1 Vegetation cover and food availability shapes the foraging activity of rodent

2 pests in and around maize fields.

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11 Abstract:

Evidence-based information for smallholder farmers on where and when to conduct 12 rodent management is vital given that most are resource poor and depend on 13 agriculture for food and income. However, there is scarce information on how the 14 foraging activity of rodent pests changes over agricultural cropping seasons. We 15 used the concepts of giving-up-density (GUD) and landscape of fear to monitor how 16 the foraging activity of rodent pests changes in and around maize (Zea mays) fields 17 over the cropping season. We tested the hypothesis that the foraging activity of 18 rodent pests will be influenced by vegetation cover, perceived predation risk and 19 food availability. Mastomys natalensis was the dominant species in all maize fields (n 20 = 3, 87.05% of the total captures). We observed that the foraging activity of rodents 21 was influenced by vegetation cover and food availability. During the germination 22 stage, rodent activity in the natural habitat and along the border was higher than 23 inside the maize fields. During land preparation, planting, weeding, maize tasselling, 24

maturity, and post-harvest stages, there was no difference in the foraging activity in and around the maize fields. During the harvest stage, the foraging activity was higher in the maize fields than along the border and in the natural habitat. These results can be used to guide smallholder farmers where and when to focus rodent control measures during different stages of the cropping season. An additional approach would be to develop strategies that could potentially increase rodent fear perceptions in cropping landscapes.

Keywords: Rodent pests, *Mastomys natalensis*, foraging activity, maize field, giving up-density, landscape of fear

34 **1.** Introduction

35 Rodent pests damage maize crops before and after harvest (Skonhoft et al., 2006; Swanepoel et al., 2017). Mostly, rodent pests damage maize crops during the 36 37 germination (Mulungu et al., 2005) and maturation stages (Mulungu, 2017). At the germination stage, rodents dig up and consume germinating maize seeds (Mulungu 38 et al., 2007) leading to either a regular distribution of damage in mosaic fields or a 39 40 more random distribution in monoculture fields (Mulungu et al., 2005). At the maturation stage, rodents consume both fresh and dry grains when the maize plants 41 are standing or on the ground (Mulungu, 2017). Population dynamics and 42 competition for available food resources partly accounts for observed heterogeneous 43 damage patterns (Mohr et al., 2003). Predation risk, land preparation methods and 44 soil type can also account for the heterogrenous damage by indirectly or directly 45 affecting the population dynamics of rodents (Mulungu et al., 2005). Therefore, either 46 random or stratified sampling methods could be used to assess rodent damage in 47 48 maize fields (Mulungu et al., 2007). In maize cropping systems, little is known both

about how the foraging activity of rodent pests changes over the cropping season
and how this may affect crop damage, particularly in relation to harbourage provided
by field margin vegetation and the maize crop itself. Maintaining field margin
vegetation is increasingly recognised as important in facilitating crop pollination and
conservation biological control of insect pests (Arnold *et al.*, 2021; Ochieng *et al.*,
2022), but such vegetation could potentially exacerbate the presence of rodent pests
(Jacob, 2008; Rodríguez-Pastor *et al.*, 2016).

Understanding the foraging activity of rodent pests is important to enable sustainable 56 control to reduce their impact and damage (Belmain, 2010; Krijger et al., 2017). 57 Foraging activity has been strongly correlated with vegetation cover in several 58 studies. In Philippines, Rattus tanezumi spent more time foraging at the centre of the 59 rice fields than on the field edges (border), where there was less vegetation cover 60 (Jones et al., 2017). Evidence suggests that rodents in agricultural landscapes 61 spend more time foraging in areas where they perceive the least fear from predation 62 (Ylonen et al., 2002). Understanding how the foraging activity of rodents changes 63 over the maize growing season could help to develop management strategies that 64 incorporate the 'landscape of fear' (LOF) concept (Laundré et al., 2001) and thereby 65 reduce rodent foraging in cropping areas. Furthermore, evidence-based information 66 on where and when to conduct rodent management can help to prevent rodent 67 outbreaks and is vital given that most farmers are resource poor and depend on 68 agriculture for food and income (Swanepoel et al., 2017; Taylor et al., 2012). 69

To monitor and/or map the foraging activity of rodents across the maize growing season, one technique that can be exploited is the giving-up-density (GUD) approach, which attempts to characterise the LOF for a species in a habitat. The LoF

is "the spatially explicit distribution of perceived predation risk as seen by a prey 73 population" (Bleicher, 2017; Gaynor et al., 2019). The perceived predation risk (cost 74 of foraging) of a population can be measured by the GUD (Brown and Kotler, 2004). 75 According to Johnson and Horn (2008), a forager abandons a patch quickly when 76 the perceived risk of predation is high, leaving behind greater density of food 77 compared to when the perceived risk of predation is low. In many crops, landscape 78 79 features can affect both domestic and wild predators that prey on rodents (Pita et al., 2009; Fischer and Schröder, 2014; St. George and Johnson, 2021), as can the 80 81 presence of farmers regularly tending their fields who may influence the spatial behaviour of rodents (Jones et al., 2017). Rodents use both direct (predator odours) 82 and indirect (habitat type and weather conditions) cues to assess the risk of 83 predation in a particular patch (Orrock et al., 2004). 84

GUDs have been successfully used to understand the foraging activity of rodents in 85 rice fields (Jones et al., 2017), maize fields (Mohr et al., 2003), wheatfields (Ylonen 86 et al., 2002) and in natural habitats (Wheeler and Hik, 2014; Yang et al., 2016; 87 Loggins et al., 2019). Despite the application of GUD studies on rodents, few papers 88 directly apply GUDs to assess rodent management strategies (Krijger et al., 2017). 89 Currently, most rodent management strategies in maize cropping systems do not 90 incorporate the rodent's landscape of fear which could increase their efficiency and 91 reduce damage to maize crops. To address these shortcomings and highlight how 92 GUD studies could refine management strategies beyond the usual measures of 93 94 abundance or activity, the current study interprets the results with consideration of rodent pest management strategies by recommending areas (in and around maize 95 fields) where farmers should focus pest control during different times of the maize 96 cropping season, i.e., areas where rodents perceive the lowest levels of predation 97

98 (Krijger *et al.*, 2017). This is the first application of GUDs and LOF in Africa to 99 understand how the foraging activity of rodent pest species in and around maize 100 fields changes across a growing season.

We tested the hypothesis that the foraging activity of rodents in a maize cropping 101 system is influenced by vegetation cover and food availability. We predicted that 102 rodents will have: (i) lower foraging activity in the maize fields than along the border 103 and in the adjacent natural habitat during the land preparation, planting, germination 104 and post-harvest stages (when the maize fields have less vegetation cover and less 105 food resources (grains)); (ii) equal foraging activity in maize fields and adjacent 106 natural habitat from the weeding to maize tasselling stages when the vegetation 107 cover in the maize fields increases; and (iii) the foraging activity will be higher in the 108 maize fields than the adjacent habitat during the maturity, and harvest stages due to 109 increased food resources (maize grains) and vegetation cover. This study will help to 110 understand how different habitats may affect anti-predator and foraging activity and 111 could guide rodent damage assessments (Jones et al., 2017) and guide future 112 ecologically-based rodent management strategies (Krijger et al., 2017) in maize 113 cropping systems. 114

115 **2. Materials and methods**

116 2.1. Experimental Design

Four maize fields located adjacent to a natural habitat in Luto agricultural camp, Kitwe, Zambia (located between 12.94S,28.17E and 12.93S,28.20E) were selected for this study (Fig. 1). The maize fields ranged from 2 to 4 hectares.

Prior to the main study, a pilot study was conducted to establish the best food (e.g., 120 groundnuts, sunflower kernels, or pumpkin seeds), feeder (e.g., plastic, or wooden 121 trays) and substrate type (sand or soil from the fields) for GUD estimates (Bedoya-122 Perez et al., 2013). The pilot study involved placing 20 seeds of a single type 123 (groundnuts, sunflower kernels, or pumpkin seeds) in separate plastic or wooden 124 trays (18 buried and 2 placed on the top) filled with either sand or soil from the fields. 125 126 Trays contained small drainage holes in the bottom to allow rain water to drain through. The trays were left in fields for three consecutive nights, counting the 127 128 number of seeds remaining each morning, and resetting to 20 seeds each night. Pilot data indicated sunflower kernels and pumpkin seeds were more difficult to 129 recover than groundnuts when counting the number of seeds remaining, especially if 130 it had rained. Hence, we settled for groundnuts as the best food for the main study. 131 Plastic trays were preferred over wooden trays because wooden trays were soaked 132 by the rains making them difficult to carry around. Rodent activity was generally 133 lower in trays filled with sand, possibly because the sand increased neophobic 134 behaviour of rodents as sand is not commonly found in the area. Therefore, we used 135 soils from the fields as the substrate type for the main study. Thus the main study 136 was developed using four plastic trays with 20 m spacing between the trays (Ylonen 137 et al., 2002) which were placed along five transects. The first transect was laid along 138 the border (field edge) of the maize field (transect #3), and two were at 20 m and 40 139 m either side of the border transect in maize fields (transects 1 and 2) and natural 140 habitat (transects 4 and 5), respectively (Fig. 2). 141

Twenty groundnuts were placed in each tray, 18 buried in soil and 2 placed on the top (Jones *et al.*, 2017). The foraging activity was monitored for three consecutive days (in the morning), with trays restocked with 20 groundnuts each day. The GUD

was assessed by counting the number of seeds remaining in the tray (Brown, 1988). 145 To confirm rodent activity at the feeding patches, a Bushnell Trophy Cam HD 146 Essential Trail camera trap was placed in one patch per field at the beginning of the 147 study (Fig. 3) (see Bedoya-Perez et al., (2013)). The camera traps were set to record 148 24 h per day with a 30 s delay between detections (Williams et al., 2018; Rich et al., 149 2017). The following parameters were set on the camera traps; take three photos 150 151 (8M pixel) per trigger, sensor level at auto, NV shutter at medium and time stamp on. The camera traps were set 20 cm (Ramesh and Downs, 2015; Meek et al., 2012) 152 153 above the ground on a wooden pole. The plastic tray was placed 1.5 m in front of the camera trap (Glen et al., 2016; Meek et al., 2012). 154

Foraging activity was assessed monthly (4-week intervals) during the maize growing 155 season (October to July), while the populations of rodents in the maize fields were 156 monitored monthly following the capture-mark-recapture (CMR) procedure in fields 157 1-3 as part of another study which examined the population dynamics of small 158 mammals in maize fields (Imakando, 2021). A 70 m x 70 m permanent trapping grid 159 was established in the centre of each maize field. Each trapping grid had seven trap 160 lines, 10 m apart. Seven trapping stations, 10 m apart, were marked on each trap 161 line. One Sherman live-trap, baited with a mixture of peanut butter and maize bran, 162 was set in each trapping station. The traps were set in the evening and checked in 163 the morning for three consecutive days in each grid. On the first capture, all animals 164 were toe-clipped using sterile scissors. This study was initially conducted during the 165 166 2018/2019 maize cropping season and repeated in the 2019/2020 maize cropping season. 167

168 2.2. Statistical analysis

An independent samples t-test, with Levene's Test for equality of variance, was used 169 170 to compare the GUD results from 2018/2019 and 2019/2020 cropping seasons. A two-way ANOVA using general linear mixed-effects model "package Ime4" (Bates et 171 al., 2019) was used to analyse the effect of distance (transect location) and crop 172 stage on angular transformed GUDs (proportion of groundnuts remaining) (Laundré 173 et al., 2001; Kasuya, 2004). Tukey's post hoc comparisons were conducted on 174 distance (transects) and crop stage using the package 'multcomp' (Hothorn et al., 175 2019). All analyses were conducted in R version 3.6.1 (R Core Team, 2019). We 176 used the minimum number of animals known to be alive (MNA) method to calculate 177 the population of rodents during each stage. 178

179 **3. Results**

180 3.1. Rodent species and population dynamics.

From the CMR data, the most common rodent species in maize fields was *Mastomys natalensis* (87.05% of the total captures, Table 1).

183 **Table 1**

184 Species composition of small mammals (rodents and shrews) captured in three 185 maize fields in Kitwe, Zambia, with species ordered by overall abundance. The 186 numbers in brackets are percentage composition of each species.

	Fields			
species	Luto 1	Luto 2	Luto 3	Overall
Mastomys natalensis	131 (72.78%)	396 (91.45%)	347 (88.75%)	874 (87.05%)
Mus minutoides	23 (12.78%)	15 (3.46%)	18 (4.60%)	56 (5.58%)
Crocidura hirta	14 (7.78%)	6 (1.39%)	11 (2.05%)	28 (2.79%)

2 (1.11%)	2 (0 000()	44 (0.040()	
∠ (I.II/0)	3 (0.69%)	11 (2.81%)	16 (1.59%)
5 (2.78%)	7 (1.62%)	1 (0.26%)	13 (1.29%)
3 (1.67%)	6 (1.67%)	1 (0.26%)	10 (1.00%)
0 (0%)	0 (0%)	2 (0.51%)	2 (0.2%)
1 (0.56%)	0 (0%)	1 (0.26%)	2 (0.2%)
0 (0%)	0 (0%)	1 (0.26%)	1 (0.1%)
0 (0%)	0 (0%)	1 (0.26%)	1 (0.1%)
1 (0.56%)	0 (0%)	0 (0%)	1 (0.1%)
180 (100%)	433 (100 %)	391 (100 %)	1004 (100%)
8	6	10	11
0.97	0.42	0.56	0.56
	3 (1.67%) 0 (0%) 1 (0.56%) 0 (0%) 0 (0%) 1 (0.56%) 180 (100%) 8	3 (1.67%) 6 (1.67%) 0 (0%) 0 (0%) 1 (0.56%) 0 (0%) 0 (0%) 0 (0%) 0 (0%) 0 (0%) 1 (0.56%) 0 (0%) 1 (0.56%) 0 (0%) 1 (0.56%) 0 (0%) 1 80 (100%) 433 (100 %) 8 6	3 (1.67%) 6 (1.67%) 1 (0.26%) 0 (0%) 0 (0%) 2 (0.51%) 1 (0.56%) 0 (0%) 1 (0.26%) 0 (0%) 0 (0%) 1 (0.26%) 0 (0%) 0 (0%) 1 (0.26%) 0 (0%) 0 (0%) 1 (0.26%) 0 (0%) 0 (0%) 1 (0.26%) 1 (0.56%) 0 (0%) 0 (0%) 1 (0.56%) 0 (0%) 0 (0%) 1 80 (100%) 433 (100 %) 391 (100 %) 8 6 10

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The density of rodents was low during the planting period and increased as the vegetation increased in the maize fields. The highest rodent density in maize fields was observed during the harvest stage and just before the fields are cleared (May-June). Population density reduced during land preparation post-harvest, especially after clearing of the fields (Fig. 4).

3.2. Changes in the foraging activity of rodent pest species in and around maizefields.

Motion sensitive camera traps confirmed that *M. natalensis* was the rodent species 195 196 that frequently visited the GUDs. An independent samples t-test was conducted to examine GUD differences between the 2018/2019 and 2019/2022 cropping seasons. 197 Levene's Test for equality of variances showed no violations, p = 0.289. In general, 198 the GUD results from the 2018/2019 season and 2019/2020 season were not 199 significant different (t(88) = 1.201, p = 0.233), so the data were combined during the 200 201 analyses. Due to differences in the planting and harvest times between farmers, the results from December and January were combined as "germination stage" while the 202 results from June and July were combined as "post-harvest" during the analyses, but 203

these were separated when constructing a heat map on spatial use. In general, the 204 foraging activity of rodents was highest (i.e., lowest GUD) during the germination 205 stage (mean GUD = 50.5) while lowest during the land preparation and post-harvest 206 stages (mean GUD = 58.0 at both crop stages). From the two-way ANOVA, overall, 207 there was a significant effect of distance for crop stage ($F_{7,40} = 11.228$, p < 0.001) 208 and the interaction between the effects of distance and crop stage on the GUD 209 210 $(F_{28,40} = 4.723, p < 0.001)$, but no effect of distance on the GUD $(F_{4,40} = 1.631, p = 1.631)$ 211 0.185).

For distance from the edge of crops and natural habitat (transect), Tukey's post-hoc 212 tests revealed that rodent activity was affected during maize germination and harvest 213 stages, whereas rodent activity was similar on all transects during the other stages 214 (see Supplementary Table S2). During the maize germination stage, rodent activity 215 was higher on transect 5 (40 m into the natural habitat; mean GUD = 37) than on 216 transects 1 (mean GUD = 59; t = -6.551, p < 0.001), 2 (mean GUD = 58; t = -6.039, 217 p < 0.001) and 3 (mean GUD = 53; t = - 3.941, p = 0.001). Additionally, rodent 218 activity was higher on transect 4 (20 meters into the natural forest; mean GUD = 43) 219 than on transects 1 (t = - 4.528, p < 0.001), and 2 (t = - 4.016, p < 0.001) during the 220 germination stage. However, rodent activity during the harvest stage was higher on 221 transect 1 (40 meters into the maize field; mean GUD = 50) than on transects 3 222 (mean GUD = 59; t = 2.935, p = 0.034), 4 (mean GUD = 60; t = 3.277, p = 0.013) 223 and 5 (mean GUD = 59; t = 2.817, p = 0.047). 224

Rodent activity was higher during the germination stage than during land preparation, planting, weeding, maturation, harvest and post-harvest crop stages [(LP vs. G; z = -5.690, p < 0.001); (P vs. G; z = -4.757, p < 0.001); (G vs. W; z =

228 3.401, p = 0.015); (G vs. M; z = 3.409, p = 0.015); (G vs. H; z = 5.418, p < 0.001); 229 and (G vs. PH; z = 6.757, p < 0.001)]. Rodent activity also was higher during the 230 maize tasselling stage than land preparation (z = -3.154, p = 0.034); and higher 231 during the weeding stage than harvest stage (z = 3.262, p = 0.024) (see 232 Supplementary Table S3). The changes in the foraging activity of rodents in and 233 around maize fields can be summarised using a heat map (Fig. 5).

234 **4.** Discussion

This is the first study to document how the foraging activity of rodents in and around 235 maize fields changes across the growing season. As predicted, the foraging activity 236 of rodents over the maize growing season was influenced by vegetation cover and 237 food availability. Higher rodent activity occurred in the adjacent natural habitat than 238 along and inside the maize field during the germination period. Uniform/equal rodent 239 activity in the adjacent natural habitat, along the border and inside maize fields 240 occurred during the land preparation, planting, weeding, maize tasselling, maturity, 241 and post-harvest stages. During the harvesting period rodent activity was 242 significantly higher inside the maize fields than along the border and adjacent natural 243 habitat. These results provide evidence-based information on how rodent foraging 244 activity changes across the maize growing season. Krijger et al., (2017) suggested 245 that focusing rodent pest management in those areas where rodents perceived the 246 lowest predation risk could be more effective and efficient. Therefore, in 247 management terms, our findings suggest that farmers are likely to have greater 248 success managing rodent pests during the germination of the maize crop by focusing 249 rodent control measures in the natural habitats adjacent to the maize fields rather 250 than inside or along the edge of maize fields. From the weeding to maturation 251

stages, equal success would be achieved if rodent control measures are 252 concentrated inside, along the edge of maize fields or in the natural habitat adjacent 253 to the maize fields. During the harvest stage, greater success in managing rodent 254 pests could be achieved if rodent control measures are concentrated inside the 255 maize fields than if rodent control measures are concentrated along the field border 256 or in the natural habitat adjacent to the maize fields. However, it is necessary to 257 258 survey the species composition in all the habitats before application of control measures to minimize non-target implications of rodent control in natural habitats. 259 260 Therefore, our findings can be used by small holder farmers to focus rodent management strategies efficiently and effectively at different stages in the maize 261 cropping season, which in turn will reduce the cost for controlling rodent pest species 262 and losses of the crops. 263

Earlier work in maize fields in Tanzania have shown that vegetation cover plays an 264 important role in the foraging, habitat preference and population dynamics of 265 rodents, particularly *M. natalensis* (Leirs et al., 1996; Mohr et al., 2003). Leirs et al., 266 (1996) reported that *M. natalensis* preferred (i.e., was more active in) areas with 267 vegetation cover while tending to avoid open spaces, especially during periods of 268 low density. Corroborating this finding, Mohr et al., (2003) used GUD and video 269 evidence to show that *M. natalensis* perceived lower predation risk in feeding 270 patches with cover than in open patches. Elsewhere, research on the foraging 271 activity of other rodents using GUDs suggests that rodent foraging activity is shaped 272 273 by the perceived predation risk (Ylonen et al., 2002; Orrock et al., 2004; Wheeler and Hik, 2014; Jones et al., 2017). Jones et al. (2017) found that the foraging activity of 274 Rattus tanezumi in rice fields in the Philippines was shaped by the perceived 275 predation risk whereby more damage was observed in the middle of the rice fields 276

(with more vegetation cover) than on the borders and rice bund, with no vegetation. 277 Ylonen et al. (2002) reported that prior to harvest of wheat in southern Australia, 278 house mice, Mus domesticus, were mainly in the crop. Similarly, Oldfield mice, 279 *Peromyscus polionotus*, in South Carolina, USA, were found to remove more seeds 280 in areas with vegetation cover than outside of cover (Orrock et al., 2004). In Canada, 281 the arctic ground squirrel, Urocitellus parryii, exhibited habitat specific strategies to 282 283 minimise predation risk by foraging more in tundra and shrub-tundra habitats while avoiding the shrub-dominated habitat, which reduced their visibility and increased 284 285 predation risk (Wheeler and Hik, 2014). All of these studies highlight the importance of vegetation cover as a feature of small mammal behaviour to avoid predation, 286 which aligns with the conclusions from our study. 287

Increased rodent activity around maize fields during the germination stage was 288 reported in other studies (Stenseth et al., 2003; Mulungu et al., 2007). However, the 289 findings in our study indicate that rodent activity was only high in the adjacent natural 290 291 habitat and along the border during germination of the maize crop. This indicates that, during the germination stage, the perceived predation risk was higher inside the 292 maize fields than along the border and adjacent natural habitat, corroborating the 293 studies by Johnson and Horn (2008) and Jones et al., (2017), who reported that 294 rodents perceived open areas to be riskier than areas with cover. Similarly, Key 295 (1990) found that pre-harvest maize damage from the African ground squirrel 296 occurred at the edges of the fields than in the middle and that they used the edges of 297 298 the field for refuge when disturbed while feeding in the fields. However, when farming methods that lead to less disturbance to rodent burrows and increased cover 299 300 and food supply, such as conservation agriculture, mice become resident in fields all the time, rather than retreating to field edges (Ruscoe et al., 2022). This indicates 301

that foraging activity of rodents in maize fields is shaped by their perceived predation
risk. Therefore, high GUDs during the land preparation stage on all transects may be
because at this stage the maize fields were cleared and, even in the natural habitat,
the vegetation cover is dry and minimal.

As the height of maize and vegetation increased inside the maize fields (from the 306 weeding to maturation stages), there was no difference in the mean GUD between 307 the natural habitat and maize field transects indicating that the perceived predation 308 was equal in the forest, along the margin and inside the maize field. This further 309 supports the contention that rodent foraging activity is shaped by vegetation cover 310 (Brown, 1988; Mohr et al., 2003). Vegetative cover provides shelter for rodents, 311 leading to reduced detection probability and capture by predators (Banasiak and 312 Shrader, 2016) and thus reduces the perceived predation risk and increases the 313 foraging activity of rodent species (Loggins et al., 2019). A limitation of our study is 314 that we are unable to comment on whether the different rodent species found in the 315 study area respond to vegetation cover in the same way. Further studies, for 316 example using camera traps, are recommended to understand whether there are 317 detectible differences in the way different small mammal species within the same 318 habitat respond to GUDs, vegetation cover and predation risk. As our study area is 319 dominated by *M. natalensis*, we can expect our results closely align with the 320 behaviour of this species. 321

Increased rodent activity inside the maize fields compared to along the border and adjacent habitat during the harvest stage suggests that, at this stage, the foraging activity was shaped by both vegetation and increased availability of food resources (Sluydts *et al.*, 2007). In addition, the harvest stage (May) coincided with the peak

rodent population (see Fig. 4) in maize fields. When presented with patches of equal 326 vegetation cover, food availability becomes important in explaining the foraging 327 activity of rodents. This finding supports the hypothesis that rodents select to forage 328 in habitats and microhabitats where the perceived risk of predation is low (Brown, 329 1988; Jacob and Brown, 2000; Ylonen et al., 2002). These findings support the 330 suggestion that rodent management during the harvest stage would be more 331 332 successful by placing baits inside the maize field than along the border or adjacent natural habitat. 333

In conclusion, GUD was successfully used to monitor rodent foraging activity in and 334 around maize fields over the maize cropping season. Rodent activity was driven by 335 vegetation cover and food availability. Based on our findings, during the germination 336 period, rodent control measures should be concentrated along the maize fields 337 edges and in the natural habitat adjacent to maize fields while during the harvest 338 period rodent control measures should be concentrated inside the maize fields. This 339 information will help smallholder farmers to be more efficient and effective in rodent 340 control by focusing their management strategies in areas of perceived reduced 341 predation risk (Krijger et al., 2017). We recommend further research, such as using 342 rodenticide baits or methods of trapping (e.g., linear trap barrier) at different times of 343 the growing season and at different distances from the maize field, to assess the 344 effect on rodent population dynamics and associated crop losses. Follow up studies 345 should also collect and include data on plant biomass on field edges and within fields 346 347 to track the changes over time and then assess how these changes affect rodent foraging activity. Additionally, farming practices such as tractor ploughing and 348 management of the vegetation around fields margins can be used to increase 349 predation risk (Brown et al., 2004: Massawe et al., 2006). Target rodent pest species 350

and non-target impacts should be surveyed in adjacent natural habitats, particularly as these habitats provide a range of ecosystem services beneficial to agricultural production (Hatt *et al.*, 2017; Lindell *et al.*, 2018; Mkenda *et al.*, 2019) where tradeoffs between the management of rodents, insects, and weeds as well as crop pollination services need careful cost-benefit assessments (Wegner and Pascual, 2011; Wratten *et al.*, 2012; Williams *et al.*, 2018).

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366 Author contributions

ICI and SRB conceived the topic. ICI, SRB, MFG and GRS conceived the research.
ICI conducted the field work and analyzed the data. All the authors contributed to the
writing of the manuscript.

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374

375 **References**

- Arnold, S.E.J., Elisante, F., Mkenda, P.A., Tembo, Y.L.B., Ndakidemi, P.A., Gurr,
 G.M., Darbyshire, I.A., Belmain, S.R., Stevenson, P.C. (2021) Beneficial insects are
 associated with botanically rich margins with trees on small farms. *Scientific Reports*.
 11, 1–11.
- Banasiak, N., Shrader, A.M. (2016) Similarities in perceived predation risk prevent temporal partitioning of food by rodents in an African grassland. *Journal of Mammalogy*. 97, 483–489.
- Bedoya-Perez, M.A., Carthey, A.J.R., Mella, V.S.A., McArthur, C., Banks, P.B.
 (2013) A practical guide to avoid giving up on giving-up densities. *Behavioral Ecology and Sociobiology*. 67, 1541–1553.
- Belmain, S.R. (2010) Developing pesticide-free rodent control for southern Africa. *Pesticides News.* 87, 9–11.
- Bleicher, S.S. (2017) The landscape of fear conceptual framework: definition and review of current applications and misuses. *PeerJ*. 5:e3772.
- Brown, J.S. (1988) Patch use as an indicator of habitat preference, predation risk,
 and competition. *Behavioral Ecology and Sociobiology*. 22, 37–47.
- Brown, J.S., Kotler, B.P. (2004) Hazardous duty pay and the foraging cost of predation. *Ecology Letters*. 7, 999–1014.

Brown, P.R., Davies, M.J., Croft, J.D., and Singleton, G.R. (2004). Can farm
management practices reduce the impact of house mouse populations on crops in
an irrigated farming system? Wildlife Research 31, 597-604.

Fischer, C., Schröder, B. (2014) Predicting spatial and temporal habitat use of rodents in a highly intensive agricultural area. *Agriculture, Ecosystems and Environment.* 189, 145–153.

Gaynor, K.M., Brown, J.S., Middleton, A.D., Power, M.E., Brashares, J.S. (2019)
Landscapes of fear: spatial patterns of risk perception and response. *Trends in Ecology and Evolution*. 34, 355–368.

St. George, D.A., Johnson, M.D. (2021) Effects of habitat on prey delivery rate and
prey species composition of breeding barn owls in winegrape vineyards. *Agriculture, Ecosystems and Environment.* 312, 107322.

Glen, A., Anderson, D., Veltman, C., Garvey, P., Nichols, M. (2016) Wildlife detector
dogs and camera traps: a comparison of techniques for detecting feral cats. *New Zealand Journal of Zoology*. 43, 127–137.

Hatt, S., Lopes, T., Boeraeve, F., Chen, J., Francis, F. (2017) Pest regulation and
support of natural enemies in agriculture: Experimental evidence of within field
wildflower strips. *Ecological Engineering*. 98, 240–245.

412 Hothorn, Bretz, F., Westfall, P., Heiberger, R.M., Schuetzenmeister, A., Scheibe, S.

413 (2019) Multcomp package (Simultaneous Inference in General Parametric Models).

414 https://cran.r-project.org/web/packages/multcomp/multcomp.pdf.

Imakando, C.I. (2021) Implications of Habitat Fragmentation on Small Diversity,

- 416 Rodent Pest Regulation and Ecologically Based Management Strategies in Kitwe,
 417 Zambia. PhD Thesis, University of Greenwich.
- Jacob, J. (2008) Response of small rodents to manipulations of vegetation height in
 agro-ecosystems. *Integrative Zoology*. 3, 3–10.
- Jacob, J., Brown, J.S. (2000) Microhabitat use, giving-up densities and temporal
 activity as short-and long-term anti-predator behaviors in common voles. *OIKOS*. 91,
 131–138.
- Johnson, M.D., Horn, C.M. (2008) Effects of Rotational Grazing on Rodents and
- 424 Raptors in a Coastal Grassland. *Western North American Naturalist*. 68, 444–452.
- Jones, C.R., Lorica, M.R.P., Villegas, J.M., Ramal, A.F., Horgan, F.G., Singleton,
 G.R., Stuart, A.M. (2017) The stadium effect: rodent damage patterns in rice fields
 explored using giving-up densities. *Integrative Zoology*. 12, 438–445.
- Kasuya, E. (2004) Angular transformation Another effect of different sample sizes. *Ecological Research*. 19, 165–167.
- Key, G. (1990) Pre-harvest crop losses to the African striped ground squirrel, *Xerus erythropus* in Kenya. *Tropical Pest Management*. 36, 223–229.
- 432 Krijger, I.M., Belmain, S.R., Singleton, G.R., Groot Koerkamp, P.W., Meerburg, B.G.
- 433 (2017) The need to implement the landscape of fear within rodent pest management
- 434 strategies. *Pest Management Science*. 73, 2397–2402.
- Laundré, J.W., Hernández, L., Altendorf, K.B. (2001) Wolves, elk, and bison:
 reestablishing the 'landscape of fear' in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*. 79, 1401–1409.

Leirs, H., Verheyen, W., Verhagen, R. (1996) Spatial patterns in *Mastomys natalensis* in Tanzania (Rodentia, Muridae). *Mammalia*. 60, 545–555.

Lindell, C., Eaton, R.A., Howard, P.H., Roels, S.M., Shave, M.E. (2018) Enhancing
agricultural landscapes to increase crop pest reduction by vertebrates. *Agriculture, Ecosystems and Environment*. 257, 1–11.

Loggins, A.A., Shrader, A.M., Monadjem, A., McCleery, R.A. (2019) Shrub cover homogenizes small mammals' activity and perceived predation risk. *Scientific Reports*. 9, 1–11.

Massawe, A.W., Rwamugira, W., Leirs, H., Makundi, R.H., Mulungu, L.S. (2006) Do farming practices influence population dynamics of rodents? A case study of the multimammate field rats, Mastomys natalensis, in Tanzania. African Journal of Ecology. 45, 293-301.

Meek, P.D., Ballard, G., Fleming, P. (2012) An introduction to camera trapping for
wildlife surveys in Australia. Canberra, Austalia: PestSmart Toolkit publication,
Invasive Animals Cooperative Research Centre.

Mkenda, P.A., Ndakidemi, P.A., Mbega, E., Stevenson, P.C., Arnold, S.E.J., Gurr,
G.M., Belmain, S.R. (2019) Multiple ecosystem services from field margin vegetation
for ecological sustainability in agriculture: Scientific evidence and knowledge gaps. *PeerJ*. 7(e8091), 1–33.

Mohr, K., Vibe-Petersen, S., Jeppesen, L.L., Bildsøe, M., Leirs, H. (2003) Foraging
of multimammate mice, *Mastomys natalensis*, under different predation pressure:
Cover, patch-dependent decisions and density-dependent GUDs. *Oikos*. 100, 459–
468.

Mulungu, L.S. (2017) Control of rodent pests in maize cultivation: the case of Africa.
In D. Watson, ed. *Achieving sustainable maize cultivation*. Burleigh Dodds Science
Publishing Limited, pp. 317–338.

Mulungu, L.S., Makundi, R.H., Massawe, A.W., Leirs, H. (2007) Relationship
between sampling intensity and precision for estimating damage to maize caused by
rodents. *Integrative Zoology*. 2, 131–135.

Mulungu, L.S., Makundi, R.H., Massawe, A.W., Machang'u, R.S., Ngowo, V., Leirs,
H. (2005) Spatial patterns and distribution of damage in maize fields due to *Mastomys natalensis* in Tanzania. *Belgian Journal of Zoology*. 135 (supplement),
183–185.

Ochieng, L.O., Ogendo, J.O., Bett, P.K., Nyaanga, J.G., Cheruiyot, E.K., Mulwa,
R.M.S., Arnold, S.E.J., Belmain, S.R., Stevenson, P.C. (2022) Field margins and
botanical insecticides enhance *Lablab purpureus* yield by reducing aphid pests and
supporting natural enemies. *Journal of Applied Entomology*. 146, 838-849.

475 Orrock, J.L., Danielson, B.J., Brinkerhoff, R.J. (2004) Rodent foraging is affected by
476 indirect, but not by direct, cues of predation risk. *Behavioral Ecology*. 15, 433–437.

477 Pita, R., Mira, A., Moreira, F., Morgado, R., Beja, P. (2009) Influence of landscape
478 characteristics on carnivore diversity and abundance in Mediterranean farmland.
479 Agriculture, Ecosystems and Environment. 132, 57–65.

480 R Core Team (2019) *R: A language and environment for statistical computing. R*481 *foundation for statistical computing.* Vienna, Austria: URL https://www.R-project.org/.

Ramesh, T., Downs, C.T. (2015) Impact of land use on occupancy and abundance of

terrestrial mammals in the Drakensberg Midlands, South Africa. *Journal for Nature Conservation*. 23, 9–18.

Rich, L.N., Miller, D.A.W., Robinson, H.S., McNutt, J.W., Kelly, M.J. (2017) Carnivore
distributions in Botswana are shaped by resource availability and intraguild species. *Journal of Zoology*. 303, 90–98.

Rodríguez-Pastor, R., Luque-Larena, J.J., Lambin, X., Mougeot, F. (2016) "Living on
the edge": The role of field margins for common vole (*Microtus arvalis*) populations in
recently colonised Mediterranean farmland. *Agriculture, Ecosystems and Environment*. 231, 206–217.

Ruscoe, W.A., Brown, P.R., Henry, S., van de Weyer, N., Robinson, F., Hinds, L.A.,
Singleton, G.R. (2022) Conservation agriculture practices have changed habitat use
by rodent pests: implications for management of feral house mice. *Journal of Pest Science*. 95, 493-503.

Skonhoft, A., Leirs, H., Andreassen, H.P., Mulungu, L.S.A., Nils, C.S. (2006) The
bioeconomics of controlling an African rodent pest species. *Environment and Development Economics*. 11, 453–475.

Sluydts, V., Crespin, L., Davis, S., Lima, M., Leirs, H. (2007) Survival and maturation
rates of the African rodent, *Mastomys natalensis*: density-dependence and rainfall. *Integrative Zoology*. 2, 220–232.

Stenseth, N.C., Leirs, H., Skonhoft, A., Davis, S.A., Pech, R.P., Andreassen, H.P.,
Singleton, G.R., Lima, M., Machang'u, R.S., Makundi, R.H., Zhang, Z., Brown, P.R.,
Shi, D., Wan, X. (2003) Mice, rats, and people: the bio-economics of agricultural
rodent pests. *Frontiers in Ecology and the Environment*. 1, 367–375.

Swanepoel, L.H., Swanepoel, C.M., Brown, P.R., Eiseb, S.J., Goodman, S.M., Keith,
M., Kirsten, F., Leirs, H., Mahlaba, T.A.M., Makundi, R.H., Malebane, P., Von Maltitz,
E.F., Massawe, A.W., Monadjem, A., Mulungu, L.S., Singleton, G.R., Taylor, P.J.,
Soarimalala, V., Belmain, S.R. (2017) A systematic review of rodent pest research in
Afro-Malagasy small-holder farming systems: are we asking the right questions? *PLoS ONE*. 12, 1–20.

Taylor, P.J., Downs, S., Monadjem, A., Eiseb, S.J., Mulungu, L.S., Massawe, A.W.,
Mahlaba, T.A., Kirsten, F., Von Maltitz, E., Malebane, P., Makundi, R.H., Lamb, J.,
Belmain, S.R. (2012) Experimental treatment-control studies of ecologically based
rodent management in Africa: Balancing conservation and pest management. *Wildlife Research*. 39, 51–61.

517 Wegner, G., Pascual, U. (2011) Cost-benefit analysis in the context of ecosystem 518 services for human well-being: A multidisciplinary critique. *Global Environmental* 519 *Change*. 21, 492–504.

Wheeler, H.C., Hik, D.S. (2014) Giving-up densities and foraging behaviour indicate
possible effects of shrub encroachment on arctic ground squirrels. *Animal Behaviour*.
95, 1–8.

523 Williams, S.T., Maree, N., Taylor, P., Belmain, S.R., Keith, M., Swanepoel, L.H. 524 (2018) Predation by small mammalian carnivores in rural agro-ecosystems: An 525 undervalued ecosystem service? *Ecosystem Services*. 30, 362–371.

Wratten, S.D., Gillespie, M., Decourtye, A., Mader, E., Desneux, N. (2012) Pollinator
habitat enhancement: Benefits to other ecosystem services. *Agriculture, Ecosystems and Environment*. 159, 112–122.

Yang, Y., Zhang, M., Yi, X. (2016) Small rodents trading off forest gaps for scatterhoarding differs between seed species. *Forest Ecology and Management*. 379, 226–
231.

Ylonen, H., Jacob, J., Davies, M.J., Singleton, G.R. (2002) Predation risk and habitat
selection of Australian house mice, *Mus domesticus*, during an incipient plague:
desperate behaviour due to food depletion. *OIKOS*. 99, 284–289.

535 Figure legends:

Fig. 1. Map showing the location of the four maize fields in Luto agricultural camp,
Kitwe, Copperbelt Province, Zambia.

Fig 2. Layout of GUD trays in and around maize fields. The distance between thetrays and transects was 20 m.

Fig. 3. Camera trap image of *Mastomys natalensis* feeding from a tray used in assessing giving up density. Camera type (Bushnell Trophy Cam HD Essential Trail Camera) produces a 'black' infrared flash that does not disturb mammal behaviour.

Fig. 4. Mean monthly rodent abundance (minimum number known to be alive) in maize fields (n = 3) in Kitwe, Zambia. The letters below the months represents seasons; WW, warm-wet season (November to April); CD, cold-dry season (April to August); HD, hot-dry season (September to October).

Fig. 5. Heat map showing rodent foraging activity across the maize growing season. The lower the mean GUD, the higher the rodent foraging activity and vice versa. The letters on the x-axis represent crop stage; LP = Iand preparation (October); P =planting stage (November); G = germination stages (December and January); W =

- weeding stage (February); MT = maize tasselling stage (March); M = maturity stage
- 552 (April); H = harvesting stage (May); and PH = post-harvest stage (June and July).