Integrative Zoology 2021; 0: 1–13 doi: 10.1111/1749-4877.12580

ORIGINAL ARTICLE

Impact of fertility versus mortality control on the demographics of *Mastomys natalensis* in maize fields

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Abstract

The multimammate mouse, *Mastomys natalensis*, is the most common rodent pest species in sub-Saharan Africa. Currently, rodenticides are the preferred method used to reduce the population of rodent pests, but this method poses direct and indirect risks to humans and other non-target species. Fertility control is a promising alternative that has been argued to be a more sustainable and humane method for controlling rodent pests. In this study, we compared the effectiveness of fertility control bait EP-1 (quinestrol (E) and levonorgestrel (P), 10 ppm) and an anticoagulant rodenticide bait (bromadiolone, 50 ppm) on the population dynamics of *M. natalensis* in maize fields in Zambia during 2 cropping seasons. *M. natalensis* was the most abundant species in maize fields (77% of total captures). Fertility control reduced the number of juveniles and suppressed population growth of *M. natalensis* at the end of the 2019–2020 cropping season. The population density initially decreased after rodenticide treatment, but the population rapidly recovered through immigration. None of the treatments influenced maize damage by rodents at germination ($F_{2,67} = 1.626$, $P = 0.204$). Applying the treatments during the maize seeding time was effective at suppressing population growth at the end of the cropping season than application the month before maize seeding. This research indicates that a single-dose delivery of EP-1 and rodenticide have comparable effects on the population dynamics of *M. natalensis*. These findings are important in developing fertility control protocols for rodent pest populations to reduce maize crop damage and improve yields.

Key words: ecologically based rodent management, levonorgestrel, multimammate mouse, quinestrol, rodent pests, rodenticide

INTRODUCTION

Rodents represent 39% of all mammalian species (Burgin *et al*. 2018). Despite their diversity, less than 10% of rodents are pest species in agricultural crops (Singleton *et al*. 2007; Capizzi *et al*. 2014). However, the considerable damage caused by outbreaks of these pest species threaten agricultural production worldwide (Brown *et al*. 2007; Leirs *et al*. 2010) causing considerable economic losses (Singleton *et al*. 1999; Mwanjabe *et al*. 2002; Makundi *et al*. 2005). In addition to the threat to agriculture, rodents are a major reservoir for many zoonotic diseases affecting livestock and human health (Meerburg

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et al. 2009). The World Health Organization has estimated more than 400 million human cases of rodent-related zoonoses occur every year (Colombe *et al*. 2019). In sub-Saharan Africa, *Mastomys* is the most important rodent pest genus for its negative impacts on cereal crop production and transmission of arenaviruses responsible for diseases such as Lassa fever (Swanepoel *et al*. 2017; Olayemi & Fichet-Calvet 2020).

For decades, second generation anticoagulant rodenticides (SGARs) have been used worldwide to control rodent populations (Buckle & Smith 2015). Despite being highly effective in controlling rodent populations (Tosh *et al*. 2011), SGARs persist in animal tissues (Erickson & Urban 2004) and accumulate in the bodies of rodents, leading to contamination of terrestrial predators, scavengers, and beneficial non-target species such as shrews (Nocera & Dawe 2008; Elliott *et al*. 2016). In addition to SGARs causing secondary poisoning, there is considerable evidence that rodents become genetically resistant through mutations to enzymes involved in the catalysis of Vitamin K (Rost *et al*. 2004; Desvars-Larrive *et al*. 2017; Berny *et al*. 2018). Commercial pest control operators, farmers, and consumers may be put at risk of poisoning when handling rodenticides or consuming contaminated food (Lefebvre *et al*. 2017; Lekei *et al*. 2017; Lohr & Davis 2018). Despite issues associated with rodenticide use, they remain the main way rodent pest problems are tackled due to the ease of use and availability (Buckle & Smith 2015). Alternative approaches which are both environmentally friendly and cost-effective need to be developed and effectively promoted to overcome this problem.

Environmentally friendly methods that have been proposed to control rodent pest species include the use of avian predators (Vibe-Petersen *et al*. 2006; Paz *et al*. 2012; Labuschagne *et al*. 2016; Machar *et al*. 2017; Luna *et al*. 2020), habitat manipulation (Massawe *et al*. 2005), and trap barrier systems (Singleton *et al*. 1998; Wang *et al*. 2017). Several plant extracts have also been explored as an avenue to control rodent populations by either inhibiting their fertility or as repellents (Tran & Hinds 2012; Fu *et al*. 2016; Hansen *et al*. 2016). With the broad relevance of these alternative strategies still under examination, one strategy that could have wide application is the use of fertility-inhibiting compounds to limit rodent populations (Zhao *et al*. 2007; Jacob *et al*. 2008; Zhang 2015; Fu *et al*. 2016). Laboratory and field studies have shown that fertility control promises to be an appropriate and long-term strategy for controlling rodent pests (Chambers *et al*. 1999; Liu *et al*. 2013; Zhang 2015; Shi *et al*. 2020). Fertility control does not immediately lower a population, but it prevents the build-up of population eruptions (Stenseth *et al*. 2001) which may be further enhanced through competitive reproductive interference of infertile individuals (Zhang 2000; Liu *et al*. 2012b).

Fertility-inhibiting hormones, quinestrol (E) and levonorgestrel (P), have demonstrated dose-dependent antifertility effects on *Mastomys natalensis* in the laboratory, particularly when the 2 hormones are equally combined in a bait, commonly referred to as EP-1 (Massawe *et al*. 2018). Massawe *et al*. (2018) showed that the optimal delivery dose of EP-1 is 10 ppm using a 1:1 ratio for quinestrol and levonorgestrel. EP-1 causes reduced sperm number and sperm quality in males and induces uterine edema in females which results in reduced pregnancy rates and litter size. However, the effectiveness of EP-1 on the population dynamics of this species in the field is yet to be documented. The population dynamics of *M. natalensis* have been well-studied, showing clear links to seasonal rainfall patterns with numbers growing with the onset of rains followed by a decline at the end of the rainy season, thereafter, remaining at low numbers until the next rainy season (Makundi *et al*. 2007). The present study seeks to compare the effectiveness of fertility control bait EP-1 and a commercially available anticoagulant rodenticide bait on the population dynamics of *M. natalensis* in maize fields in Zambia. We hypothesize that a single application of a commercially available anticoagulant rodenticide would have similar effects on the population dynamics of *M. natalensis* over a maize cropping season as a single application of a fertility control bait (EP-1). We also tested the hypothesis that damage caused by rodents to maize at germination will not be influenced by the treatment applied. Further, we tested the hypothesis that the recruitment of *M. natalensis* will be similar in both treatments.

MATERIAL AND METHODS

Study area

There were 3 treatments in this study: fertility, rodenticide, and control. Six maize fields (2 for each treatment, randomly assigned) were selected for the study in Luto (5 fields) and Mwekera (1 field) agricultural camps on the Copperbelt Province of Zambia (Fig. 1). In both camps, the farmers start to prepare the fields around October with seeding taking place from mid-November through to early January. The maize germination is typically from early-December through to the end of January (depending on the maize variety) while the maize is harvested from mid-April until the end of May.

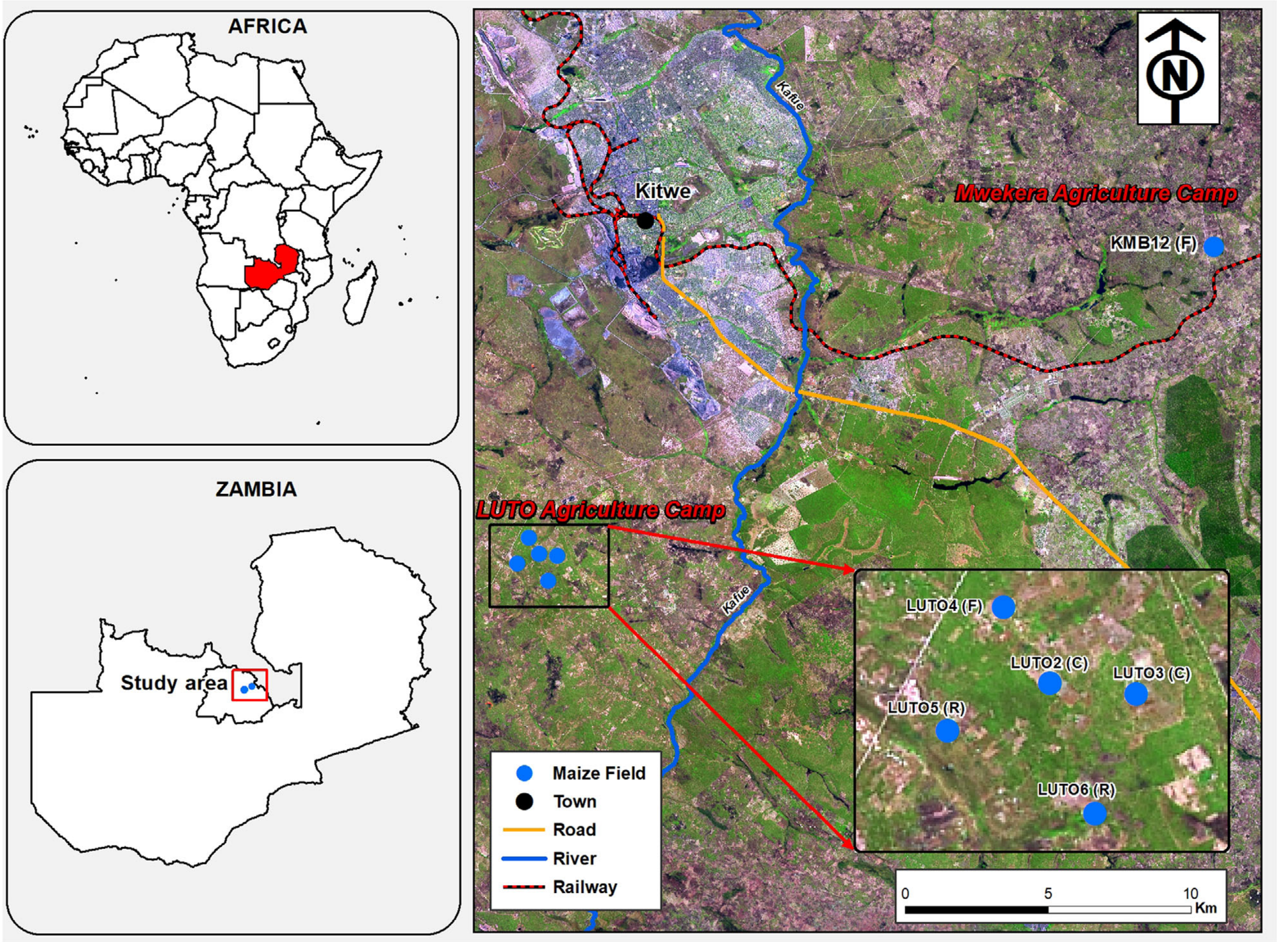

Figure 1 Location of the study sites in Kitwe, Copperbelt Province, Zambia.

Experimental design

In each field, a 200 m × 200 m baiting grid was marked using wooden poles. To establish the initial population density of rodents in the fields, a capture–mark–recapture (CMR) technique (Krebs 1999) was followed. A 0.49 ha (70 m × 70 m) observation plot (trapping grid) was established in the center of each 200 m × 200 m baiting grid. Each trapping grid had 49 trapping/bait stations, located 10 m apart, in a square grid. Labeled bricks were placed at each trapping station to maintain the same station every month. A Sherman trap baited with a mixture of peanut butter and maize meal was placed at each station. The traps were checked early morning for 3 consecutive days. The captured rodents were marked by toe-clipping using sterile dissecting scissors. Toe-clipping was used because it does not directly affect the movement, body weight, or survival of the animal (Silvy *et al*. 2012; Borremans *et al*. 2015). The date of capture, sex, sexual condition of adult females (adult females with a perforated vagina, lactating and pregnant were labeled as sexually active while adult females with a closed vagina and no visible signs of pregnancy or lactating were labeled as not sexually active), age status, trapping station, species, toe-clipping code, and body weight (using a Pesola spring balance, to the nearest 0.1 g) were recorded in the field before releasing the captured animal at point of capture. The population dynamics of rodents in the trapping grids was monitored monthly throughout the maize growing season.

Bait formulation and application

Two “baiting grids” were baited with a fertility control bait (EP-1) 10 ppm, which is a 1:1 mixture of levonorgestrel and quinestrol, that is, each compound contained at 5 ppm (Massawe *et al*. 2018)); another 2 grids were baited with Scientific Supa-kill (wheat impregnated with bromadiolone—50 ppm—as active ingredient) and 2 further grids were baited with plain untreated bait (control fields). EP-1 and control baits were prepared following published methods and contained similar food ingredients to that found in the rodenticide bait (Massawe *et al*. 2018). Each baiting grid was stratified into 10 m square grids (180 square grids). Approximately 5 g (Liu *et al*. 2012a; Fu *et al*. 2013) of each bait was placed in the center of each 10 m × 10 m squared grid. Each baiting grid of 200 m × 200 m had approximately 900 g of bait. To protect the bait from non-target animals, such as birds, the bait was placed in sections of bamboo cuttings (see Figure S1, Supplementary Information). The distance between the baiting grids in each village was at least 300 m (Christensen 1996; Leirs *et al*. 1997; Mulungu *et al*. 2015) to reduce the likelihood of rodent dispersal among plots. In the 2018–2019 growing season, the treatments were applied a month before maize seeding (i.e. around mid-October). Based on results from another study on rodent foraging activity in and around maize fields in Zambia (Imakando, unpublished data), we moved the baiting session to a week before maize germination (i.e. maize planting time, third week of December) in the 2019–2020 growing season but using the same maize fields. The treatments were applied at the same time to investigate their potential impact on population growth over the maize cropping season, when normally rodent numbers are growing in response to food availability.

Assessment of crop damage and recruitment

Rodent damage assessments to maize crops at the germination stage were conducted using a systematic row sampling technique—sampling every 5th row in a 70 × 70 m field (Mwanjabe & Leirs 1997; Mulungu *et al*. 2007; Meheretu *et al*. 2014) for the 2019/2020 growing season. Due to time limitations and logistical challenges, damage assessments were not conducted in the 2018/2019 season. Recruitment, proportion of new individuals entering the population, from the first session after treatment to the end of the cropping season was compared between the treatments. Recruitment was calculated as R (%) = [(new captures/total captures) × 100%]. Recruitment was divided into 3 categories to test the hypothesis that there is, (i) in the first 2 sessions after treatment (short term treatment effect) no difference between control and fertility treatment, but higher recruitment in the rodenticide treatment due to increased recolonization replacing the animals that were killed by the rodenticide, (ii) after 3 to 5 sessions after treatment (medium term treatment effect), no difference between control and rodenticide treatment (the recolonization after rodenticide treatment and reproduction in both treatments but where lower recruitment in the fertility treatment was due to reduced reproduction), and (iii) beyond 6 sessions after treatment (long-term treatment effects), no difference in recruitment between control and both treatments because the impact of the EP-1 (fertility treatment) on reproduction has diminished.

Data analyses

We estimated the population size of *M. natalensis* in each field for every session using the minimal number of animals alive (MNA) (Krebs 1999). Although MNA estimates are known to be less accurate than other methods, it has advantages under low densities conditions. We also estimated the population size for each plot for every session using a more accurate method, the Mh Jacknife estimator in DENSITY 5.0 software (Efford 2014). To compare the population size, and how this changed over the growing season between treatments, we applied generalized linear mixed model (GLMM) with negative binomial distribution for MNA counts using the package MASS (Brian *et al*. 2019). Treatment, session, and the interaction between treatment and session were entered as fixed effects in the model. We also inserted field in the GLMM as a random effect to account for pseudoreplication and heteroscedastic variance (Gillies *et al*. 2006; Jamil *et al*. 2013). Adding field as a random effect, in our model, also allowed us to generalize our conclusions to other fields (Bolker *et al*. 2008). To check for normality, we used Q-Q plots of the random effects (Jamil *et al*. 2013). When using density estimates as the response variable, we used a linear mixed effects model. An ANOVA was conducted to compare the damage at germination, recruitment, and population growth at the end of the cropping season between treaments. Further, we used a Welch 2 sample *t*-test to compare the recruitment in the first session after treatment for each treatment in the 2 growing seasons. All statistical analyses were in R version 3.6.1 (R Core Team 2019). To generate graphs, we used the package ggplot2 (Wickham 2016).

RESULTS

Species composition

Over the 2 maize growing seasons, a total of 1415 individuals (from 2752 total captures) of small mammals

Table 1 Species composition of captured rodents and shrews at all sites for 2018–2019 and 2019–2020 maize growing seasons. Numbers in brackets are percent contribution of each species and species are ordered by abundance; n = number of captures

		Treatments			
Small mammal species	n	Control	EP-1	Rodenticide	Overall
Mastomys natalensis	2280	439 (88.3)	337 (77.3)	319 (70.1)	1095 (77.4)
Mus minutoides	128	28 (5.6)	38 (8.2)	37 (8.1)	103 (7.28)
Steatomys pratensis	141	12 (2.4)	26 (5.6)	42 (9.2)	80 (5.65)
Gerbilliscus leucogaster	68	6 (1.2)	27 (5.8)	15 (3.3)	48 (3.39)
Crocidura hirta	78	8 (1.6)	24 (5.2)	13 (2.9)	45 (3.18)
Saccostomus campestris	24	3 (0.6)	6 (1.3)	10 (2.2)	19 (1.34)
Steatomys sp.	9	-	1 (0.2)	8 (1.8)	9 (0.64)
Aethomys sp.	13	-	1 (0.2)	8 (1.8)	9 (0.64)
Lemniscomys rosalia	7	-	1 (0.2)	3 (0.7)	4 (0.28)
Elephantulus brachyrhynchus	3	-	2 (0.4)	-	2 (0.14)
Rattus rattus	1	1 (0.2)	-	-	1 (0.07)
Total	2752	497 (100)	463 (100)	455 (100)	1415 (100)
Species richness	-	7	10	9	11

representing 9 species of rodents and 2 species of shrews were captured from 4998 trapping nights. *M. natalensis* was the most abundant species (>70% of captures) in all the treatments (Table 1).

Population dynamics

In the 2018–2019 maize growing season, there were no statistical differences between the 3 treatments in terms of mean population size (see Tables S1 and S2, Supporting Information, for full details), indicating comparable levels of infestation. Although the effect of time (session) on population size was not statistically significant for all treatments ($P = 0.106$, 0.143, and 0.398 for control, fertility and rodenticide, respectively—see Tables S1 and S2, Supporting Information, for full details), the number of *M. natalensis* individuals changed within the different treatment groups, but this depended on the treatment (Fig. 2). For the control treatment, there was a positive correlation between time (session) and population size (slope = 0.051). This indicated that more unique individuals entered the population over the growing season. For the fertility treatment, a negative correlation was found between time and population size (slope = −0.017). This means that over time there were fewer individuals in the fields treated with EP-1. For the rodenticide treatment, we found a very weak positive correlation between time (session) and population size (slope = −0.01). This means that there were almost the same numbers of individuals before and after the treatment in the rodenticide-treated fields. However, the population growth at the end of the cropping season was not different between treatments ($F_{2,3} = 0.93$, $P = 0.485$; population growth 70% ± 26%, 32% ± 60%, −10% ± 77% for the control, fertility, and rodenticide treatments, respectively).

In the 2019–2020 maize growing season, mean population size was greater for the fertility fields compared with the control and rodenticide fields ($t = -2.043$, $P = 0.007$. See Table S2, Supporting Information). The effect of time (session) on population size was statistically significant for all treatments ($P < 0.001$, 0.002, and 0.003 for control, fertility and rodenticide, respectively. See Table S2, Supporting Information), and the number of *M. natalensis* individuals changed within the different treatment groups over the growing season depending on the treatment (Fig. 3). For the control treatment, there was a strong positive correlation between session and population size (slope = 9.445). For the fertility and rodenticide treatments, we found a weak positive effect of time (session) on population size when compared to the control treatment (slope = 0.756 and slope = 1.682 for

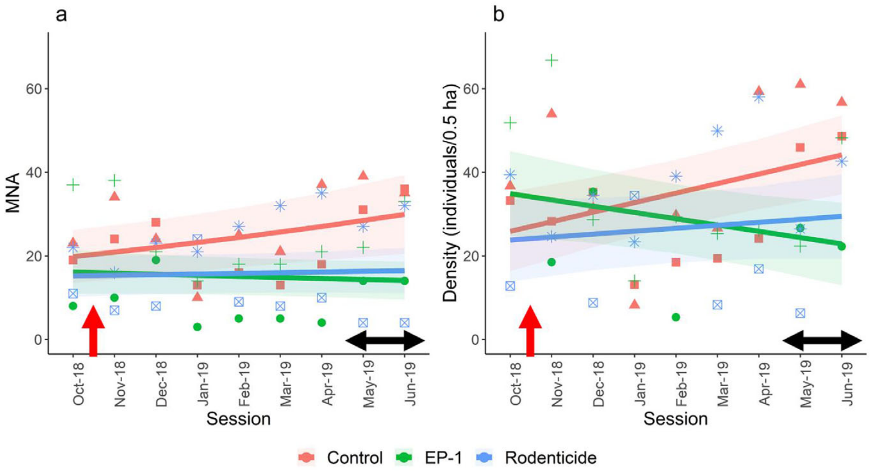

Figure 2 Predicted linear response of *Mastomys natalensis* population size over time (session) for the different treatments, (a) based on minimum number of alive animals (MNA) and (b) based on density estimations. Red line and shading (±SE) represent control fields; green line and shading (±SE) represent EP-1 fields; blue line and shading (±SE) represent rodenticide fields. Each session refers to a month when trapping took place during the 2018–2019 growing season. The arrows indicate when the baits were applied (red arrow) and when the maize was harvested (black arrow).

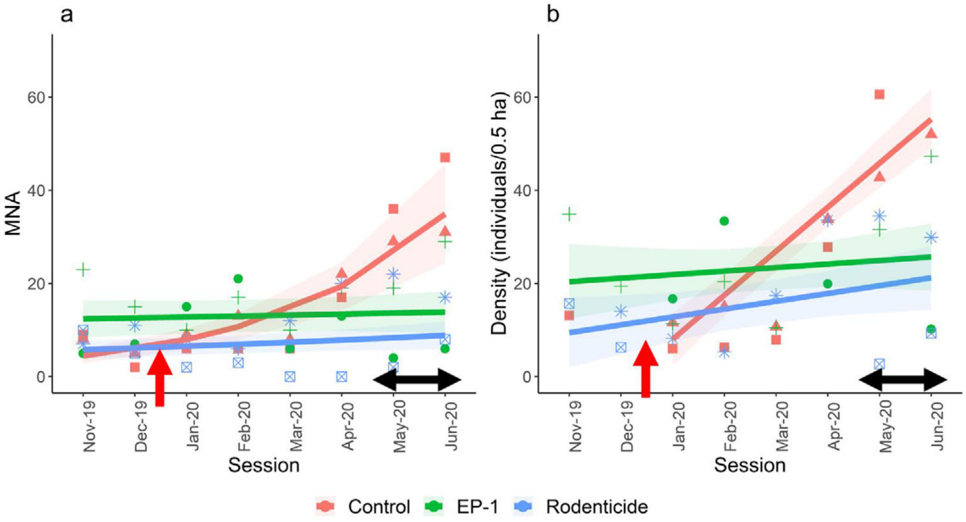

Figure 3 Predicted linear response of *Mastomys natalensis* population size over time (session) for the different treatments (a) based on minimum number of alive animals (MNA) and (b) based on density estimations. Red line and shading (±SE) represent control fields; green line and shading (±SE) represent EP-1 fields; blue line and shading (±SE) represent rodenticide fields. Each session refers to a month when trapping took place during the 2019–2020 growing season. The arrows indicate when the baits were applied (red arrow) and when the maize was harvested (black arrow).

the fertility and rodenticide treatments, respectively. See Table S2, Supporting Information). Hence the change in density of *M. natalensis* in the fertility and rodenticide treatments was similar throughout the growing season. This means that there were similar numbers of individuals before and after the treatment in the fertility and rodenticide treated fields. The population growth at the end of the cropping season was higher in the control than fertility and rodenticide treatments ($F_{2,3} = 9.519$, $P = 0.05$; population growth 355% ± 95%, 23% ± 4%, 66% ± 107% for the control, fertility, and rodenticide treatments, respectively).

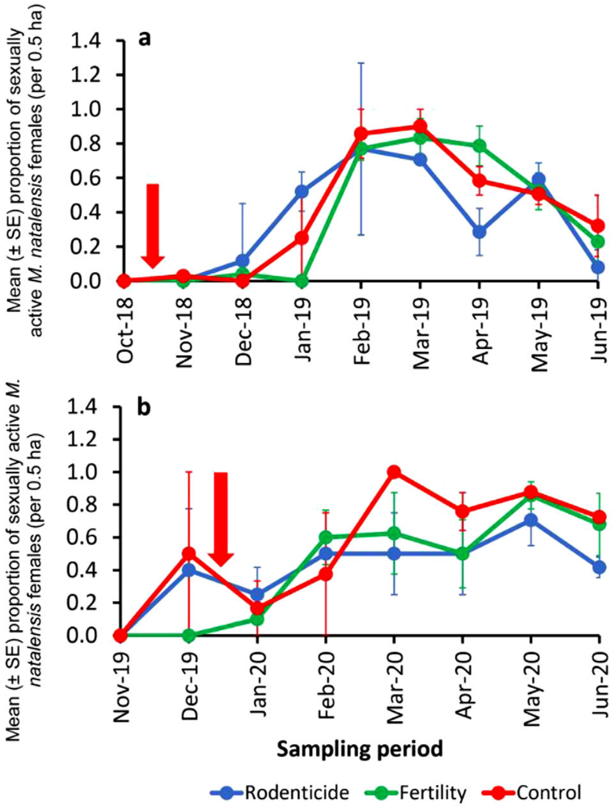

Figure 4 Mean (± SE) monthly proportion of sexually active female *Mastomys natalensis* in each treatment over the growing season: (a) for the 2018–2019 growing season and (b) for the 2019–2020 growing season. Red line represents control fields; green line represents EP-1 fields; blue line represents rodenticide fields. The black arrow indicates the time when the treatments were applied in the fields.

Breeding activity

Overall, the proportion of sexually active *M. natalensis* females in the treatments was not different from the control in both seasons ($F_{2,24} = 0.034$, $P = 0.967$ and $F_{2,21} = 0.534$, $P = 0.594$ in the 2018–2019 and 2019–2020 growing seasons, respectively) (Fig. 4). The overall sex ratio was also not different between treatments and control in both cropping seasons ($F_{2,24} = 0.28$, $P = 0.758$ and $F_{2,21} = 2.308$, $P = 0.124$ in the 2018–2019 and 2019–2020 growing seasons, respectively).

In both seasons, EP-1 reduced the number of juveniles (individuals weighing <20 g (Mulungu *et al.* 2013)) in the population for up to 6 sessions after the treatments were applied (Fig. 5). However, when compared to the other treatments, the difference in number of juveniles was not significant in both seasons ($F_{2,24} = 2.54$, $P = 0.0999$ and $F_{2,21} = 1.135$, $P = 0.34$ in the 2018–2019 and 2019–2020 growing seasons, respectively).

Recruitment

Although recruitment values were generally higher in rodenticide treatment in the first session after treatment compared to fertility treatment and control, the overall recruitment of *M. natalensis* individuals in the treatments was not different, $F_{2,21} = 1.149$, $P = 0.336$ and $F_{2,15} = 0.536$, $P = 0.596$ in the 2018–2019 and 2019–2020 growing seasons, respectively (Fig. 6). In 2018, the recruitment was also not different between the treatments and the control in the short term ($F_{2,3} = 3.782$, $P = 0.151$), medium term ($F_{2,6} = 0.415$, $P = 0.678$), and long term ($F_{2,6} = 0.563$, $P = 0.597$). Similarly, the recruitment was also not different between the treatments and the control in the short term ($F_{2,3} = 1.437$, $P = 0.365$), medium term ($F_{2,6} = 1.003$, $P = 0.421$), and long term ($\chi^2 = 4.507$, df = 2, $P = 0.106$) in the 2019–2020 growing season.

In the first session after treatments, recruitment was higher in the rodenticide fields in the 2019–2020 season than in the 2018–2019 season ($t = -108.25$, $P = 0.006$), but not different in the fertility ($t = -0.076$, $P = 0.947$) and control ($t = -1.568$, $P = 0.259$) fields.

Damage assessment

Rodent damage at the maize germination stage was not different between treatments, $F_{2,67} = 1.626$, $P = 0.204$ (Fig. 7). Variability was much higher in the fertility treatment; however, the treatment was not expected to have any impact at the germination stage.

DISCUSSION

The fertility treatment was effective in controlling the wild populations of *M. natalensis* in maize fields by suppressing the population growth and reduced the number of juveniles during the growing season. The most effective time for applying the baits is around the maize seeding time (a week before germination). It was not expected that the contraceptive bait would reduce damage to maize seedlings, but it would be the best time in with respect to limiting breeding, which is clearly linked to rainfall at the start of the cropping season. This reduced numbers at the time of crop harvest. The dominance of *M. natalensis* in cultivated fields has also been reported by other researchers (Makundi *et al.* 2010; Mayamba *et al.* 2019; Mlyashimbi *et al.* 2019), and is the most important rodent pest species in agricultural crops in sub-Saharan Africa

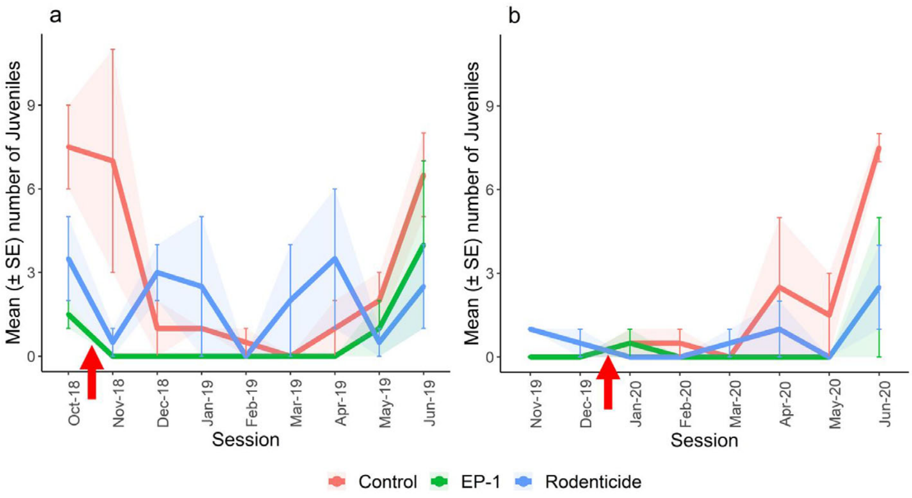

Figure 5 Mean (±SE) number of *Mastomys natalensis* juveniles in each treatment per session: (a) for the 2018–2019 growing season and (b) for the 2019–2020 growing season. Red line and shading (±SE) represent control fields; green line and shading (±SE) represent EP-1 fields; blue line and shading (±SE) represent rodenticide fields. Each session refers to a month when trapping took place.

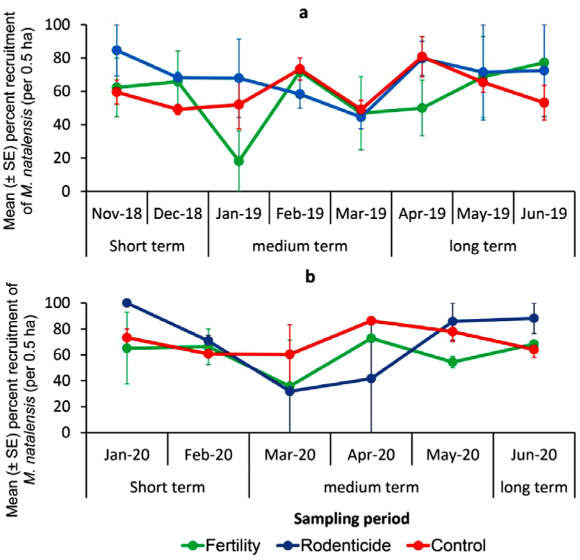

Figure 6 Mean (±SE) monthly recruitment of *Mastomys natalensis* individuals after treatments: (a) for the 2018–2019 growing season and (b) for the 2019–2020 growing season. Red line represents control fields; green line represents EP-1 fields; blue line represents rodenticide fields. Recruitment "R (%)" = [(new captures/total captures) × 100%].

(Swanepoel *et al*. 2017). *M. natalensis* is abundant in cultivated fields because of its adaptability as a generalist and rapid rate of colonization (Hurst *et al*. 2013; Mayamba *et al*. 2019).

Our findings showed that EP-1 suppressed *M. natalensis* population growth and reduced the number of juveniles in the population over the maize cropping season in both years. These results are consistent with the laboratory observation that EP-1 limits fertility in *M. natalensis* (Massawe *et al*. 2018). Massawe *et al*. (2018) showed that EP-1 causes reduced sperm number and sperm quality in males and induces uterine edema in females which results in reduced pregnancy rates and litter size. Additionally, EP-1 has been shown to reduce pregnancy rates and litter size in field populations of Mongolian gerbils (Fu *et al*. 2011, 2013), Djungarian hamsters (Wan *et al*. 2006), and Plateau pikas (Liu *et al*. 2012a). Although we did not calculate pregnancy rates, the fact that the proportion of sexually active females was not different between the treatments, but the number of juveniles was reduced for about 6 sessions (6 months) in fertility treatment indicates that the pregnancy rates were likely lower in the fertility treatment due to antifertility effect of EP-1 (Massawe *et al*. 2018).

None of the treatments reduced damage by rodents to maize crops at germination. Mwanjabe and Leirs (1997) also found no difference in damage caused by rodents to maize at germination in rodenticide-treated and untreated fields in Tanzania. Jacob *et al*. (2006) also reported that a single dose of fertility treatment, either through surgical or hormonal-based sterilization of female Ricefield rats, *Rattus argentiventer*, did not decrease crop damage in rice. Although rodenticides lowered population

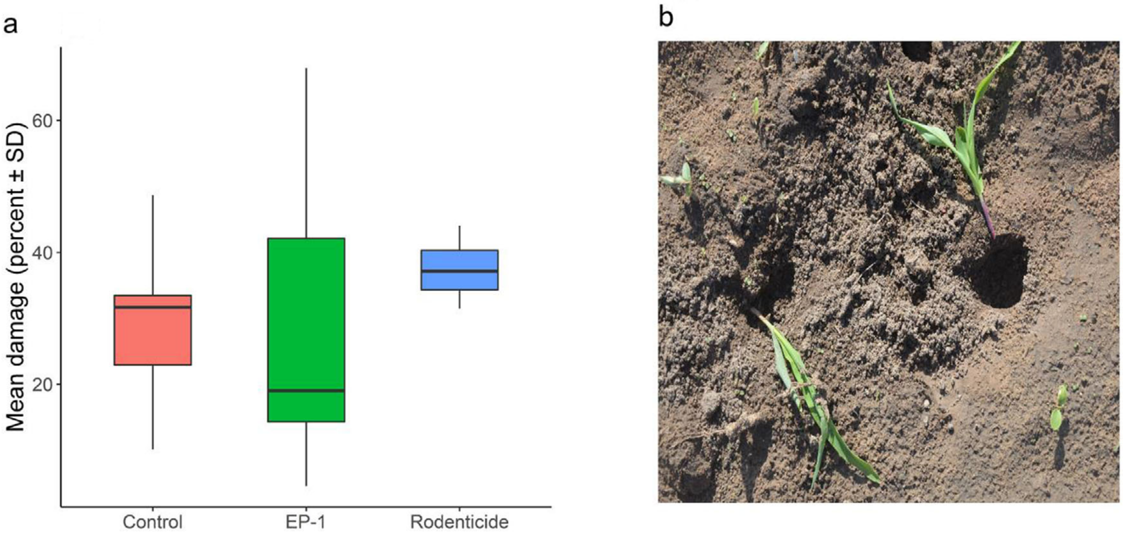

Figure 7 Mean (±SD) damage caused by rodents to maize crop at the germination stage for 2019–2020 growing season: (a) mean damage in different treatments and (b) example of rodent damage at germination stage. Red represents control fields; green represents EP-1 fields; blue represents rodenticide fields.

densities in the short term, increased rates of recruitment after rodenticide use lead to population resurgence (Leirs *et al*. 1997; Stenseth *et al*. 2001; Singleton *et al*. 2007), and hence rodenticide use does not lead to either reduced population density or damage to maize at germination (Mwanjabe & Leirs 1997). However, we found that fertility control caused more variability in seedling loss. Our damage estimates and the large variations are like those reported in the review by Swanepoel *et al*. (2017) for rodent damage to maize at germination in sub-Saharan Africa. More research, with an adequate level of temporal and spatial replication, is required to understand better the relationship between fertility control of *M. natalensis* populations and damage to maize crops.

Another possible explanation why our treatments did not have significant effects on the recruitment and damage at germination could be because of the immigration of untreated individuals. For example, Jacob *et al*. (2006) observed that immigration of untreated Ricefield rats and their contribution to reproduction and recruitment reduced treatment effects. Therefore, we recommend repeating the trials with larger baiting plots (>200 m × 200 m) to minimize these effects through the immigration of fertile individuals (Jacob *et al*. 2006). Combining fertility control with other control measures which directly reduce population size, such as use of rodenticides before commencement of fertility control, might help to reduce crop damage, especially in fields where the infestation rates are high. Alternatively, using multiple doses of fertility compounds could lead to more pronounced effects (population growth suppression) of fertility control on the demographics of *M. natalensis* over the cropping season. This is because some species are known to recover from the anti-fertility effects of the EP-1. For example, in Mongolian gerbils the anti-fertility effects of quinestrol are reversed within 3 months of treatment (Shen *et al*. 2011a,b). Therefore, laboratory studies to assess the reversibility, if any, of the anti-fertility effects of EP-1 in *M. natalensis* are urgently required to establish how many doses might be needed in a maize growing season (which typically lasts between 4 to 5 months from planting to harvest) to effectively reduce damage to maize crops at germination and harvest stages.

Population growth at the end of the cropping season was significantly suppressed by both treatments, when compared to control treatment, when the baiting was moved closer to the germination period (i.e. in the 2019–2020 cropping season) than when the baiting took place a month before maize seeding (i.e. 2018–2019 cropping season). Increased rodent activity during the germination period (Stenseth *et al*. 2003; Mulungu 2017) could have increased the chances of individuals consuming the baits. This finding is supported by our results in the rodenticide fields where recruitment, in the first session after treatment, was higher in the 2019–2020 season (100%) than in the 2018–2019 season (85%), meaning more rodents consumed the bait in the 2019–2020 season than in the 2018–2019 season. Our observations from another study (Imakando, unpublished data) on the foraging behavior of rodents in and around maize fields also showed that there is more rodent activity during the germination period than when the fields are being prepared. Reduced population at the end of the cropping season is very important because, other work has shown, this could lead to decreased population-dependent damage to agricultural crops (Jacob *et al*. 2006).

In conclusion, our results have shown that a single application of a rodenticide has comparable effects on the population dynamics of *M. natalensis* over a maize cropping season as a single application of a fertility control bait (EP-1). Further, we showed that recruitment after treatments and damage caused by rodents to maize at germination was not influenced by both treatments. We also have shown that applying the baits a week before the germination period is better than applying a month before maize seeding in terms of suppressing the population growth at the end of the cropping season for fertility control and rodenticide application. This information will be critical to developing effective ecologically based rodent management strategies (fertility control) for rodent pest populations in maize fields. A fertility control approach could be the way forward to reduce rodent damage to maize crops and improve food security and income for smallholder famers.

ACKNOWLEDGMENTS

We thank Remmy Kopeka, Bridget Mayani, and Cluasin Chulu for their valuable assistance during the field work. We thank Darius Phiri for the help in designing the study map. We thank Bram Vanden Broecke for the R-script used in initial data analysis. We thank the farmers of Mwekera and Luto agricultural camps for hosting the project. We also thank DNPW for the research permit. We thank the Ministry of Agriculture (Kitwe Office) for facilitating collaboration with the farmers. This research was supported by the Commonwealth Scholarship Commission, UK with partial funding from the African Union (grant # AURG II-1-006-2016 EcoRodMan) and the International Partnership Program of Chinese Academy of Sciences (grant # 152111KYSB20160089).

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Results from the generalized linear mixed model with MNA as response variable comparing the population size, and how this changed over the growing season between treatments

Table S2 Results from the linear mixed effect model using density estimates (from density software) as response variable comparing the population size, and how this changed over the growing season between treatments

Figure S1 Photo of a rodent eating the bait inside a bamboo cutting, captured using a camera trap.

Cite this article as:

Imakando CI, Fernández-Grandon GM, Singleton GR, Belmain SR (2021). Impact of fertility versus mortality control on the demographics of *Mastomys natalensis* in maize fields. *Integrative Zoology* **00,** 1–13.