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Comparative study of movement patterns of ***Mastomys natalensis*** in irrigated rice and fallow fields in eastern Tanzania

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8

9 **Comparative study of movement patterns of *Mastomys natalensis* in irrigated rice**  
10 **and fallow fields in eastern Tanzania.**

11

12 **Running title: Movement patterns of *Mastomys natalensis***

13

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25

## 26 **Abstract**

27 A 2-year capture-mark-recapture study was conducted to estimate home ranges and  
28 weekly travel distance of *Mastomys natalensis* (Smith 1834) in an irrigated rice  
29 ecosystem and fallow fields. We found that adults have larger home ranges than  
30 subadults in fallow fields but not in rice fields, indicating that fallow fields are more

31 suitable for breeding. Travel distances were larger in rice fields, especially in the  
32 transplanting stage, during which rice fields are flooded and provide less food, causing  
33 movements into neighbouring fallow fields that then temporarily experience higher  
34 population density. A decrease in travel distance was observed in rice fields during the  
35 maturity stage, which can be explained by higher food availability and a more suitable,  
36 non-flooded situation. Movement of *M. natalensis* in rice-fallow mosaic landscapes thus  
37 seems to be driven by food availability and flooding status of the rice fields, which can  
38 be attributed to land use practices.

39

40 **Keywords:** fallow land, home range, *Mastomys natalensis*, movement, land use, rice  
41 field

42

### 43 **1. Introduction**

44 *Mastomys natalensis* (Smith 1834) is the most important rodent pest species, which is  
45 found in large numbers in different habitats in Sub-Saharan Africa (Mulungu *et al.*,  
46 2011; Leirs, 1994). Its widespread distribution indicates a broad habitat tolerance and  
47 makes it an effective colonizer of disturbed (e.g. by agriculture) habitats (Mulungu *et al.*,  
48 2011; Massawe, 2003). Although its spatial behaviour has been studied almost  
49 exclusively in maize or fallow habitats, recent results indicate that its spatial behaviour  
50 may be affected differently in another type of agricultural habitat (Mulungu *et al.*,  
51 2014a). In rice fields, *M. natalensis* generally seems to exhibit an aggregated spatio-  
52 temporal distribution (including relocations to refuges adjacent to rice fields), while in

53 fallow fields its distribution is less aggregated, approaching a seemingly random  
54 distribution (Mulungu *et al.*, 2014a; Borremans *et al.*, 2014).

55         There are several environmental factors that can affect the spatial patterns of  
56 populations and shape unique movement patterns. These factors include resource  
57 availability, predation risk, mating system, and the abiotic environment. The distribution  
58 of these factors in space is usually heterogenous and mosaic-like (Ims, 1995).  
59 Understanding the spatio-temporal scales at which organisms perceive and respond to  
60 their environment is a central issue in ecology (Wiens, 1976, 1989; Bowman *et al.*,  
61 2000). Farming practices have been shown to have an impact on rodent spatial behavior  
62 (Jacob *et al.*, 2003). In West Java, for example, rice-field rats (*Rattus argentiventer*)  
63 react to harvest-induced changes in habitat structure by relocating their home ranges on  
64 average 300–400 m to piles of rice straw on the fields and to unharvested areas,  
65 resulting in a post-harvest decrease of home-range size, which may indicate an  
66 immediate response to increased predation risk (Jacob *et al.*, 2003).

67         More specifically, numerous factors in an irrigated rice ecosystem could  
68 determine the spatial patterns of *M. natalensis*, such as the physical characteristics, the  
69 connectivity with fallow fields, the presence of bunds and the embedding of suitable  
70 habitat in an agricultural mosaic system (Kozakiewicz, 1993; Peles *et al.*, 1999;  
71 Romanowski *et al.*, 2008). These properties may also affect population growth rate,  
72 body condition, home range compaction, foraging, parasitism, breeding and genetic  
73 variation (Patterson and Malcolm, 2010).

74 Home ranges of *M. natalensis* typically range from 200 m<sup>2</sup> to 2000 m<sup>2</sup> in  
75 grassland and bush land habitats (Hoffmann, 1999). Male and female home ranges do  
76 not seem to differ and sexually active individuals of both sexes were found to have  
77 larger home ranges (Borremans *et al.*, 2014; Leirs *et al.*, 1996). Seasonal variations in  
78 home range sizes were not found for this species (Borremans *et al.*, 2014; Christensen,  
79 1996; Hoffmann, 1999; Leirs *et al.*, 1996; Oguge, 1995).

80 Hoffmann (1999) reported an effect of habitat type on movement, where shorter  
81 travel distances were recorded in habitats with higher food quantity and quality,  
82 implying that *M. natalensis* movement is strongly determined by food availability.  
83 Similarly, home range size and travel distance decrease have been tentatively linked to  
84 increased food availability in an experimental study (Monadjem and Perrin 1998).

85 This study aims to determine the movement and home range of *M. natalensis* in  
86 irrigated rice areas using data collected by employing Capture – Mark – Recapture  
87 techniques, with the intention of providing useful information on the ecology of *M.*  
88 *natalensis*.

89

## 90 **2. Materials and Methods**

### 91 *Study area*

92 This study was conducted at Hembeti village (06<sup>0</sup>16'S, 37<sup>0</sup>31'E), in Mvomero District,  
93 Morogoro, Tanzania (Fig. 1). The study area has a bimodal rainfall pattern consisting of  
94 a short rainy season from October to December and a long rainy season from March to  
95 June. Farmers in the study area produce rice crops twice per year, first from January to

96 June and second from July to December. Farmers depend strongly on irrigation in the  
97 second rice crop production. Land preparation and rice transplanting are done during the  
98 first month of each season (January and July for the wet and dry season, respectively).  
99 This is followed by a vegetative crop stage (February-March for the wet season and  
100 August-September for the dry season). Booting stages occur in April and October, and  
101 rice crops reach physiological maturity in May and November, after which farmers  
102 harvest (June and December). Food availability to rodents is higher around and during  
103 the maturity stages, and more vegetative cover is present from the vegetative until the  
104 harvest stage. Flooding occurs during the transplanting, vegetative and booting stages.

#### 105 *Rodent trapping*

106 A capture-mark-recapture study was carried out from June 2010 to May 2012. Four 70  
107 m x 70 m permanent trapping grids (two in rice fields and two in fallow mosaics) were  
108 established, separated by at least 300 m. This distance is more than 20 times the average  
109 home range radius of *M. natalensis* (Borremans *et al.*, 2014; Leirs *et al.*, 1996) which is  
110 the major rodent pest species in the study area (Mulungu *et al.*, 2013). Each grid  
111 consisted of seven parallel lines, 10 m apart, and seven trapping stations per line, also 10  
112 m apart (total of 49 trapping stations/grid). One Sherman LFA live trap (8 x 9 x 23 cm,  
113 H.B. Sherman Traps Inc., Tallahassee, FL, U.S.A.) was placed at each trapping station  
114 and all were set for three consecutive nights at intervals of four weeks. Traps, baited  
115 with peanut butter mixed with maize bran/flour, were placed in the afternoon and  
116 inspected in the morning. During flooding of rice fields (i.e. transplanting and vegetative

117 crop growth stages), the traps were placed on small islands made of dried grasses. The  
118 grids were located in a mosaic landscape containing a mix of rice and fallow fields.

### 119 *Rodent sampling*

120 All captured animals were taken to the field laboratory and identified to species level  
121 (Kingdon, 1997), with >95% in both habitats (rice fields and fallow land) identified as  
122 *M. natalensis* (Mulungu *et al.*, 2013). All animals were marked by toe clipping using  
123 individual-specific number coding at the time of first capture, which has been shown not  
124 to affect *M. natalensis* movement or home range (Borremans *et al.*, 2015). Weight,  
125 trapping station, sex and reproductive status (perforated or closed vagina in females and  
126 scrotal or non-scrotal testes in males) were recorded. Animals were then released at the  
127 exact place of capture.

### 128 *Spatial patterns*

129 For each individual, two measures of space use were estimated, a home range proxy and  
130 the weekly travel distance. The area bound by the outer capture locations was calculated  
131 using a minimum convex polygon (MCP) with an added boundary strip of 5 m (half the  
132 distance between neighbouring traps; Stickel, 1954). Although this method is an often  
133 used but rough proxy for home range, it was not possible to use more sophisticated  
134 probabilistic methods because they require a much larger number of recaptures.  
135 However, as the purpose of this study is to compare space use between different types of  
136 habitat and not to estimate absolute sizes of home ranges, the MCP method is sufficient.  
137 Following the method described in Borremans *et al.* (2014), all individuals that were  
138 captured within 12 m from the edge of the trapping grid were removed from the

139 analyses, in order to account for edge effects on home range size estimation and to  
140 minimize the proportion of transient animals. For most of the analyses, all locations  
141 where an individual was captured were used for MCP estimation. In order to study the  
142 effect of breeding status on home range size, home ranges were recalculated for adults  
143 and subadults by including only those locations where an individual was trapped during  
144 its adult or subadult period.

145 Because home ranges span several months, it would be impossible to correlate home  
146 range estimates with monthly variables like crop growth stages, season, or population  
147 density. For this reason, we also calculated the distance between a capture location and  
148 the preceding capture location. This was done for each time an individual was captured  
149 (except the first time) by calculating the distance between that capture location and the  
150 preceding one and dividing this distance by the interceding time period, resulting in a  
151 movement measure expressed in m/week.

#### 152 *Density estimation*

153 The abundance of the rodent population during each 3-night trapping session 1 (during  
154 which the population was assumed to be closed) was estimated using the commonly  
155 used heterogeneity estimator  $M(h)$  in the program CAPTURE (White *et al.*, 1982). The  
156  $M(h)$  estimator allows for variability in individual capture probabilities and appears to  
157 be quite robust (Parmenter *et al.*, 2003). This estimator has been widely used to evaluate  
158 *M. natalensis* densities from field data originating from the same trapping grids  
159 (Mulungu *et al.*, 2013) and thus permits comparison with previous study. In the study  
160 area, the population density of the *M. natalensis* varied with habitat and months and is

161 not correlated with rainfall (Mulungu *et al.*, 2013) as previously thought in mosaic and  
162 maize dominated crop fields (Leirs *et al.*, 1993; 1994). Fallow land in rice irrigated  
163 ecosystem had a more abundant population than rice fields. The highest population peak  
164 was observed during the dry season from July to October.

### 165 *Statistical testing*

166 Effects of breeding status (adult or subadult), body weight, sex, rice growth stage,  
167 population density, and habitat type (rice or fallow) and season (wet or dry) were  
168 analysed using ANOVA of linear mixed regression models with individuals included as  
169 random effects. Because home range size is positively correlated with the number of  
170 recaptures, this variable was included in the models. Statistical significance was  
171 assumed when  $p < 0.05$ . Data manipulation, home range and movement estimation and  
172 statistical analyses were performed using R 3.0.1 (R Core Team, 2013) using packages  
173 lme4 (Bates *et al.*, 2013), adehabitat (Calenge, 2006), gpclib (Peng *et al.*, 2013),  
174 maptools (Bivand & Lewin-Koh, 2013), Matrix (Bates & Maechler, 2013). All results  
175 are shown with standard error.

176

## 177 **3. Results**

### 178 *Home range*

179 An overview of home range sizes in rice and fallow fields is shown in Table 1. Home  
180 range sizes did not differ significantly between sexes ( $M = 467 \pm 25 \text{m}^2$  vs  $F = 442 \pm 25 \text{m}^2$ ;  
181  $F_{1,336} = 0.621$ ,  $p = 0.431$ ) or habitats (rice:  $464 \pm 34 \text{m}^2$ , fallow:  $448 \pm 21 \text{m}^2$ ;  $F_{1,335} = 0.172$ ,  $p$   
182  $= 0.678$ ). Breeding status did not significantly affect home range size (adult =

183  $338 \pm 18 \text{m}^2$ , subadult  $= 294 \pm 20 \text{m}^2$ ;  $F_{1,438} = 2.732$ ,  $p = 0.099$ ), but there was a significant  
184 interaction between breeding status and habitat ( $F_{1,438} = 7.969$ ,  $p = 0.005$ ), where in  
185 fallow land, home ranges of adults were larger than those of subadults ( $F_{1,314} = 9.729$ ,  $p$   
186  $= 0.002$ ), while this difference was not significant in rice fields ( $F_{1,124} = 1.797$ ,  $p =$   
187  $0.183$ ).

### 188 *Movement*

189 Movement since the last capture event, measured as m/week, differed between sexes (M  
190  $= 4.2 \pm 0.2 \text{m/week}$ ,  $F = 3.6 \pm 0.1 \text{m/week}$ ;  $\chi^2 = 5.323$ ,  $df = 1$ ,  $p = 0.021$ ), but did not  
191 correlate with breeding status (adult  $= 2.7 \pm 0.2 \text{m/week}$ , subadult  $= 2.7 \pm 0.2 \text{m/week}$ ;  $\chi^2 =$   
192  $0.162$ ,  $df = 1$ ,  $p = 0.687$ ). Body weights in rice fields ( $43.7 \pm 0.9 \text{g}$ ) were lower than those  
193 in fallow fields ( $48.5 \pm 0.5 \text{g}$ ;  $\chi^2 = 4.123$ ,  $df = 1$ ,  $p = 0.042$ ), but travel distance did not  
194 correlate with body weight ( $\chi^2 = 0.011$ ,  $df = 1$ ,  $p = 0.916$ ). In rice fields, movements  
195 were on average larger than in fallow fields (Figure 2;  $\chi^2 = 6.815$ ,  $df = 1$ ,  $p = 0.009$ ), but  
196 there was a significant three-way interaction between habitat, season and growth stage  
197 ( $\chi^2 = 28.699$ ,  $df = 10$ ,  $p = 0.001$ ), where, in rice fields, the travel distance was  
198 significantly lower in the dry season during the maturity stage, while in fallow fields it  
199 was only significantly lower in the wet season during the transplanting stage. No  
200 significant overall travel difference was observed between seasons ( $\chi^2 = 0.033$ ,  $df = 1$ ,  $p$   
201  $= 0.855$ ). There was a significant interaction between habitat and population density ( $\chi^2$   
202  $= 14.552$ ,  $df = 1$ ,  $p < 0.001$ ), where increasing densities correlated with decreasing travel  
203 distances in fallow fields (Effect estimate  $= -0.018 \pm 0.006$ , while the opposite was true in  
204 rice fields (Effect estimate  $= 0.012 \pm 0.006$ ). The number of times an individual was

205 recaptured correlated negatively with travel distance ( $\chi^2 = 141.6$ ,  $df = 1$ ,  $p < 0.001$ ) and  
206 was lower in rice fields than in fallow fields ( $3.9 \pm 0.1$  vs  $5.0 \pm 0.1$  times recaptured;  $\chi^2 =$   
207  $10.135$ ,  $df = 1$ ,  $p = 0.002$ ).

208

#### 209 **4. Discussion**

##### 210 *Home range*

211 The aim of this study was to investigate space use patterns of *M. natalensis* in rice fields,  
212 and whether they differ from those in fallow fields. Home range sizes in our study were  
213 consistent with those found in previous studies on *M. natalensis* (Borremans *et al.*, 2014;  
214 Leirs *et al.*, 1996; Monadjem & Perrin, 1998), and were not significantly different  
215 between rice and fallow fields, suggesting that *M. natalensis* is resident in both types of  
216 habitat. While there was no significant home range size difference between rice and  
217 fallow fields, we did observe an interesting interaction between breeding status and field  
218 type, where home ranges of adults were larger than those of subadults in fallow fields,  
219 but not in rice fields. This may be because of high density in fallow land as compared to  
220 rice fields as reported by Mulungu *et al.* (2013) in the same study site leading to intense  
221 intra-specific competition hence larger home range for resource and foraging space  
222 (Mulungu *et al.*, 2015).

223 Home ranges were not significantly different between sexes. This finding is consistent  
224 with previous observations (Borremans *et al.*, 2014, Leirs *et al.*, 1996, Hoffmann, 1999).  
225 Also, season did not seem to significantly affect home range size, indicating that  
226 resources are sufficiently available throughout the year in the study area (Mulungu *et al.*,

227 2014). Similar results were reported by Oguge (1995), Christensen (1996), Leirs *et al.*  
228 (1996) and Hoffmann (1999).

### 229 *Movement*

230 Knowledge of travel distance within and movement between different elements of the  
231 habitat mosaic are important for developing an understanding of how the environment is  
232 utilised and perceived by the rodent. In the current study, significant differences in short-  
233 term movement (i.e. within home ranges) were found between sexes, where males  
234 moved longer distances than females. This was also found by Leirs *et al.* (1996).  
235 Considering that breeding occurs throughout the year (Mulungu *et al.*, 2013), this  
236 movement difference may indicate that *M. natalensis* males use a scramble competition  
237 (SC) strategy, as previously suggested by Kennis *et al.* (2008), where males move  
238 around more in order to increase chances of encountering receptive females. While  
239 Borremans *et al.* (2014) found that, as in our study, home ranges of males and females  
240 did not differ and concluded that this lack of difference indicated that a dominance  
241 hierarchy may be more likely than SC, we now observe that higher movement rates  
242 seem to occur within home ranges, supporting the SC hypothesis. However, our results  
243 did not show a significant difference between adult and subadult movement, which  
244 would not be in line with the SC hypothesis. This could however be due to the much  
245 lower sample size in the analyses that include breeding status, as the dataset had to be  
246 subdivided into adult and subadult categories. Indeed, even the significant effect of sex  
247 disappears in the regression analysis using the subdivided dataset, suggesting that the

248 statistical power may be too low to detect movement differences between adults and  
249 subadults.

250         The current study shows that *M. natalensis* individuals move longer distances in  
251 rice fields than in fallow land, especially during rice transplanting. Similar reported by  
252 Leirs *et al.* (1996), where mouse movements were larger in maize fields than in fallow  
253 fields. We also observed a lower number of recaptures in rice fields, suggesting that the  
254 larger travel distances in rice fields are correlated with more frequent movements  
255 outside the trapping grid, perhaps to neighbouring fallow fields. This pattern is strongest  
256 during the transplanting stage, which is a period during which rice fields are flooded  
257 thus providing little food. The adjacent fallow land therefore seems to provide a stable  
258 habitat into which mice can retreat during periods when rice fields are less suitable. This  
259 is further supported by the fact that population densities in rice and fallow fields are very  
260 similar throughout the year except during the transplanting stage, when densities are,  
261 remarkably, twice as high in fallow than in rice fields ( $73.5 \pm 1.2$  vs.  $33.0 \pm 2.0$  individuals  
262 per ha).

263         In this study, travel distance was observed to be smaller in rice fields during crop  
264 maturity, indicating that food quality and quantity may be a determinant of mouse  
265 movement. Indeed, Mulungu *et al.* (2014b) found that seeds/grains of rice and weeds  
266 predominated, both in frequency and volume, in stomachs of *M. natalensis* rats trapped  
267 in both rice fields and fallow land.

268         To conclude, the larger home ranges of adults in fallow fields and the temporary  
269 movements from rice into fallow fields during transplanting suggest that fallow fields

270 provide a stable breeding habitat for *M. natalensis*, and that movements in this rice-  
271 fallow mosaic landscape are mainly driven by food availability and perhaps the flooding  
272 status of the rice fields.

273

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419 Table 1. Home range sizes (mean  $\pm$  standard error) of sexes and breeding status in rice  
 420 and fallow fields. N denotes sample size

Category	Habitat	
	Rice	Fallow
Male	445 $\pm$ 44m <sup>2</sup> (N=49)	477 $\pm$ 30m <sup>2</sup> (N=102)
Female	483 $\pm$ 53m <sup>2</sup> (N=50)	427 $\pm$ 28m <sup>2</sup> (N=140)
Adult	280 $\pm$ 29m <sup>2</sup> (N=60)	360 $\pm$ 22m <sup>2</sup> (N=160)
Subadult	351 $\pm$ 43m <sup>2</sup> (N=67)	270 $\pm$ 21m <sup>2</sup> (N=157)
Female adult	234 $\pm$ 37m <sup>2</sup> (N=29)	321 $\pm$ 28m <sup>2</sup> (N=89)
Male adult	324 $\pm$ 44m <sup>2</sup> (N=31)	409 $\pm$ 36m <sup>2</sup> (N=71)
Female subadult	349 $\pm$ 54m <sup>2</sup> (N=40)	276 $\pm$ 31m <sup>2</sup> (N=98)
Male subadult	353 $\pm$ 72m <sup>2</sup> (N=27)	259 $\pm$ 24m <sup>2</sup> (N=59)

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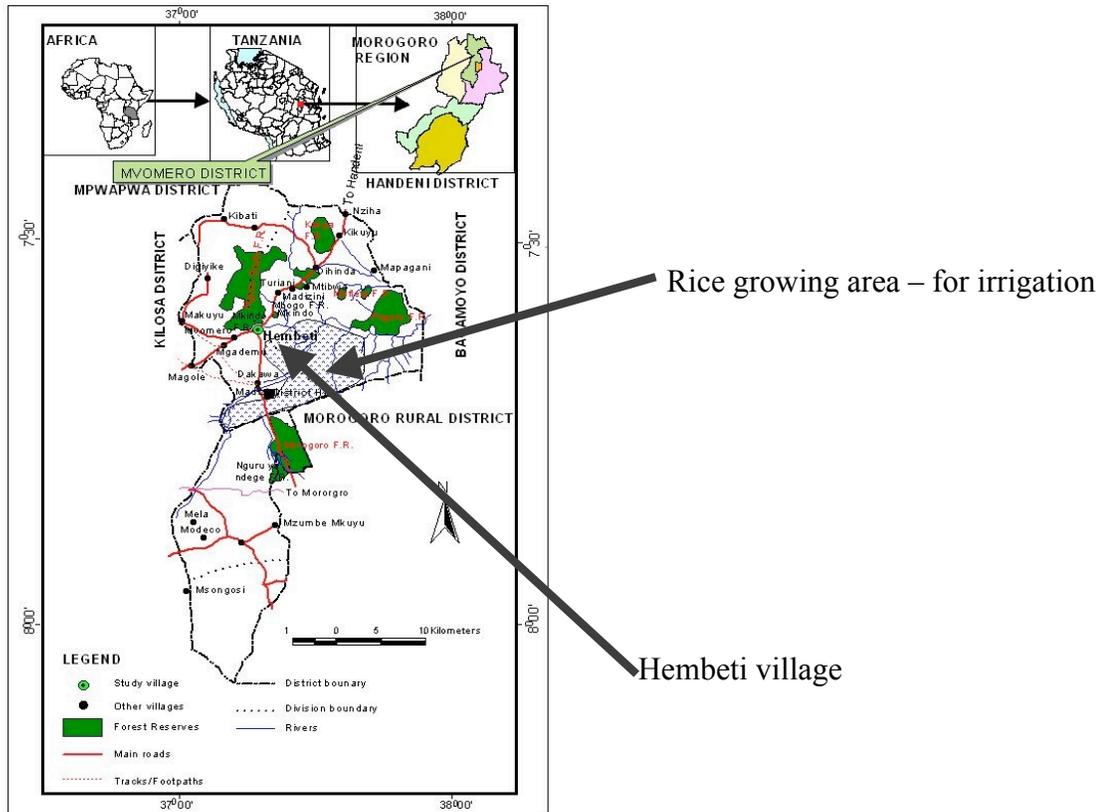
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431 Figure 1: Map of Mvomero District, showing the location of the study area.

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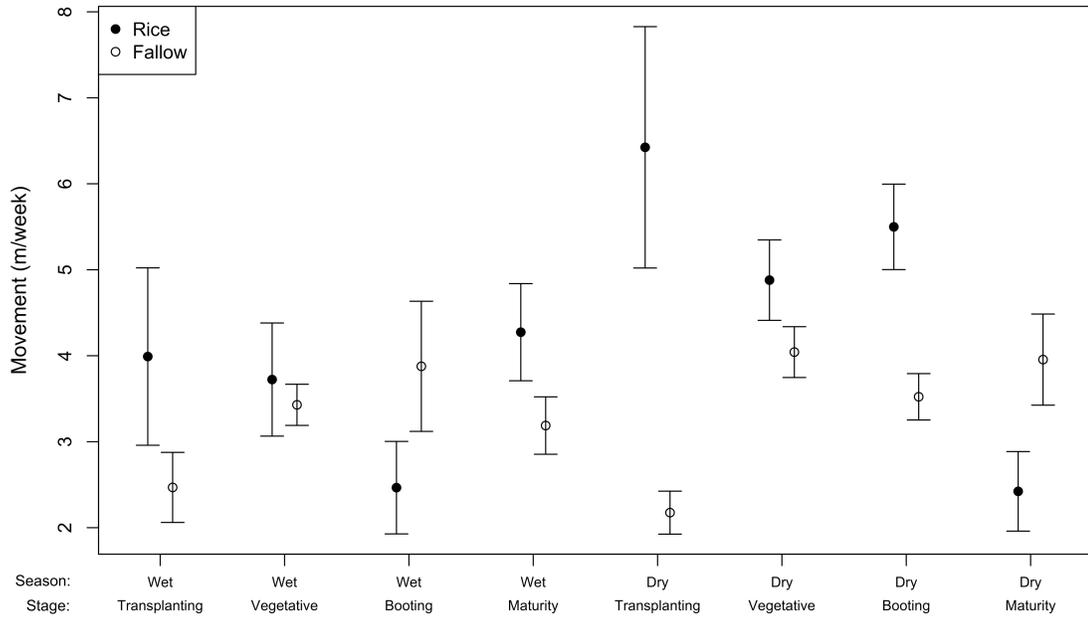
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442 Figure 2. Movement (mean  $\pm$  standard error) for the dry and wet season (for all animals)

443 and for the different rice crop growth stages in rice and fallow fields. In rice fields, food

444 availability is higher around and during the maturity stages, and more vegetative cover is

445 present from the vegetative until the harvest stage. Flooding occurs during the

446 transplanting, vegetative and booting stages.