swaziland and Namibia and 100 traps per grid in Tanzania). Smaller grids were necessary in Swaziland and Namibia due to smaller fragmented habitats in comparison to Tanzania. Traps were baited with peanut butter mixed with maize bran/maize flour each afternoon and were inspected in the morning. Captured animals were taken to the field laboratory for processing. Animals were identified to genus or species level, toe-clipped for new animals, weighed and their reproductive status recorded. State of maturity or reproductive status as described and illustrated in Gurnell & Flowerdew (1990) was used. The position of the testes and condition of the vagina and nipples were noted as indicators of current breeding, previous breeding or juvenile status. Males were recorded as been in breeding if the testes were scrotal or abdominal and if the epididymal gubernacula is externally visible or not. Females were recorded as sexually

Table 1. Rodent species diversity and proportional composition in Tanzania, Namibia and Swaziland.

Species	Tanzania	Namibia	Swaziland
Mastomys natalensis	2286 (74.38)	222 (53.2)	217 (97.74)
Aethomys chrysophilus	239 (7.77)	0 (0)	0 (0)
Arvicanthis neumanni	30 (0.97)	0 (0)	0 (0)
Acomys spinosissimus	202 (6.57)	0 (0)	0 (0)
Gerbilliscus visina	199 (6.47)	0 (0)	0 (0)
Gerbilliscus leucogaster	0 (0)	116(27.8)	0 (0)
Lemniscomys griselda	84 (2.73)	0 (0)	0 (0)
Lemniscomys zebra	16 (0.52)	0 (0)	0 (0)
Mus minutoides	2 (0.065)	20 (4.79)	0 (0)
Grammomys sp.	1 (0.03)	0 (0)	0 (0)
Rattus rattus	1 (0.03)	0 (0)	0 (0)
Saccostomus campestris	0 (0)	48 (11.51)	0 (0)
Steatomys pratensis	0 (0)	11 (2.63)	0 (0)
Others	13 (0.42)	0 (0)	5 (2.25)
Total	**3073 (100)**	**417 (100)**	**222 (100)**

Numbers in brackets are percentage composition of each species.

active when the vagina was perforated or when they were visibly pregnant and whether nipples are swollen due to lactation. Pregnancies were identified by palpation. Animals were later released at the station of capture. The data were recorded and entered into a CMR data input program for analysis. Population size was estimated for each three-day trapping session using the M(h) estimator of the program CAPTURE for a closed population, which allows for individual heterogeneity (variations) in trapping probability. This estimator was selected after examining the data set through a series of tests looking for time, behaviour and heterogeneity effects. A discriminant function procedure selects the most appropriate model for the data based on these tests (White *et al.* 1982). A Student's *t*-test was used to compare both between and within grid variations in population abundances. Percentage number of breeding females (sexually active females) was calculated as a percentage of the total number of females captured in each month in the entire study period.

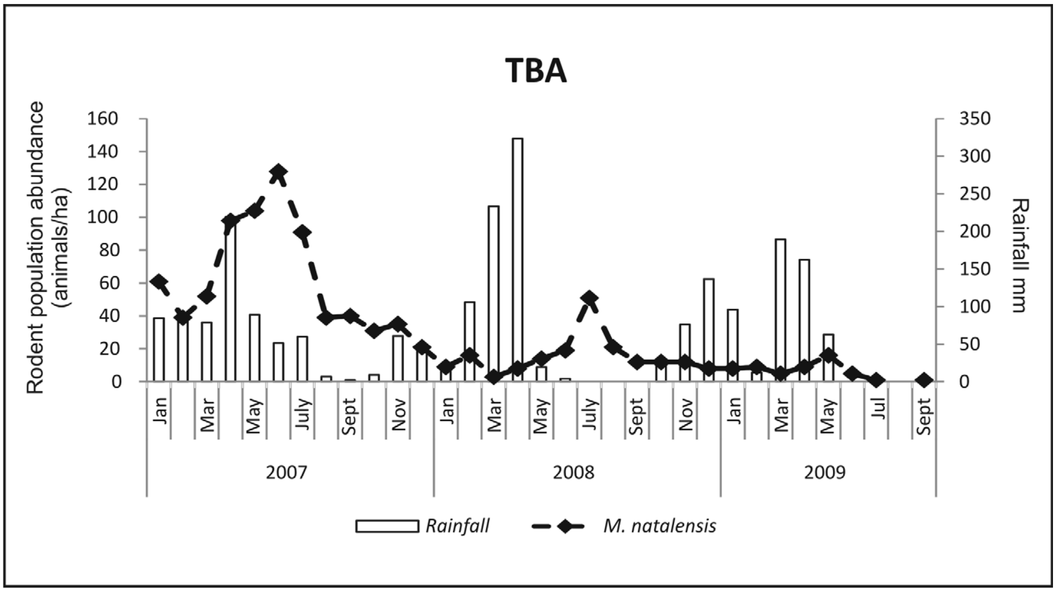
RESULTS

Species composition in the different study sites

In Tanzania, a total of 3073 individual animals belonging to 10 species of rodents (Table 1) and one shrew (*Crocidura* sp.) were captured in a total of 19 200 trap nights (16% trap success). *Mastomys natalensis* comprised more than 70% of the total capture. In Namibia, a total of 417 rodents (5 species – Table 1) were captured in 7076 trap nights (5.9% trap success), *M. natalensis* comprised more than 50%. The other species were *Gerbilliscus leucogaster, Saccostomus campestris, Mus minutoides* and *Steatomys pratensis.* In Swaziland, a total of 222 rodents were captured out of 5880 trap nights (3.8% trap success). Except for one unidentified species all the other captures were *M. natalensis.*

Rodent population abundance in Tanzania, Namibia and Swaziland

Temporal variations in population density changes were observed between seasons and years in the three countries (Figs 1A,B, 2 & 3). The highest population density of *M. natalensis* was observed in Tanzania in the TBB grid (137 animals/ha) in July 2007, where as the other species combined had densities of <10 animals/ha. Inter-annual variations in density of rodents were observed between grids, but in 2008 and 2009 the population densities were generally low in the two grids. In Namibia (Fig 2), rodent population densities were low throughout the study period, with abundance of *M. natalensis* in NKA being 20 animals/ha in 2007 and less than 12 animals/ha throughout 2008. For the other species, the population of *Saccostomus sp* reached 10 animals /ha, while *G. leucogaster* had a population density of 22 animals/ha during June 2007. In NKB only two



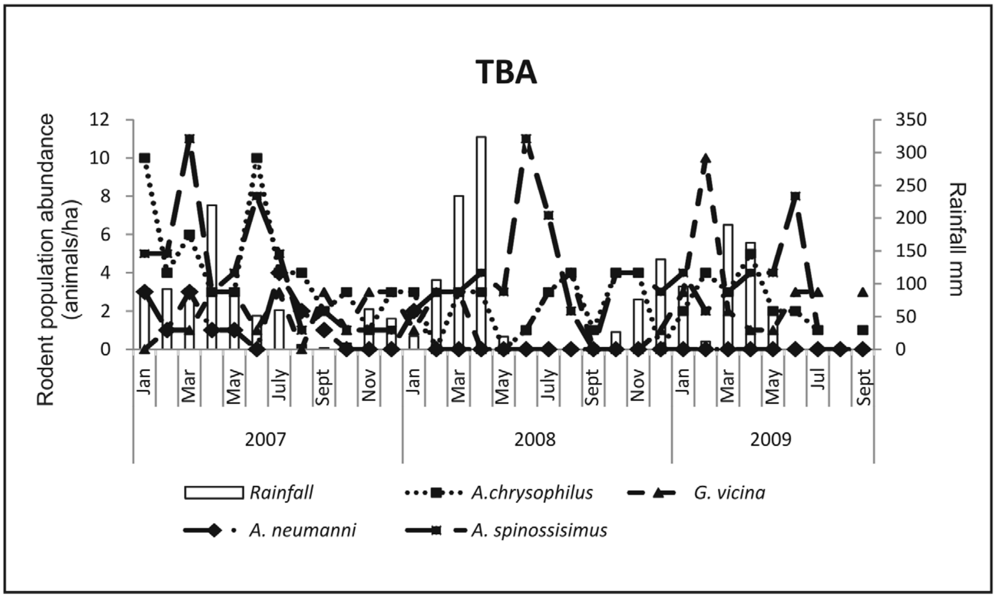


Fig. 1A. Rodent population densities (Mh estimator of the program CAPTURE) and fluctuations in time in the TBA study grid in Central Tanzania

species were captured (*M. natalensis* and *G. leucogaster*) with population densities of each species being ≤10 animals/ha.

In Swaziland, inter-annual variations in population density of *M. natalensis* were evident in both grids, with lowest population density (<4 animals/ha) in January–March in 2008 and 2009 (Fig. 3). The peak population density in SLA occurred in April 2008 (60 animals/ha) and June 2009 (34 animals/ha). In SLB trapping started late in November 2008 and, therefore, the data available are for 2009 when population density was highest in January (20 animals/ha) and lowest in March and November (2 animals/ha).

Significant temporal variations in rodent population density were observed in each of the three

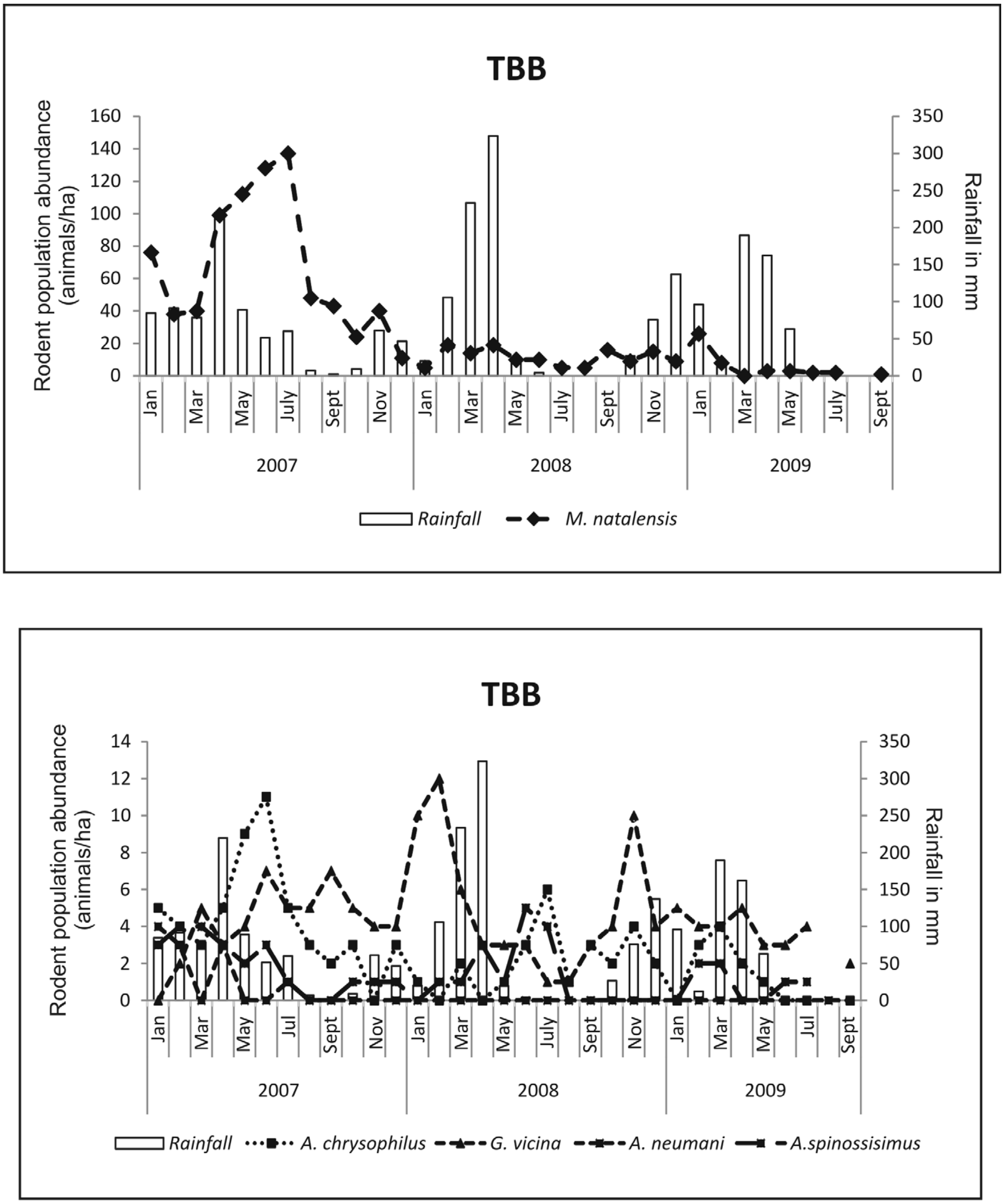
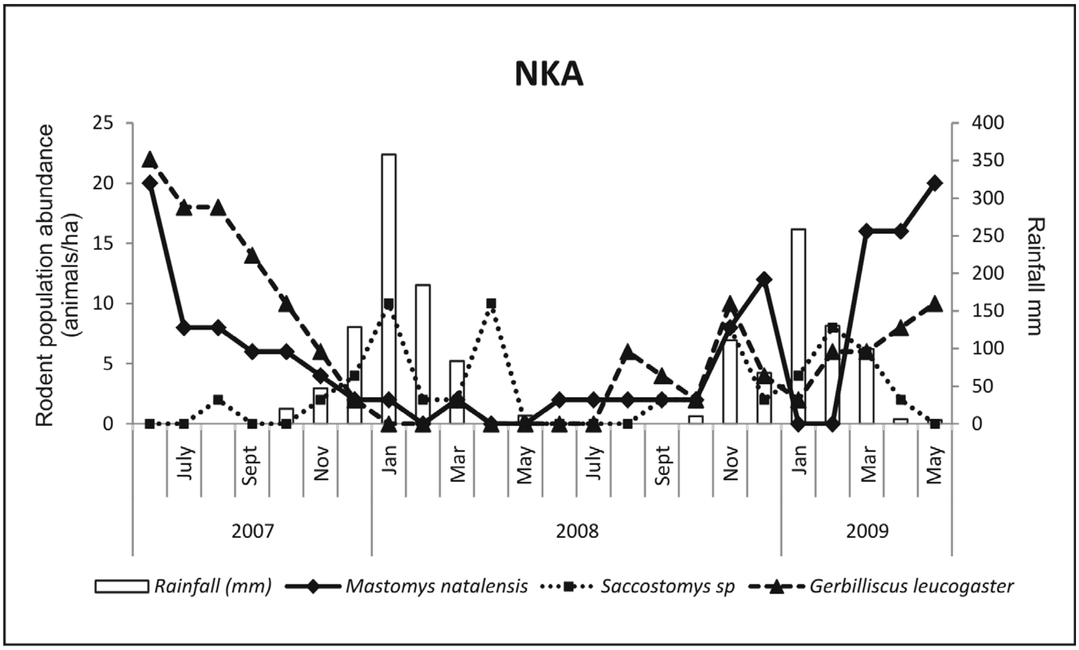


Fig. 1B. Rodent population densities (Mh estimator of the program CAPTURE) and fluctuations in time in the TBB grid in Central Tanzania

countries. In Tanzania, within-grid variation in densities were observed for the four dominant species: *M. natalensis* t = 12.463, P = 0.001; *A. chrysophilus* t = 107.804, P = 0.001; *G. vicina* t = 126.581, P = 0.001; and *A. spinosissimus* t = 104.536, P = 0.001. However, there were no significant differences (P > 0.05), in population density between grids TBA and TBB for *M. natalensis* and *A. chrysophilus,* while between grid population density differences were significant for *G. vicina* (t = 4.124, P = 0.0025) and *A. spinosissimus* (t = 6.573, P = 0.001). In Namibia, significant



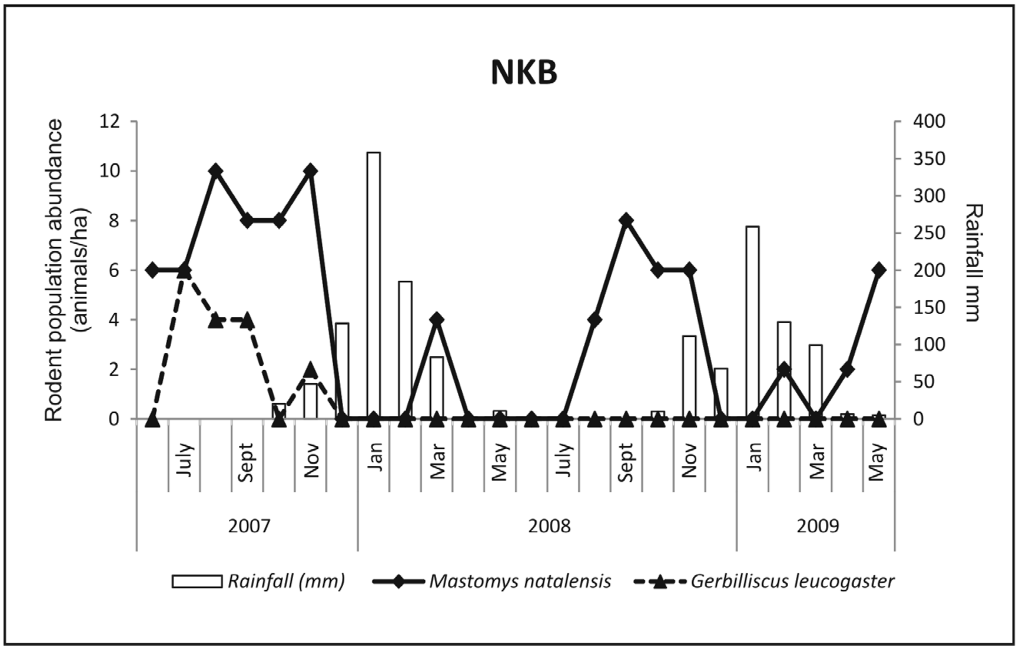


Fig. 2. Rodent population densities (Mh estimator of the program CAPTURE) and fluctuations in time in the two study grids in Namibia.

within-grid differences in population density were observed for *M. natalensis* (t = 67.448 P = 0.001), *S. campestris* (t = 137.00; P = 0.001) and *G. leucogaster* (t = 57.121; P = 0.001) in NKA. In NKB, *M. natalensis* (t = 83.424; P = 0.001) and *G. leucogaster* (t =115.936; P = 0.001) showed significant temporal differences in population density. For the two dominant rodent species in

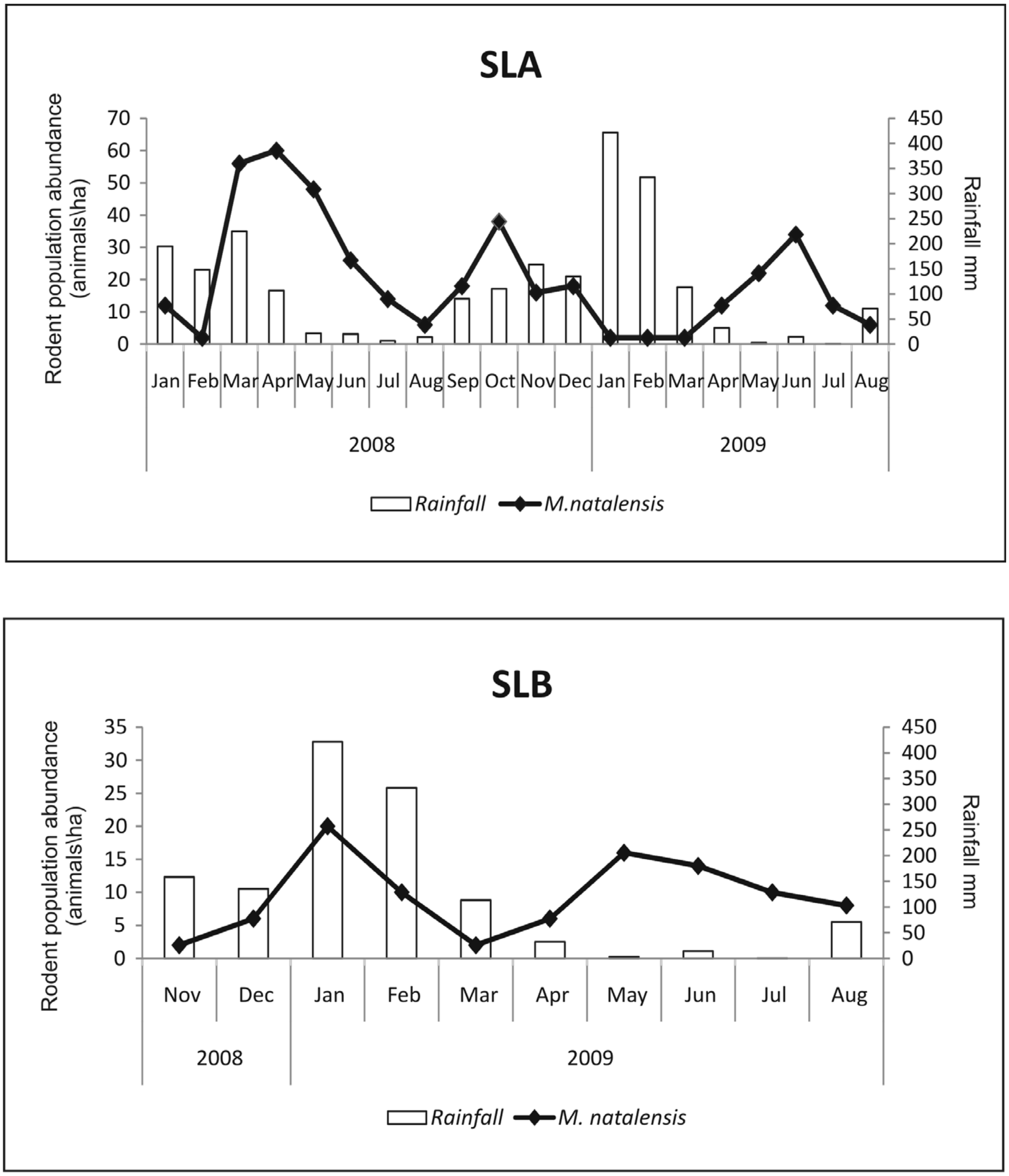


Fig. 3. Rodent population densities (Mh estimator of the program CAPTURE) and fluctuations in time in the two study grids in Swaziland.

Namibia, there were significant differences between grids in the population density of *G. leucogaster* (t = 4.916; $P < 0.05$), but not for *M. natalensis* ($P > 0.05$). In Swaziland, significant variations in the population density of *M. natalensis* were observed in the two grids (SLA1, t = 7.974; P = 0.001), SLB (t = 19.576; P = 0.001).

Breeding patterns of *M. natalensis*

Mastomys natalensis was the only species common in Tanzania, Namibia and Swaziland and was captured in large numbers. This allowed an analysis of breeding patterns for this species in the three countries. Figure 4 shows the proportion of the population of *M. natalensis* in active breeding condition in the three countries. In Tanzania, *M. natalensis* breeding season was synchronized to the rainfall pattern, with high proportions of female animals (>70%) in active breeding condition during the wet season in 2007, 2008 and 2009. Onset of active breeding in females was also evident in Namibia, with more animals in breeding condition during and immediately after the rainy season. In Swaziland, the breeding activity in female *M. natalensis* was extended but peaked during the wettest months of the rainy season. There was a small proportion or no animals at all in active reproduction during the driest months (August–January in Central Tanzania; June–October in Namibia and May–August in Swaziland).

DISCUSSION

The differences in species composition (ten species in Tanzania, three in Namibia and only one species in Swaziland) could be attributed to habitat differences, heterogeneity and complexity; this study could not address any diversity gradient between the geographical areas. It is, however, deduced that geographical and habitat differences affect population dynamics of the rodent species. Some populations exhibit fine-scale variability in demographic parameters, a phenomenon that suggests the contribution of local, rather than regional processes (Krohne & Burgin 1990; Bowman *et al.* 2000). The influence of rainfall on rodent population dynamics, particularly of *M. natalensis* in sub-Saharan Africa, has been reported by various authors (Duplantier & Granjon 1988; Telford 1989; Leirs *et al.* 1996; Monadjem 1998; Mahlaba & Perrin 2003; Makundi *et al.* 2005). Since *M. natalensis* was common to the three countries, any generalizations could only be made for this species. *Mastomys natalensis* appears to have adapted to local rainfall conditions in Tanzania, Namibia and Swaziland whereby breeding takes place in the wet season, with corresponding increases in population density. Breeding and population fluctuations of *M. natalensis,* which are synchronized, with the patterns of rainfall have been reported by various authors in sub-Saharan Africa and are attributed to the direct effects on primary productivity (Delany 1976; Fiedler 1988; Leirs *et al.* 1992; Makundi *et al.* 2009). Food availability affects maturation and survival, which increase during the wet season (Sluydts *et al.* 2008). When rains are extended and plentiful several generations with different productivity can occur (Leirs *et al.* 1993). Other habitat-related factors (e.g. availability of cover and nesting places), predation pressure (Van Gulck *et al.* 1998; Vibe-Petersen *et al.* 2006), intra-specific and inter-specific competition (Leirs *et al.* 1997) can influence rodent densities. From an ecological context, these factors are important in their overall regulatory effect on populations of rodents. For *M. natalensis,* studies in Tanzania have shown that predation and diseases do not have much influence on population dynamics (Van Gulck *et al.* 1998). However their influence on rodent population dynamics in Namibia and Swaziland is not known. Maximum population densities of approx. 140 animals/ha in 2007, 20 animals/ha in 2007 and 120 animals/ha in 2008 were observed in Tanzania, Namibia and Swaziland, respectively. In Tanzania, rainfall was much lower in 2009 than in 2007 and 2008 and population peak for *M. natalensis* was correspondingly lower than in the preceding years. The major question from this study is whether rainfall factor can explain the geographical variation in breeding patterns and densities changes over the wide area studied. It is important to note that *M. natalensis* is distributed throughout sub-Saharan Africa to southernmost South Africa (Kingdon 1974), and therefore demographically, between localities with different climate, we would expect differences in respect of when they breed and when populations rise and fall. The observed differences in the time of breeding and density changes on one hand, and the synchrony with rainfall patterns on the other, suggests a strong influence of rainfall on demographic processes of *M. natalensis* in the three countries. Previous studies in Tanzania indicated different patterns in rodent population density fluctuations that also corresponded with the respective rainfall regime in an area (Makundi *et al.* 2005). The studies conducted in Tanzania also showed that there is a causal relationship between rainfall and breeding, recruitment and population fluctuations of *M. natalensis* and several other species of rodents (Leirs 1992; Makundi *et al.* 2005; Sluydts *et al.* 2007; Makundi *et al.* 2009). It has also been observed that the duration and amount of the rainfall, irrespective of the timing will have some influence on the demographic characteristics of the local rodent fauna (Fiedler 1988; Telford 1989; Leirs 1995). Odhiambo *et al.* (2008 a,b) reported an increase in food availability for rodents in the form of seeds, foliage, roots and arthropods during the wet season in Central and Southern Tanzania, thus increasing the carrying capacity of suitable habitats for rodents. The observed patterns of

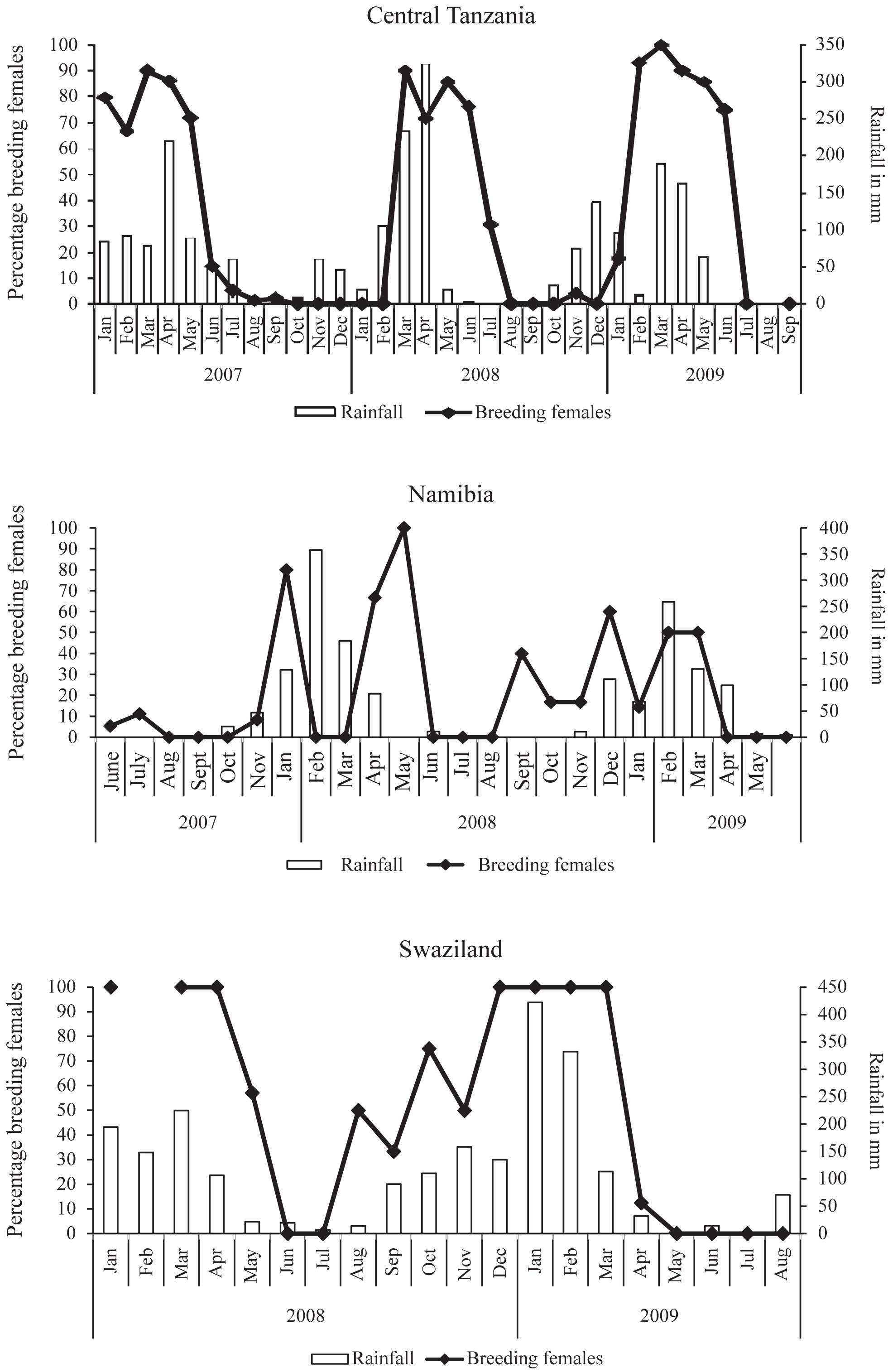


Fig. 4. Percentage number of breeding females *Mastomys natalensis* in Tanzania, Namibia and Swaziland.

population dynamics in the current study, do strongly suggest therefore that the causal relation of rainfall with breeding and density changes of M. *natalensis* observed in Tanzania will also apply in Swaziland and Namibia and probably in other countries in sub-Saharan Africa. Similar variations in rodent population fluctuations have been reported in various other locations in Africa (Hubert & Adams 1985; Fiedler 1988; Bekele & Leirs 1997). Delany (1986) reported that African murid rodent populations generally respond to rainfall through breeding which can be initiated by the appearance of new vegetation that may contain chemical substances that promote reproduction following rainfall (Van de Graaf & Balda 1973; Linn 1991).

The current study suggests that to develop 'Ecologically-based Rodent Management (EBRM)' in Africa, we need to establish how stochasticity in the environment affects the demographic processes, which determine the abundance of rodents in the field. The EBRM is basically a proactive rodent management system, based on the understanding of the ecology of the pest species. Such systems are under-developed in sub-Saharan Africa and therefore underline the need to increase our knowledge on the ecology of pest species. This knowledge will play an important role in the planning and implementation of management strategies of the pest rodent species. Over the 2–3 years of study in Tanzania, Namibia and Swaziland, the rodent populations, especially of *M. natalensis*, showed remarkable changes in density, varying annually and seasonally. Rainfall in the three countries was considered a key environmental determinant of fluctuating rodent densities, and therefore there is a potential for predicting impending outbreaks for this species. Leirs *et al.* (1996) used a logistic regression model to estimate the likelihood of a rodent outbreak occurring in areas with a bimodal rainfall pattern in Tanzania. This model allows for predictions that span over one agricultural season. Since each geographical area that was studied in southern Africa has its unique rainfall pattern, knowledge on how it influences the demographic processes of rodent species locally must be known for sound management strategies to be put in place. EBRM should focus on ecological management practices applicable at the community level such as community based intensive trapping, field hygiene, removing cover and sources of food, etc. These actions were promoted recently in Tanzania, Namibia and Swaziland during implementation of the ECORAT Project with evidence of rodent population reduction in the field, domestic areas and in houses (Belmain *et al.* 2008; ECORAT Report 2009).

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