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
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 (Swanepeol 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 anti-fertility 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.
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 $R (%) = \frac{[\text{new captures/total captures}] × 100\%}{\text{new captures/total captures}}$. 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 Jackknife 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 pseudo-replication 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 treatments. 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.

| 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)  |

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 \((P = 0.106, 0.143, \text{ and } 0.398\) 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 \((\text{slope } = 0.051)\). 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 \((\text{slope } = -0.017)\). 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 \((\text{slope } = -0.01)\). 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 \((F_{2,3} = 0.93, P = 0.485; \text{ population growth } 70\% \pm 26\%, 32\% \pm 60\%, -10\% \pm 77\% \text{ for the control, fertility, and rodenticide treatments, respectively})\).

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, \text{ and } 0.003 \text{ 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 \((\text{slope } = 9.445)\). For the fertility and rodenticide treatments, we found a weak positive effect of time (session) on population size when compared to the control treatment \((\text{slope } = 0.756 \text{ and slope } = 1.682 \text{ for}}

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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).
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.
Fertility control of rodent pests

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%].

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

(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).
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 farmers.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

REFERENCES

Berny P, Esther A, Jacob J, Prescott C (2018). Development of resistance to anticoagulant rodenticides in rodents. In: van den Brink N, Elliott J, Shore R, Ratner B, eds. Anticoagulant Rodenticides and Wildlife. Emerging Topics in Ecotoxicology (Principles, Approaches and Perspectives), Vol. 5. Springer, Cham.

Bolker BM, Brooks ME, Clark CJ et al. (2008). Generalized linear mixed models: A practical guide for ecology and evolution. Trends in Ecology & Evolution 24, 127–35.

Borremans B, Sluydts V, Makundi RH, Leirs H (2015). Evaluation of short-, mid- and long-term effects of toe clipping on a wild rodent. Wildlife Research 42, 143–8.

Brian R, Venables B, Bates DM, Firth D, Ripley MB (2019). Package ‘MASS’: support functions and datasets for venables and Ripley’s MASS. Version 7.3-51.4, 1–169.

Brown PR, Huth NI, Banks PB, Singleton GR (2007). Relationship between abundance of rodents and damage to agricultural crops. Agriculture, Ecosystems and Environment 120, 405–15.

Buckle AP, Smith RH (2015). Rodent Pests and Their Control, 2nd edn. CABI, Wallingford, UK, p. 432.

Burgin CJ, Colella JP, Kahn PL, Upham NS (2018). How many species of mammals are there? Journal of Mammalogy 99, 1–14.

Capizzi D, Bertolino S, Mortelliti A (2014). Rating the rat: Global patterns and research priorities in impacts and management of rodent pests. Mammal Review 44, 148–62.

Chambers LK, Singleton GR, Hinds LA (1999). Fertility control of wild mouse populations: The effects of hormonal competence and an imposed level of sterility. Wildlife Research 26, 579–91.

Christensen JT (1996). Home range and abundance of Mastomys natalensis (Smith, 1834) in habitats affected by cultivation. African Journal of Ecology 34, 298–311.

Colombe S, Jancoles M, Riviere A, Bertherat E (2019). A new approach to rodent control to better protect human health; first international meeting of experts under the auspices of WHO and Pan American Health Organization. Weekly Epidemiological Record 94, 197–212.

Desvars-Larrive A, Pascal M, Gasqui P et al. (2017). Population genetics, community of parasites, and resistance to rodenticides in an urban brown rat (Rattus norvegicus) population. PLoS ONE 12, e0184015.
Efford M (2014). Density 5.0: software for spatially explicit capture-recapture. Available from URL: http://www.otago.ac.nz/density

Elliott JE, Rattner BA, Shore RF, Van Den Brink NW (2016). Paying the piper: Mitigating the impact of anticoagulant rodenticides on predators and scavengers. *BioScience* **66**, 401–7.

Erickson W, Urban D (2004). *Potential Risks of Nine Rodenticides to Birds and Nontarget Mammals: A Comparative Approach*. Office of Prevention, Pesticides and Toxic Substances, United States Environmental Protection Agency, p. 225.

Fu H, Bao D, Duhu M *et al.* (2016). Anti-fertility effects and mechanism of the plant extract shikonin on mice. *Journal of Biosciences and Medicines* **4**, 30–9.

Fu H, Zhang J, Shi D *et al.* (2011). Effects of a contraceptive compound (EP-1) on population growth of wild Mongolian gerbils (*Meriones unguiculatus*). *Acta Theriologica Sinica* **31**, 404–11.

Fu H, Zhang J, Shi D, Wu X (2013). Effects of levonorgestrel-quinestrol (EP-1) treatment on Mongolian gerbil wild populations: A case study. *Integrative Zoology* **8**, 277–84.

Gillies CS, Hebblewhite M, Nielsen SE *et al.* (2006). Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* **75**, 887–98.

Hanssen HC, Stolter C, Imholt C, Jacob J (2016). Plant secondary metabolites as rodent repellents: A systematic review. *Journal of Chemical Ecology* **42**, 970–83.

Hurst ZM, McCleery RA, Collier BA *et al.* (2013). Dynamic edge effects in small mammal communities across a conservation-agricultural interface in Swaziland. *PLoS ONE* **8**, e74520.

Jacob J, Rahmini, Sudarmaji (2006). The impact of imposed female sterility on field populations of rice-field rats (*Rattus argentiventer*). *Agriculture, Ecosystems and Environment* **115**, 281–4.

Jacob J, Singleton GR, Hinds LA (2008). Fertility control of rodent pests. *Wildlife Research* **35**, 487–93.

Jamil T, Ozinga WA, Kleyer M, ter Braak CJF (2013). Selecting traits that explain species-environment relationships: A generalized linear mixed model approach. *Journal of Vegetation Science* **24**, 988–1000.

Krebs CJ (1999). *Ecological Methodology*, 2nd edn. Addison Wesley Longman, Menlo Park, CA.

Labuschagne L, Swanepoel LH, Taylor PJ, Belmain SR, Keith M (2016). Are avian predators effective biological control agents for rodent pest management in agricultural systems? *Biological Control* **101**, 94–102.

Lefebvre S, Fourel I, Queffelec S *et al.* (2017). Poisoning by anticoagulant rodenticides in humans and animals: Causes and consequences. In: Malangu N, ed. *Poisoning: From Specific Toxic Agents to Novel Rapid and Simplified Techniques for Analysis*. IntechOpen Limited, London, UK, pp. 11–32.

Leirs H, Sluydts V, Makundi R (2010). Rodent outbreaks in sub-Saharan Africa. In: Singleton GR, Belmain SR, Brown PR, Hardy B, eds. *Rodent Outbreaks: Ecology and Impacts*. International Rice Research Institute, Los Banos, Philippines, pp. 269–80.

Leirs H, Verhagen R, Sabuni CA, Mwanjabe PS, Verheyen W (1997). Spatial dynamics of *Mastomys natalensis* in a field-fallow mosaic in Tanzania. *Belgian Journal of Zoology* **127**, 29–38.

Lekei E, Ngowi AV, London L (2017). Acute pesticide poisoning in children: Hospital review in selected hospitals of Tanzania. *Journal of Toxicology* **2017**, 1–8.

Liu M, Qu J, Yang M *et al.* (2012a). Effects of quinestrol and levonorgestrel on populations of plateau pikas, *Ochotona curzoniae*, in the Qinghai-Tibetan Plateau. *Pest Management Science* **68**, 592–601.

Liu M, Wan X, Yin Y *et al.* (2012b). Subfertile effects of quinestrol and levonorgestrel in male rats. *Reproduction, Fertility and Development* **24**, 297–308.

Liu Q, Qin J, Chen Q, Wang D, Shi D (2013). Fertility control of *Rattus nitidus* using quinestrol: Effects on reproductive organs and social behaviour. *Integrative Zoology* **8**, 9–17.

Lohr MT, Davis RA (2018). Anticoagulant rodenticide use, non-target impacts and regulation: A case study from Australia. *Science of the Total Environment* **634**, 1372–84.

Luna PA, Bintanel H, Viñuela J, Villanúa D (2020). Nest-boxes for raptors as a biological control system of vole pests: High local success with moderate negative consequences for non-target species. *Biological Control* **146**, e104267.

Machar I, Harmacek J, Vrublova K, Filippovova J, Brus J (2017). Biocontrol of common vole populations by avian predators versus rodenticide application. *Polish Journal of Ecology* **65**, 434–44.

Makundi RH, Bekele A, Leirs H, Massawe AW, Rwamugira W, Mulungu LS (2005). Farmer’s perceptions of rodents as crop pests: Knowledge, attitudes and
practices in rodent pest management in Tanzania and Ethiopia. *Belgian Journal of Zoology* **135**, 153–7.

Makundi RH, Massawe AW, Mulungu LS (2007). Reproduction and population dynamics of *Mastomys natalensis* Smith, 1834 in an agricultural landscape in the Western Usambara Mountains, Tanzania. *Integrative Zoology* **2**, 233–8.

Makundi RH, Massawe AW, Mulungu LS, Katakeba A (2010). Species diversity and population dynamics of rodents in a farm fallow field mosaic system in Central Tanzania. *African Journal of Ecology* **48**, 313–20.

Massawe AW, Makundi RH, Zhang Z et al. (2018). Effect of synthetic hormones on reproduction in *Mastomys natalensis*. *Journal of Pest Science* **91**, 157–68.

Massawe AW, Rwanugira W, Leirs H, Makundi RH, Mulungu LS (2005). Influence of land preparation methods and vegetation cover on population abundance of *Mastomys natalensis* in Morogoro, Tanzania. *Belgian Journal of Zoology* **135**, 187–90.

Mayamba A, Byamungu RM, Makundi RH et al. (2019). Species composition and community structure of small pest rodents (Muridae) in cultivated and fallow fields in maize-growing areas in Mayuge district, Eastern Uganda. *Ecology and Evolution* **9**, 7849–60.

Meerbong BG, Singleton GR, Kijistra A (2009). Rodentborne diseases and their risks for public health. *Critical Reviews in Microbiology* **35**, 221–70.

Meheretu Y, Suluyts V, Welegerima K et al. (2014). Rodent abundance, stone bund density and its effects on crop damage in the Tigray highlands, Ethiopia. *Crop Protection* **55**, 61–7.

Mlyashimbi ECM, Vanden Broecke B, Mariën J et al. (2019). Soil type influences population dynamics and survival of the Multimammate rat (*Mastomys natalensis*) in semi-arid areas in Tanzania. *Crop Protection* **124**, 104829.

Mulungu LS (2017). Control of rodent pests in maize cultivation: The case of Africa. In: Watson D, ed. *Achieving Sustainable Maize Cultivation*, Vol 2. Burleigh Dodds Science Publishing Limited, Cambridge, pp. 317–38.

Mulungu LS, Borremans B, Ngowo V et al. (2015). Comparative study of movement patterns of *Mastomys natalensis* in irrigated rice and fallow fields in eastern Tanzania. *African Journal of Ecology* **53**, 473–9.

Mulungu LS, Makundi RH, Massawe AW, Leirs H (2007). Relationship between sampling intensity and precision for estimating damage to maize caused by rodents. *Integrative Zoology* **2**, 131–5.

Mulungu LS, Ngowo V, Mdogo M et al. (2013). Population dynamics and breeding patterns of multimammate mouse, *Mastomys natalensis* (Smith 1834), in irrigated rice fields in Eastern Tanzania. *Pest Management Science* **69**, 371–7.

Mwanjabe PS, Leirs H (1997). An early warning system for IPM-based rodent control in smallholder farming systems in Tanzania. *Belgian Journal of Zoology* **127**(Suppl.), 49–58.

Mwanjabe PS, Sirima FB, Lusingu J (2002). Crop losses due to outbreaks of *Mastomys natalensis* (Smith, 1834) Muridae, Rodentia, in the Lindi region of Tanzania. *International Biodeterioration and Biodegradation* **49**, 133–7.

Nocera JJ, Dawe KL (2008). Managing for habitat heterogeneity in grassland agro-ecosystems influences the abundance of masked shrews (*Sorex cinereus*). *Journal of Sustainable Agriculture* **32**, 379–92.

Olayemi A, Fichet-Calvet E (2020). Systematics, ecology, and host switching: Attributes affecting emergence of the Lassa virus in rodents across western Africa. *Viruses* **3**, 312.

Paz A, Jarea D, Arroyo L et al. (2012). Avian predators as a biological control system of common vole (*Microtus arvalis*) populations in north-western Spain: Experimental set-up and preliminary results. *Pest Management Science* **69**, 444–50.

R Core Team (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available from URL: https://www.R-project.org/

Rost S, Fregin A, Ivaskevicius V et al. (2004). Mutations in *VKORC1* cause warfarin resistance and multiple coagulation factor deficiency type 2. *Nature* **427**, 537–41.

Shen W, Guo Y, Shi D, Wang D, Hai S (2011a). Antifertility effect of quinestrol in male Mongolian gerbils (*Meriones unguiculatus*) and its reversibility. *Acta Theriologica Sinica* **31**, 171–8.

Shen W, Shi D, Wand D, Guo Y, Hai S, Yue Z (2011b). Quinestrol treatment induced testicular damage via oxidative stress in male Mongolian gerbils (*Meriones unguiculatus*). *Experimental Animals* **60**, 445–53.

Shi L, Li X, Ji Z et al. (2020). The reproductive inhibitory effects of levonorgestrel, quinestrol, and EP-1 in Brandt’s vole (*Lasiopodomys brandtii*). *PeerJ* **8**, e9140.

Silvy NJ, Lopez RR, Petersen MJ (2012). Techniques for marking wildlife. In: Silvy NJ, ed. *The Wildlife
Techniques Manual: Research, 7th edn. The John Hopkins University Press, Baltimore, pp. 230–57.

Singleton GR, Brown PR, Jacob J, Aplin KP, Sudarmaji (2007). Unwanted and unintended effects of culling: A case for ecologically-based rodent management. *Integrative Zoology* **2**, 247–59.

Singleton GR, Hinds LA, Leirs H, Zhang Z (1999). Ecologically-based management of rodent pests – re-evaluating our approach to an old problem. In: Singleton GR, Hinds LA, Leirs H, Zhang Z, eds. *Ecologically-Based Management of Rodent Pests*. Australian Centre for International Agricultural Research, Canberra, pp. 17–29.

Singleton GR, Sudarmaji, Suriapermana S (1998). An experimental field study to evaluate a trap-barrier system and fumigation for controlling the rice field rat, *Rattus argentiventer*, in rice crops in West Java. *Crop Protection* **17**, 55–64.

Stenseth NC, Leirs H, Mercelis S, Mwanjabe P (2001). Comparing strategies for controlling an African pest rodent: An empirically based theoretical study. *Journal of Animal Ecology* **38**, 1020–31.

Stenseth NC, Leirs H, Skonhoft A et al. (2003). Mice, rats, and people: The bio-economics of agricultural rodent pests. *Frontiers in Ecology and the Environment* **1**, 367–75.

Swanepoel LH, Swanepoel CM, Brown PR et al. (2017). A systematic review of rodent pest research in Afro-Malagasy small-holder farming systems: Are we asking the right questions? *PLoS ONE* **12**, e0174554.

Tosh DG, Shore RF, Jess S et al. (2011). User behaviour, best practice and the risks of non-target exposure associated with anticoagulant rodenticide use. *Journal of Environmental Management* **92**, 1503–8.

Tran TT, Hinds LA (2012). Fertility control of rodent pests: A review of the inhibitory effects of plant extracts on ovarian function. *Pest Management Science* **69**, 342–54.

Vibe-Petersen S, Leirs H, De Bruyn L (2006). Effects of predation and dispersal on *Mastomys natalensis* population dynamics in Tanzanian maize fields. *Journal of Animal Ecology* **75**, 213–20.

Wang D, Li Q, Li K, Guo Y (2017). Modified trap barrier system for the management of rodents in maize fields in Jilin Province, China. *Crop Protection* **98**, 172–8.

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.