

## Reproduction and survival of rodents in crop fields: the effects of rainfall, crop stage and stone-bund density

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### Abstract

**Context.** Reproduction and survival are two of the most important demographic factors that play a major role in changing population abundances of pest species over time and space, solid understanding of which is a useful input to forecast future population changes for proactive management.

**Aims.** We investigated the effects of rainfall, crop-development stage and density of stone bunds on reproductive patterns, and the effects of stone-bund density and sex on survival probabilities of two widespread rodent species (*Mastomys awashensis* and *Arvicanthis dembeensis*) in Ethiopian highlands.

**Methods.** Rodent population dynamics were monitored from April 2007 to February 2011, using capture–mark–recapture (CMR) technique in four 60 × 60 m permanent square grids for four consecutive cropping seasons. Two of the grids represented fields with low stone-bund density (LSBD, ~15 m apart) and the other two represented fields with high stone-bund density (HSBD, ~10 m apart).

**Key results.** Reproduction was seasonal, commencing during the wet season following the rain and continuing through the early dry season. We found an increase in the abundance of reproductively active female individuals of both species towards the milky and fruiting crop stages and around harvest period. We found no strong difference in survival probability between the two rodent species with variation in stone-bund density and sex.

**Conclusion.** Stone bunds play a minor role in the reproduction and survival of the rodent species at the observed abundances.

**Implications.** In terms of pest management, the high local survival rates estimated for both rodent species matter more than survival differences owing to variations in stone-bund density and sex.

**Additional keywords:** *Arvicanthis dembeensis*, Ethiopia, *Mastomys awashensis*, pest control.

Received 17 June 2014, accepted 27 December 2014, published online 22 May 2015

### Introduction

Agricultural-pest control managers are interested in understanding several aspects of the pest species they are dealing with, including the demography of the pest species, so as to help them design and implement appropriate management techniques (Witmer 2007). Reproduction and survival are two of the most important demographic factors that play a major role in changing population abundances over time and space, solid understanding of which is a useful input to forecast future population changes for

proactive management (Leirs *et al.* 1997a; Witmer 2007). Variations in the demographic factors in small mammals is a result of both density-dependent and density-independent processes (Leirs *et al.* 1997a; Aars and Ims 2002; Sluydts *et al.* 2007; Goswami *et al.* 2011). Density-independent factors such as type of crop, habitat complexity and climate are important considerations in design and implementation of ecologically based management strategies (Singleton *et al.* 2005; Witmer 2007; Power 2010; Chaplin-Kramer *et al.* 2011).

Rodent populations in sub-Saharan African agroecosystems often show pronounced temporal variations in numbers and structure (Leirs *et al.* 1994, 1997b). It appears that the generally accepted driving factor for the variations is a bottom-up trophic mechanism that involves a combination of intrinsic and extrinsic factors, including rainfall, plant biomass, reproduction and survival. This scenario has been rigorously reported elsewhere (Leirs *et al.* 1994; Brown and Singleton 1999; Madsen and Shine 1999; Previtali *et al.* 2009; Sluydts *et al.* 2009). The central issue is that seasonal rodent breeding is stimulated by sprouting annual and perennial vegetation following seasonal rains and that reproductive output and survival rates are affected by the quality and quantity of plant biomass.

In Meheretu *et al.* (2014), we highlighted that rainfall in the Tigray highlands of northern Ethiopia show considerable seasonal and annual variability, affecting agricultural production and cropping patterns. In response, crop fields are covered with stone bunds to curb soil erosion by runoff (Vancampenhout *et al.* 2006). Stone bunds are rock walls built from large basaltic or limestone rock fragments reinforced by gravel and soil (Nyssen *et al.* 2001). They are built following the contours of the topography, with an average height of ~1 m. In general, the morphology (height, width and length) of the stone bunds in crop fields is influenced by factors such as type of topography (e.g. slope, gully), size of neighbouring farms and amount of rock fragments in the field (Nyssen *et al.* 2001). The stone bunds have already demonstrated the advantages of reduced runoff and increased crop yield (Vancampenhout *et al.* 2006; Pender and Gebremedhin 2007). However, the most widely voiced negative effect of the stone bunds was that they act as refugia for rodents, and that high stone-bund densities in crop fields are associated with a high rodent abundance, leading ultimately to more crop damage (Gebremichael and Herweg 2000; Nyssen *et al.* 2001, 2007; Beshah 2003; Meheretu *et al.* 2010, 2014).

The two dominant, sometimes irrupting, pest rodents in Ethiopia and more generally in sub-Saharan Africa (Leirs *et al.* 2010) belong to two important genera, the multimammate mouse, *Mastomys*, and the African grass rat, *Arvicanthis* (Bekele *et al.* 2003; Meheretu *et al.* 2014). Several studies have documented the reproductive patterns of several species belonging to the two genera in Ethiopia (Bekele and Leirs 1997; Bekele *et al.* 2003; Gebresilassie *et al.* 2004, 2006; Wube 2005; Nyssen *et al.* 2007). However, virtually no information exists on the reproduction pattern and survival of *Mastomys awashensis* (Lavrenchenko, Likhnova & Baskevich, 1998) and *Arvicanthis dembeensis* (Ruppel, 1842), two of the dominant pest rodents in the northern highlands of Ethiopia. We also know little as to how these two species manage to coexist in the agroecosystem while sharing similar resources.

In an attempt to provide an insight into the pattern of reproduction of the rodent species in relation to variations in rainfall patterns and crop developmental stages and into the effect of variation in the density of stone bunds on survival probabilities, we monitored the rodent species in experimental grids for four consecutive cropping seasons. We predicted reproductive patterns of both species to follow rainfall patterns and crop developmental stages, and the abundance of reproductive females and survival probabilities to vary with variation in stone-bund density.

## Materials and methods

The study was conducted in four rainfed crop fields in the May Zeg-Zeg catchment (~200 ha) near the town of Hagera Selam (13°40'N, 39°10'E), northern Ethiopia, from April 2007 to February 2011. The altitude of the study area is ~2600 m asl and the morphology of the Hagera Selam area is typical for the Tigray highlands (see Nyssen *et al.* 2010 for a detailed description). The area has an annual average rainfall of 762 mm (as reported for 1970–2005 by Nyssen *et al.* 2010) and the main rainy season runs from June to September. Crop production depends mainly on this rain and cropped fields are the dominant land use (~65%) in the study area. The typical land use is crop fields in the flat areas and lesser slopes and rangeland and exclosures (guarded communal areas where grazing and farming are prohibited) on the steep slopes. The remaining native vegetation is largely dominated by *Acacia etbaica* (Schweinf.) and *Euclea schimperi* (A.DC.) Dandy.

The experimental grids were situated on a basaltic Vertic Cambisol soil, where stone bunds were built in the past two decades to prevent soil erosion (Nyssen *et al.* 2008). The main crops grown were wheat (*Triticum* sp.), barley (*Hordeum vulgare* L.), a mixture of wheat and barley, and teff (*Eragrostis tef* (Zucc.) Trotter); these are staple crops in the highlands. Cereal grains, such as wheat and barley, are sown after the early rains in June; crops reach milky stage in August, mature in October and are harvested in November. Other commonly cultivated crops include grass pea (*Lathyrus sativus* L.), horse bean (*Vicia faba* L.) and lentil (*Lens culinaris* Medikus). Rainfall data for Hagera Selam were obtained from the National Meteorological Agency; the Hagera Selam weather station is ~2 km from the study area.

Complete description of the study area and the methodology used for trapping the animals were outlined in Meheretu *et al.* (2014). In brief, a capture–mark–recapture (CMR) study was conducted, in which rodents were live-trapped in four 60 × 60 m permanent square grids set in four crop fields. Trapping was performed for three consecutive nights, at intervals of 4 weeks, from April 2007 to February 2011. Two of the grids represented fields with low stone-bund density (LSBD) and the other two represented fields with high stone-bund density (HSBD). We defined LSBD grids as those with stone bunds spaced at a distance of ~15 m apart and HSBD grids as those with stone bunds spaced ~10 m apart. All farming practices were conducted according to the conventional farming system followed by the farmers in the area. Crop variety and agronomic practices were kept the same (synchronised) in each grid each year.

### Rodent reproduction

Females were considered as reproductively active when they exhibited perforated vagina or perforated vagina and were pregnant or perforated vagina and were lactating; and reproductively inactive when they exhibited plugged vagina. We estimated monthly abundance of reproductively active females of *M. awashensis* and *A. dembeensis* in the HSBD and LSBD grids from our four-season monthly CMR trapping data by using the  $m(h)$  estimator of the Program CAPTURE (White *et al.* 1982), which has been reported as quite robust (Parmenter *et al.* 2003). It has also been used recently to estimate abundance in African rodents (see Lima *et al.* 2003; Sluydts *et al.* 2009;

Massawe *et al.* 2011). We excluded males from the analysis because one male is able to breed with several females and, therefore, males are not a limiting factor. Statistical significance was declared at  $P$ -values of  $<0.05$ .

### Survival and recapture analysis

We estimated apparent survival ( $\Phi$ ) and recapture ( $p$ ) probabilities of the two rodent species in HSBD and LSBD grids from individual encounter histories generated from our CMR data. Apparent survival refers to the combined probability that an animal survives from Capture  $i$  to Capture  $i+1$  and that it has not emigrated (White and Burnham 1999). To ensure that the most general model to be used as a reference model in the analysis adequately fits to our data, we carried out a goodness-of-fit (GOF) test before analysis (Lebreton *et al.* 1992; Burnham and Anderson 1998), using program U-Care (v.2.3.1) (GOF; Choquet *et al.* 2003). The GOF test will indicate whether our CMR data follow the main assumptions of the capture–recapture model (Pradel 1993) or violates them, that is, the presence of transient animals and/or immediate trap-dependence.

We were interested to find out whether survival and recapture probabilities of the two rodent species varied with variation in stone-bund density and sex. Survival and recapture probabilities were estimated with the CMR methodology (Lebreton *et al.* 1992; Pradel *et al.* 1997) by using Program MARK version 6.0 (White and Burnham 1999). The estimations were conducted on the basis of the monthly sessions of individual capture–recapture histories. Selection of the best-fitting model among candidate models was performed on the basis of Akaike's information criterion corrected for small sample sizes (AICc) (Lebreton *et al.* 1992; Burnham *et al.* 1995; Johnson and Omland 2004). The first top models should be accepted as not significantly different if the difference in their AICc is  $<2$  (Burnham and Anderson 1998).

## Results

### Reproduction versus rainfall, crop stage and stone-bund density

Overall, the abundance of reproductively active females of *M. awashensis* and *A. dembeensis* followed a similar pattern during the survey period both in HSBD and LSBD grids (Fig. 1). On the basis of the general pattern of reproductive activity observed each year, we divided the reproductive period of the rodents into the following three 'seasons': wet season (June to September), early dry season (October to January) and dry season (February to May). Generally, reproduction commenced in the middle of the wet season almost each year and continued through to the early dry season. The first reproduction peaks were observed during the wet season and the second peaks during the early dry season. There was little or no reproductive activity during the dry season. Abundance of reproductively active females was relatively higher during the early dry season than during the wet season in both grids (less obvious in 2009; Fig. 1). On average, while the wet season reproduction peaks were delayed for 2–3 months from the onset of the main rainfall in June, the early dry season reproduction peaks were delayed for ~6 months. Note that the first peaks of reproduction coincided with the reproductive stages of the crop (milky and fruiting stages), and the second peaks occurred approximately at harvest.

### Proportion of males

As summarised in Table 1, seasonal abundance of males of both *M. awashensis* and *A. dembeensis* in the population did not vary over the study period and with variation in the density of the stone bunds.

### Survival and stone-bund density

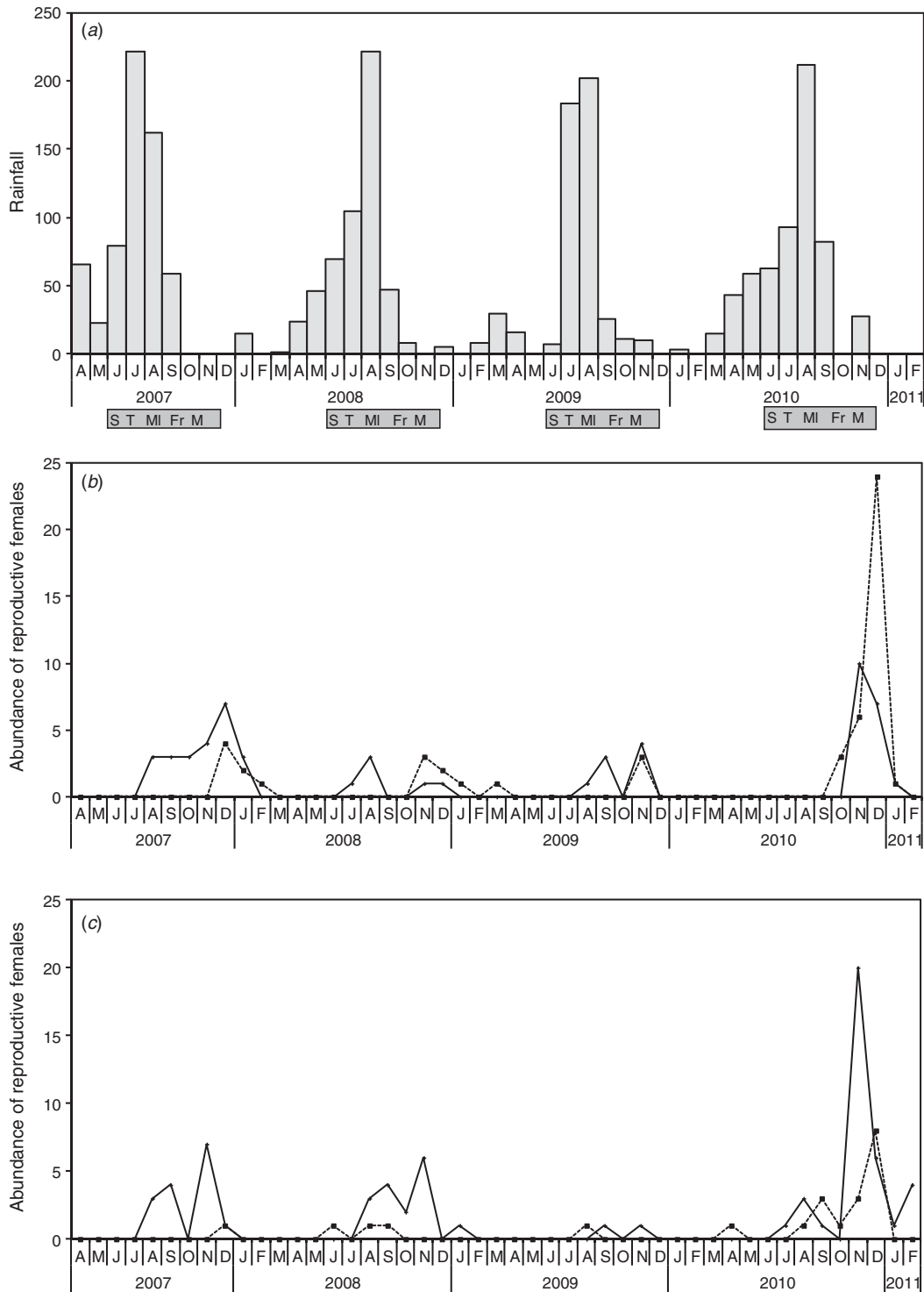
The GOF test for *M. awashensis* showed no transient effects ( $N(0,1)$  statistic for transients = 1.6211;  $P=0.105$ ), but a significant trap dependency (trap happiness;  $N(0,1)$  signed statistics for trap-dependency = -3.4311;  $P=0.0006$ ). Similarly, the GOF test for *A. dembeensis* showed no transient effects ( $N(0,1)$  statistic for transients = 1.2833;  $P=0.1994$ ), but a significant trap dependency (trap happiness;  $N(0,1)$  signed statistics for trap dependency = -3.0043;  $P=0.00266$ ). To deal with the violation of the assumption for trap dependency, the capture-history data were transformed by splitting the capture histories according to the method explained in Pradel (1993) by using the program U-Care (Choquet *et al.* 2003). This will result in the estimation of two capture probabilities, conditional on whether or not rodents were captured on the previous occasion, i.e. immediate trap dependency.

The best model describing survival and recapture probabilities for *M. awashensis* showed the same (constant,  $\Phi(\cdot)$ ) survival rates over time, and recapture probability varying with trap effect ( $p_{(m)}$ ) (available as Supplementary Material Table S1). The probability of *M. awashensis* surviving between two consecutive 4-week trapping sessions was estimated as 0.81 (CI: 0.76–0.85; Fig. 2). Six-month survival can be calculated using  $(0.81)^6 = 0.282$ . Thus, ~28% of the local *M. awashensis* population is likely to survive over a 6-month period. Here, the probability of capture differed between rodents that were captured on the previous occasion ( $P=0.24$ , CI: 0.20–0.28) and those that were not ( $P=0.058$ , CI: 0.039–0.085).

By contrast, the model with the lowest AICc describing survival and recapture probabilities for *A. dembeensis* showed that survival rate varied with stone-bund density ( $\Phi_{(stb)}$ ) and recapture probability with trap effect ( $p_{(m)}$ ) (Supplementary Material Table S1). However, this model was not significantly different from the second-best model that describes no difference in survival with varying stone-bund density, and recapture probability varying with trap effect ( $p_{(m)}$ ). Monthly survival probability for *A. dembeensis* was estimated as 0.66 with CI of 0.38–0.86 in LSBD grids and 0.85 with CI of 0.77–0.91 in HSBD grids (Fig. 2). Capture probability for rodents captured at Occasion  $t$  on the condition they were captured at  $t-1$  was estimated as 0.23 (CI: 0.18–0.30), whereas those not captured on the previous occasion had a probability of being captured of only 0.028 (0.014–0.059). Note that the estimates for *A. dembeensis* have larger confidence intervals than those for *M. awashensis* because of low capture–recapture data. Effective sample size (total number of capture events) was 331 for the *A. dembeensis* dataset, compared with 630 for the *M. awashensis* datasets.

### Male versus female survival

The GOF test of pooled *M. awashensis* data (HDSB plus LDSB) for survival difference between sexes showed no transient effect



**Fig. 1.** (a) Bar graph representing monthly mean rainfall with shaded boxes at the bottom showing crop stages. Monthly abundance of reproductively active *Mastomys awashensis* (solid lines) and *Arvicanthis dembeensis* (broken lines) females in (b) high (HSBD) and (c) low stone-bund density (LSBD) grids. Fr, fruiting stage; H, harvest; M, maturation stage; MI, milky stage; S, sowing stage; T, tillering stage.

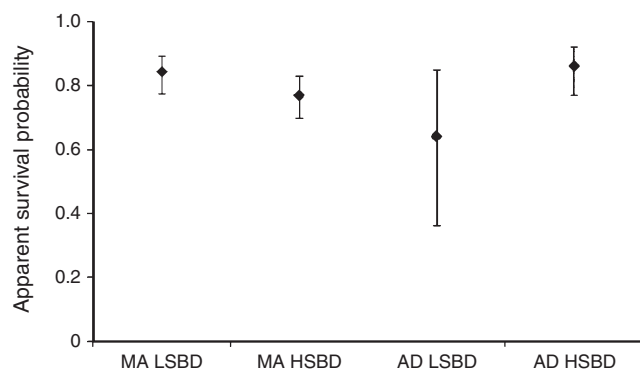
( $N(0,1)$  statistic for transients = 1.7466;  $P=0.08$ ) but a significant trap dependency (trap happiness;  $N(0,1)$  signed statistics for trap dependency = -3.3178;  $P=0.0009$ ). The data for *A. dembeensis*

also showed the same pattern ( $N(0,1)$  statistic for transient = 1.4441;  $P=0.14871$  and  $N(0,1)$  signed statistic for trap dependency = -2.7594;  $P=0.0058$ ). The AICc ranking of

**Table 1.** Seasonal average abundance of male *Mastomys awashensis* (MA) and *Arvicanthis dembeensis* (AD) trapped in high (HSBD) and low stone-bund density (LSBD) grids

The wet season comprised June to September and the dry season comprised October to May. Trapping did not take place in wet 2011

Year	HSBD				LSBD			
	MA		AD		MA		AD	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
2007	6.3	2.6	1.5	4.0	9.3	1.8	1.0	0.2
2008	3.5	3.8	1.8	7.9	4.3	4.3	0.5	1.5
2009	5.3	3.1	0.8	2.5	3.5	0.8	0	0.1
2010	1.5	4.1	0	2.9	2.3	4.0	0	1.0
2011	–	6.5	–	4.0	–	0.5	–	2.5
Average	4.1	4.0	1.0	4.3	4.8	2.3	0.4	1.0

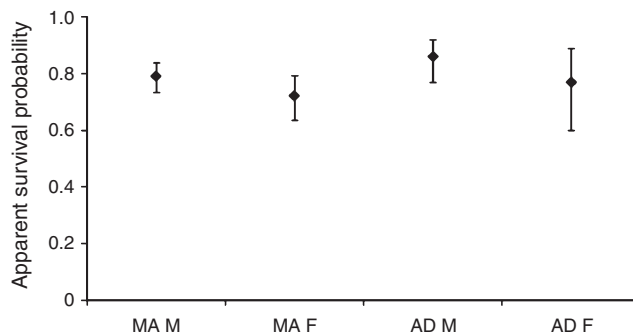


**Fig. 2.** Apparent survival estimates with 95% confidence interval for *Mastomys awashensis* (MA) and *Arvicanthis dembeensis* (AD) in high (HSBD) and low (LSBD) stone-bund density grids.

the models for both species is shown in Supplementary Material Table S2 available for this species. The models including differences in survival between the two sexes and trap dependency in the recapture parameter could not be clearly distinguished from the model, with survival being similar between the sexes in terms of AICc. This means that there is no strong support in the data to justify the hypothesis of difference in survival between the sexes (Fig. 3). The corresponding recapture probabilities had no variation in sex modelled and were estimated being 0.25 (0.21–0.29) and 0.075 (0.05–0.11) in *M. awashensis* and 0.23 (0.18–0.29) and 0.028 (0.013–0.058) in *A. dembeensis*.

## Discussion

Cereal crops in northern Ethiopian highlands are sown after the early rains in June, crops reach milky stage in August, mature in October and are harvested in November. Between harvesting and the next sowing (December to May), the crop fields remain fallow. Consequently, both rodent species in both HSBD and LSBD grids showed a strong seasonal reproduction following the rainfall and crop development. Reproduction commenced in the wet season and continued through the early dry season. The highest abundance of reproductively active females was observed in the early dry season, which roughly coincides with crop-harvesting period. A substantial proportion of reproductively



**Fig. 3.** Apparent survival estimates with 95% confidence interval for male (M) and female (F) *Mastomys awashensis* (MA) and *Arvicanthis dembeensis* (AD) (data were pooled for high and low stone-bund density grids).

active females was also observed in the wet season, roughly coinciding with the milky and fruiting crop stages. Small mammals inhabiting seasonally varying habitats show seasonal reproductive patterns synchronised with the most favourable periods of the year as a strategy to maximise reproductive success (Bronson 1985; Gittleman and Thompson 1988). Several African rodent species are known to time their reproductive period with occurrence of rainfall events and plant productivity, to maximise growth and survival of newly born individuals by benefiting from availability of high-quality food and suitable environmental conditions (Neal 1981; Leirs *et al.* 1994, 1997b; Bekele and Leirs 1997; Makundi *et al.* 2007; Medger *et al.* 2010). Correct identification of these periods in the life cycle of the pest species is, therefore, critical for designing effective population management before these crop stages are attained. Breeding females consume more food for fetal growth and development and store some for later lactation, in addition to self-support and maintenance (Bronson 1985; Speakman 2008), hence causing more crop damage.

The absence of marked variation in the abundance of reproductively active females with variation in stone-bund density suggested that the density of stone bunds has a limited role in providing cover to reproductive females at the observed abundance. Alternatively, given that the population dynamics of the rodents are likely to be density dependent, we did not detect variation in the abundance of reproductively active females with the variation in stone-bund density because the density of the rodents was too low during the study period. We hypothesised that stone bunds built close to each other provide better nesting sites and cover (against potential predators) to breeding individuals than do stone bunds built far from each other. From Fig. 1, it seemed that the predominantly nocturnal *M. awashensis* performed better in both grids than did the diurnal *A. dembeensis*, for the most part in LSBD grids. However, this was not statistically supported because of large variation in the sample size between the two species. The presence of more females in the early dry season than in the wet season (less obvious in 2009) suggested that some female members of the new generation born during the wet season might have successfully joined the female population of the previous generation later in the years.

In the current study, the rodent population in the crop fields did not show sex-biased capture probability. Male-biased capture probabilities can occur as a result of intersexual difference in

home-range size, where males show large home-ranges and increased movement (e.g. in search of mates), and therefore increased capture probability relative to females (Christensen 1996; Morris *et al.* 2011). However, in our study, capture probability did not differ between males and females; instead, there was a strong component of immediate trap dependency. Low female survival could also be the underlying reason because females have high energy costs during reproduction and these are not easily compensated towards the end of the reproductive period when food available in the fields is insufficient. Nevertheless, we could not find evidence to support sex-biased mortality in these species. In fact, we did not detect large differences in survival probabilities between the sexes.

Our results indicated no difference in survival probability between *M. awashensis* and *A. dembeensis* in LSBD and HSBD grids. Although it seems that the heavier and diurnal *A. dembeensis* survived better (85%) in HSBD grids than in LSBD grids (66%) over a 4-week period, this finding was not statistically supported. Diurnal rodent species are more conspicuous to avian and mammalian predators than are nocturnal species (Ebensperger and Blumstein 2006) and large-bodied rodent species face more difficulty in hiding under vegetation against predators than do small-bodied species (Bozinovic and Medel 1988; Norrdahl and Korpimäki 1998), both of which suggest that more cover and a larger home range are needed for *A. dembeensis*. Trap happiness, that is, an individual captured at a previous occasion was more likely to be recaptured (Pradel 1993), was observed in both rodent species. However, although survival of both rodent species did not differ with variation in stone-bund density and sex, the rates of local survival estimated for both species were relatively high. For instance, 8 of 10 *M. awashensis* individuals present in a grid at a given time were able to survive for the next 4 weeks and about three were able to survive for the next 5 months. Therefore, in terms of pest management, the high local survival rates estimated for both species would be more worrying than variations in survival owing to differences in stone-bund density and sex. Hence, stone bunds play a minor role in the reproduction and survival of the rodent species at the observed abundances.

## Acknowledgements

We are grateful to the Flemish Interuniversity Council (VLIR-IOUS), Belgium, for funding the research. We thank the Departments of Biology in Mekelle (Ethiopia) and Antwerp (Belgium) Universities for provision of field and laboratory facilities, and Mekelle University–Institutional University Cooperation Project (MU–IUC) for facilitating the fieldwork. The assistance of Kokob Girmay, Nahusenay Teamer, Mulugeta Hagos, Selamawit Girmay, Eleni Girmay, the late Berhe Hadush, Haile Gebregiorgis, Kasu Kiros, Bisrat Haile, Samson Gebremeskel and Nurhussen Mustfa is highly appreciated.

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