

Original Contribution

Movement Patterns of Small Rodents in Lassa Fever-Endemic Villages in Guinea

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Abstract: The Natal multimammate mouse (*Mastomys natalensis*) is the reservoir host of Lassa arenavirus, the etiological agent of Lassa fever in humans. Because there exists no vaccine for human use, rodent control and adjusting human behavior are currently considered to be the only options for Lassa fever control. In order to develop efficient rodent control programs, more information about the host’s ecology is needed. In this study, we investigated the spatial behavior of *M. natalensis* and other small rodents in two capture-mark-recapture and four dyed bait (Rhodamine B) experiments in Lassa fever-endemic villages in Upper Guinea. During the capture-mark-recapture studies, 23% of the recaptured *M. natalensis* moved between the houses and proximate fields. While *M. natalensis* was found over the entire study grid (2 ha), other rodent species (*Praomys daltoni*, *Praomys rostratus*, *Lemniscomys striatus*, *Mus* spp.) were mostly trapped in the surrounding fields. Distances between recapture occasions never exceeded 100 m for all rodent species. During the dyed bait experiments, 11% of *M. natalensis* and 41% of *P. daltoni* moved from the fields to houses. We conclude that commensal *M. natalensis* easily moves between houses and proximate fields in Guinea. We therefore consider occasional domestic rodent elimination to be an unsustainable approach to reduce Lassa virus transmission risk to humans, as *M. natalensis* is likely to reinvade houses quickly from fields in which rodents are not controlled. A combination of permanent rodent elimination with other control strategies (e.g., make houses rodent proof or attract predators) could be more effective for Lassa fever control, but must be further investigated.

Keywords: *Mastomys natalensis*, Lassa virus, Rhodamine B, Capture-mark-recapture, Rodent control

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INTRODUCTION

The Natal multimammate mouse, *Mastomys natalensis* (Smith, 1834), is the natural host of Lassa virus (LASV), an arenavirus that causes Lassa hemorrhagic fever (LF) in humans (Monath 1987). In West Africa, these rodents thrive in houses and surrounding fields of rural villages where they shed the virus through feces, urine and saliva

(McCormick et al. 1987; Walker et al. 1975). Humans can become infected by ingestion of contaminated food or water, inhalation of virus particles, touching contaminated objects or by direct consumption of the rodents (Stephenson et al. 1984; McCormick 1999; Bonwitt et al. 2016). Secondary human-to-human transmission is also possible and occurs typically within households or health care facilities (Carey et al. 1972; Fisher-Hoch et al. 1995; Lo Iacono et al. 2015). Annually around 200,000 people are affected, with a fatality rate of 1–2% (Monath 1987; McCormick 1999; World Health Organization 2016). Since no human vaccine exists and therapeutic options are limited to the broad-spectrum antiviral ribavirin, rodent control and adjusting human behavior are currently considered to be the only options for LASV prevention (Bausch et al. 2010; Fisher-Hoch et al. 2000; Hastie et al. 2017).

In order to develop sustainable rodent control programs, basic knowledge of the rodent's spatial behavior is essential to determine when and where to control and to anticipate recolonization events (Singleton et al. 1999, 2010). Since *M. natalensis* is the most important rodent pest species in sub-Saharan Africa, plenty of information can be found in the literature and outbreak forecast models have been developed (Leirs 1994; Leirs et al. 1997; Monadjem and Perrin 1998; Massawe et al. 2011; Borremans et al. 2015). While most of these studies investigated *M. natalensis* living in large agricultural fields or natural savannah habitat in East or Southern Africa, little attention has been paid to its ecology in LF-endemic areas in West Africa (Swanepoel et al. 2017). Here, the rodent flourishes in houses and surrounding cultivations of rural villages, where it reaches between 95 and 98% of all indoor captures (Demby et al. 2001; Fichet-calvet et al. 2009). The reason why *M. natalensis* is found in houses in remote areas in West Africa could be the absence of competing *Rattus* species (Demby et al. 2001), which are suggested to scare away *M. natalensis* from buildings in East and South Africa (Monadjem et al. 2011). Because several environmental factors (e.g., resource availability, predation risk or mating system) can affect rodent behavior considerably, additional research is needed to better understand *M. natalensis*' ecology in these commensal environments (Mulungu et al. 2015; Fichet-Calvet et al. 2007).

To our knowledge, only one longitudinal survey investigated the spatial behavior of *M. natalensis* in LF-endemic areas. Fichet-Calvet et al. 2007 trapped rodents inside houses and surrounding cultivations in three villages in Upper Guinea. They found clear seasonal fluctuations in abundance

according to habitat type. While *M. natalensis* was as numerous inside as outside houses during the rainy season, its abundance increased significantly inside but decreased outside houses during the dry season. This pattern suggests a change in habitat preference driven by fluctuations in food availability. When the dry season starts, the harvest is cut and the crops are stored inside the houses. At the same time, fields are left fallow or burned for the cultivation of crops the following year. These environmental conditions might attract *M. natalensis* from the surrounding fields to the houses where they find food and shelter. Because houses in these villages typically consist of one room in which the harvest is stored close to the bed, the living space of humans and *M. natalensis* seems to overlap almost completely during the dry season (Bonwitt et al. 2017). An increased transmission risk of LASV to humans can therefore be expected and is also noted by clinicians who observed more LF cases in local hospitals during this period (McCormick et al. 1987; Bausch et al. 2001; Asogun et al. 2012).

In this study, we examined the spatial behavior of *M. natalensis* in LF-endemic villages during the dry season at three levels. First, we investigated if *M. natalensis* moves from the surrounding fields to the houses, as hypothesized by Fichet-Calvet et al. (2007). Secondly, we reported the mean and maximum distances that this rodent moved between captures, which we used as an indicator of its home-range size. Finally, we investigated the rodent's microhabitat choice within and close to the village. Although we were mainly interested in the spatial behavior of *M. natalensis* as the reservoir host of LASV, we included other captured rodent species in our analysis as well. These rodents are not reservoirs of LASV, but spillover infections to these animals (*Praomys daltoni*, *Praomys rostratus*, *Lemniscomys striatus*, *Mus matthei/minutoides*) have been observed (Fichet-Calvet et al. 2014). We performed two types of experiments: capture-mark-recapture (CMR) experiments in which traps were set in both houses and surrounding fields, and Rhodamine B (RB) experiments in which colored bait was set in the fields and rodents were trapped inside houses.

METHODS

Selection of Study Sites

Because we wanted to build on the results of Fichet-Calvet et al. 2007, we chose the same area used in that study for

our experiments, which is the prefecture of Faranah in Upper Guinea. This area was chosen for its high mean human LASV seroprevalence (approx. 35%) and the abundance of *M. natalensis* in the houses (Demby et al. 2001; Lukashovich et al. 1993). In Faranah, the rainy season starts in April and continues until October with an annual mean rainfall of 1458 mm. Four rural villages were selected: Tambaya (10°18'25"N; 10°51'45"W), Silimi (09°58'32"N, 10°39'07"W), Brissa (10°13'00"N, 10°41'20"W) and Yarawalia (9°57'18"N, 10°43'56"W). They were chosen because of their remote location from a paved road, a size not exceeding 1000 inhabitants (Tambaya 1000, Silimi 960, Brissa 655, and Yarawalia 570 inhabitants), and less than 45 min driving time from Faranah. Experiments were performed during the beginning of the dry season in the months October and November of the years 2015 and 2016. This period was chosen because the harvest is recently stored inside the houses and the fields are left fallow, which we hypothesized to be the main drivers for *M. natalensis* to enter the houses.

Capture-Mark-Recapture Studies

Two capture-mark-recapture (CMR) experiments were performed: one in Tambaya (14/10/2015–6/11/2015) and a second in Silimi (17/10/2016–8/11/2016). The two villages

were chosen for biosafety reasons, as the LASV prevalence in the rodent population was zero in Tambaya and low in Silimi (1/42) in comparison with other villages in this area (Fichet-Calvet et al. 2016).

During 1 month, rodents were live-trapped every week for three consecutive nights using Sherman live traps (Sherman Live Trap Co., Tallahassee, FL, USA). Trapping was done in 2-ha rectangular grids of 20 × 10 traps spaced 10 m apart. The grids were located on the edge of the villages in a way that both houses and surrounding fields were included. The habitat type was noted for each location where a trap was set: inside a house, or outside in bush, grass, cultivations or open-space (public square) habitat (Fig. 1). The traps were baited (with a mixture of peanuts, dry fish and wheat flour) in the evening and checked in the morning. Captured rodents were taken to a small building, where species, sex, weight and reproductive status were recorded (Leirs 1994; Sluydts et al. 2007). Identification of rodent species was based on external morphology following Kingdon et al. 2013. Mice were considered to be adults if signs of sexual activity were observed (scrotal testes in males, perforated vagina, lactating nipples or pregnancy in females). All animals were individually marked by toe clipping or tattooing (Leirs 1994; Hess 2009; Borremans et al. 2015) and released at the same location as where they

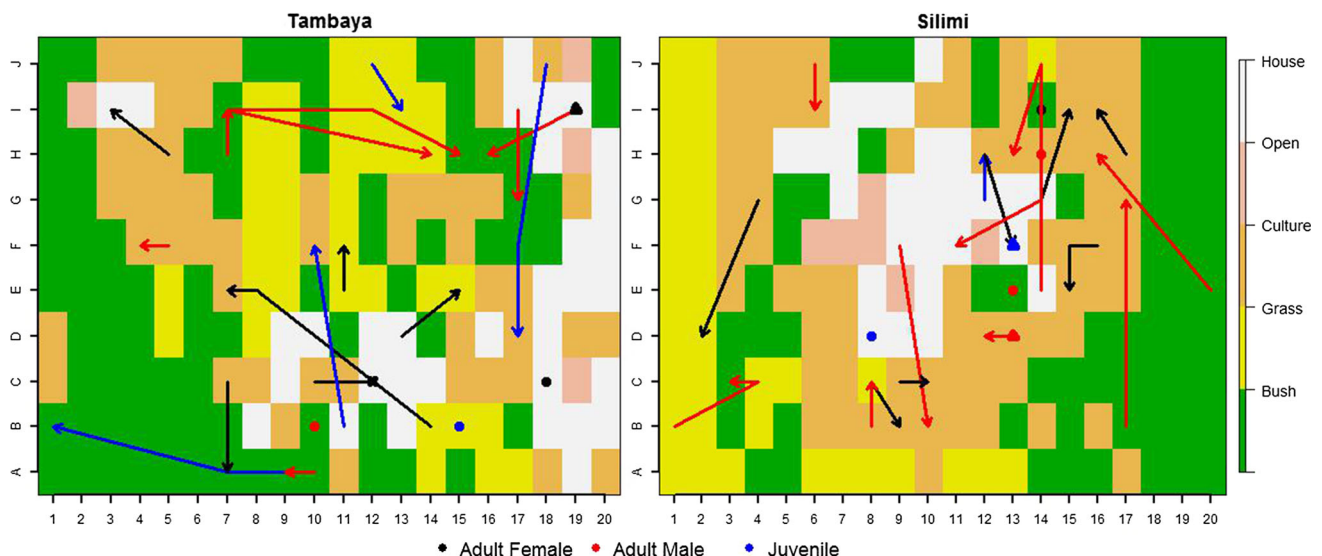


Figure 1. Movements of recaptured *M. natalensis* during the capture-mark-recapture experiments in Tambaya (left) and Silimi (right). Traps were spaced 10 m apart. Arrows represent the direction and minimum distance that an individual moved between two successive captures. Points (two times) and triangles (three times) represent recaptures on the same location. Colors of the arrows indicate sex and reproductive status of the animals (red = male and adult, black = female and adult, blue = juvenile). The colors of the different coordinates represent the habitat type where the trap was placed (white = house, pink = open space, orange = cultivations, yellow = grass, green = bush).

were previously captured (even if they were captured inside a house).

The mean distance between successive captures (MDSC) and maximum distance between all captures (MDAC) were calculated for each recaptured individual based on the Euclidian distance between trapping locations. The MDSC was used as an indicator of home-range size which could not be calculated directly due to the low number of recaptures per animal (Monadjem and Perrin 1998; Slade and Russell 1998). The R-packages ‘colorRamps’ and ‘fields’ were used for the plotting of habitat types, rodent movements and capture locations in the village (R Core Team 2016).

Microhabitat choice was analyzed by relating habitat type per trapping station to trapping success per station (i.e., total number of rodents captured on that station/number of trapping occasions). The habitat type around each station was determined and divided into five categories: house (indoor), cultivations (outdoor, surrounded by agricultural plants), bush (outdoor, surrounded by trees or shrubs > 1 m), grass (outdoor, surrounded by *Poaceae* plants) or open space (outdoor, no vegetation). We did not include the habitat ‘open space’ in the analyses because there were only a few stations placed in this habitat. The relation was analyzed with a generalized linear model (GLM) with negative binomial distribution (*glm.nb* function in R), as there was considerable evidence of overdispersion when we used a Poisson distribution. Multiple comparisons (*glht* function in R) between the different vegetation types were analyzed by a Tukey’s test using the Rpackage ‘Multcomp’ (R Core Team 2016). Separate analyses were performed for the two villages, as rodent diversity and abundance differed considerably between them. We only retained rodent species of which there were at least 25 captures (i.e., *M. natalensis*, *P. daltoni*, *P. rostratus*, *Mus* spp. and *L. striatus*).

Rhodamine B Experiments

Rhodamine B (RB) is a dye that, once ingested, becomes incorporated into keratinous structures of animals where it is detectable for up to several weeks under fluorescent light (Jacob et al. 2002). The dye is often used to examine dispersal of mammals and was previously shown to be effective to study rodent movements (Mohr et al. 2007; Monadjem et al. 2011; Rahelinirina et al. 2009). Four RB experiments were performed: two in Brissa (first 23/10/2015–11/11/2015; second 26/10/2016–14/11/2016) and two

in Yarawalia (first 1/11/2015–18/11/2015; second 4/11/2016–23/11/2016). These villages were chosen for practical reasons, as they are part of ongoing studies in which LASV viral prevalence was followed in the rodent population for several years.

For the preparation of the bait, 2 g RB powder (Sigma-Aldrich) was mixed in 1 kg of conventional bait (Monadjem et al. 2011). Bait stations were filled with 50 g RB bait and placed in (one to three) fields close to the village border in a grid formation spaced 5 m apart (Fig. 3). The number of bait stations differed between the 2 years: While 100 bait stations were placed in both villages in the year 2015, 200 stations were placed in both villages in 2016. The stations stayed in the field for eight consecutive days, where they were rebaited each 2 days and checked for signs of consumption. Eight days after removal of the stations, 120 traps were placed in 60 houses that were randomly chosen along a transect from the RB fields to the village center. In order to be sure that rodents were willing to eat the bait, 50 additional traps were placed in the RB fields. All traps were baited during three consecutive evenings and checked every morning. Captured rodents were humanely killed, measured morphometrically (as described in Fichet-Calvet et al. 2007) and checked for external signs of RB. The whiskers (including the follicle) and a piece of the fur were removed, put in small ziploc bags and stored in a – 20°C freezer until further analysis followed. Coordinates of the houses where rodents were trapped were recorded with a GPS.

At least six whiskers and a piece of the fur were eventually placed on a microscope slide in a drop of water and covered with a coverslip. Slides were examined for signs of RB under a fluorescence microscope (UV light at 530–585 nm) at low magnification and always compared with a positive and negative control sample. Distances between the houses and the fields were estimated based on the GPS coordinates and calculated with the ‘Vincenty (ellipsoid)’ method from the Rpackage ‘geosphere’. Locations of the RB fields and houses were plotted in Google Maps (with the Rpackage ‘ggmap’) (R Core Team 2016).

Ethical Statement

During all manipulations, standard procedures for BSL3 work in the field were followed (Mills et al. 1995). The investigation and permission to conduct research on wild animals were approved by the National Ethics Committee of Guinea (permit n° 12/CNERS/12 and 129/CNERS/16) and carried out in accordance with the approved guide-

lines. The experiments were performed in collaboration with the local health authorities (Prefecture de Faranah) and in agreement with the village chiefs. Trapping and releasing of rodents in houses was only performed if permission was obtained from the individual house owners.

RESULTS

Capture-Mark-Recapture Study

During 4800 trap nights, we captured 378 animals of which 109 individuals were recaptured a total of 203 times (Table 1). The exact number of times that individuals were recaptured is presented per species in the additional information table 1.

The species richness and evenness differed considerably between the two villages (Table 1). Almost all animals trapped in Tambaya were *M. natalensis* (94%), and only one other rodent (*P. daltoni*) and *Crocidura* species were found. *M. natalensis* was also the most abundant rodent in Silimi (37%), but other rodents [*P. daltoni* (5%), *P. rostratus* (20%), *L. striatus* (11%) and *Mus* spp. (14%)] were captured frequently as well. Other trapped species in Silimi were *Grammomys butingi*, *Uranomys ruddi*, *Lophuromys sikapusi*, *Gerbilliscus guineae*, *Rattus rattus* and *Crocidura* spp. Although we could not identify all individuals to the species level, we know from previous

studies that three sibling species of *Mus* (*M. mattheyi*, *M. minutoides* and *M. baoulei*) and *Crocidura* (*C. theresae*, *C. buettikoferi* and *C. lamottei*) can occur in this area (Fichet-calvet et al. 2009).

Direct movements into or out of houses or recaptures in the same house were mainly found for *M. natalensis* (Fig. 1 and additional information table 2). We captured three *M. natalensis* (two in Tambaya and one in Silimi) first inside and afterward outside a house, eight *M. natalensis* (five in Tambaya and three in Silimi) first outside and afterward inside a house, one *M. natalensis* (in Silimi) in one house and later in another house, and six *M. natalensis* (four in Tambaya and two in Silimi) always in the same house. In addition, we captured two *P. daltoni*, one *P. rostratus*, one *L. striatus* and two *M. musculus* (all in Silimi) first inside and later outside a house, two *P. daltoni* and one *L. striatus* first outside and later inside a house, and one *P. daltoni* two times in the same house. Outdoor movements between different vegetation types were observed for fifteen *M. natalensis*, seven *P. daltoni*, twelve *P. rostratus*, eleven *L. striatus*, three *Crocidura* spp and seven *Mus* spp. captures (additional information: table 2).

Distances between captures were small for all rodent and shrews: the mean distance between successive captures (MDSR) lay between 10.0 and 40.6 m and maximum distance between all captures (MDAR) between 10.0 and 60.4 m depending on the species (Table 1). Some indi-

Table 1. Data by Species and Village on the Number of Unique and Recaptured Individuals, Number of Total Recapture Occasions, Mean Distance Between Successive Recaptures (MDSR), Mean Distance Between All Recaptures (MDAR), Sex (Males/Females) and Reproductive Activity (Active/Non-active) Ratios of Recaptured Individuals.

Village	Species	Unique individuals	Recaptured individuals	Total recaptures	MDSR (m)	MDAR (m)	Sex ratio	Reproductive ratio
Tambaya	<i>Mastomys natalensis</i>	123	22	31	19.7 ± 3.7	25.1 ± 5.4	1:1.4	1:0.3
	<i>Praomys daltoni</i>	4	2	7	40.4 ± 9.7	60.4 ± 10.4	1:0	1:0
	<i>Crocidura</i> spp.	4						
Silimi	<i>Mastomys natalensis</i>	91	23	28	17.2 ± 3.4	18.6 ± 3.6	1:1.1	1:0.2
	<i>Praomys rostratus</i>	49	22	64	23.8 ± 4.3	32.4 ± 5.0	1:6.1	1:0
	<i>Praomys daltoni</i>	13	8	21	27.5 ± 7.6	40.8 ± 11.8	1:1.8	1:0.3
	<i>Lemniscomys striatus</i>	27	12	18	40.6 ± 9.8	49.4 ± 13.8	1:1.8	1:0.3
	<i>Mus</i> spp.	35	11	18	27.2 ± 4.4	34.7 ± 7.4	1:1.8	1:0.1
	<i>Grammomys butingi</i>	2	1	4	22.5	41.2	0:1	1:0
	<i>Uranomys ruddi</i>	2	1	1	20	20	1:0	1:0
	<i>Lophuromys sikapusi</i>	2	1	1	10	10	1:0	1:0
	<i>Gerbilliscus guineae</i>	2	1	1	31	31	1:0	0
	<i>Rattus rattus</i>	2						
	<i>Crocidura</i> spp.	22	5	9	14.0 ± 5.1	16.5 ± 7.2	1:0.3	1:0

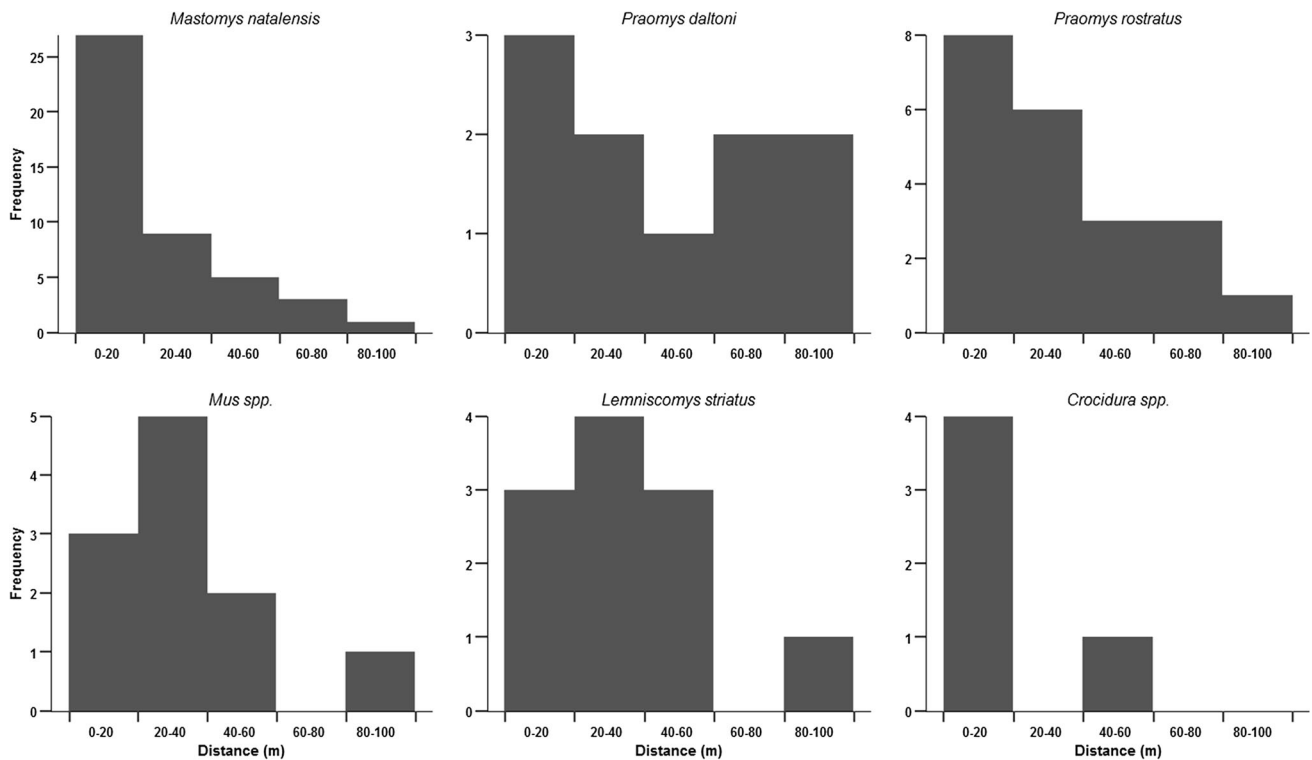


Figure 2. Maximal distances between all recaptures (MDAR) for *M. natalensis*, *P. daltoni*, *P. rostratus*, *Mus* spp., *L. striatus* and *Crocidura* spp during the capture-mark-recapture experiments in Tambaya and Silimi. Bars represent the number of individuals that moved between a certain MDAR interval.

Table 2. Average Number of Captured Individuals Per Trap Over All Trapping Nights.

Species	Tambaya					Silimi				
	House	Open	Cultivations	Bush	Grass	House	Open	Cultivations	Bush	Grass
<i>Mastomys natalensis</i>	1.42		0.54	0.62	0.89	1.35	0.50	0.76	0.23	0.36
<i>Praomys rostratus</i>						0.15	0.17	0.48	0.70	0.88
<i>Praomys daltoni</i>	0.06		0.02	0.05	0.11			0.28	0.20	0.06
<i>Lemniscomys striatus</i>						0.04	0.17	0.25	0.22	0.33
<i>Mus</i> spp.						0.12	0.33	0.30	0.28	0.27
Number of traps	33	4	50	77	36	26	6	71	64	33

Results are given per habitat type for the five most abundant rodent species in the villages Tambaya and Silimi.

viduals moved larger distances, but the MDAR never exceeded 100 m for all species (Fig. 2).

Differences in microhabitat choice were observed for all rodent species, but significant differences were only found for *M. natalensis* and *P. rostratus* (Table 2; additional information table 3 for the p values). In both villages, we trapped significantly more *M. natalensis* inside houses than in bush vegetation patches (z value = 0.35, p = <0.01). We also trapped more *M. natalensis* in houses compared to

cultivations in Tambaya (z value: 3.22, p = <0.01), and in houses compared to grass in Silimi (z value = 0.38, p < 0.01). We trapped almost no other rodent species inside houses, but only *P. rostratus* was captured significantly more frequently in grass patches compared to houses (z value = -2.59, p = <0.01). Significant differences between vegetation types were only found for *M. natalensis*, which we trapped more often in cultivations compared to bush vegetation in Silimi (z value = 0.31, p = <0.01).

Table 3. Number of Rhodamine B-positive Individuals Per Total Number of Individuals that were Captured During the Rhodamine B Experiments in the Villages Brissa and Yarawalia.

Species	2015				2016			
	Brissa		Yarawalia		Brissa		Yarawalia	
	Houses	Field	Houses	Field	Houses	Field	Houses	Field
<i>Mastomys natalensis</i>	2/60	6/8	7/35	4/5	4/36	4/6	5/25	9/9
<i>Praomys daltoni</i>	0/1	6/6	5/14	1/1	2/2	3/3		2/2
<i>Praomys rostratus</i>								1/1
<i>Rattus rattus</i>					0/1			1/1
<i>Mus</i> spp.		0/2				0/1		
<i>Lemniscomys striatus</i>				1/1				1/1
<i>Crocidura</i> spp.				0/1				1/1

Rhodamine B Experiment

During 2040 trap nights, we captured 223 animals of which 174 individuals were trapped inside a house and 49 in a RB field (Table 2). The most dominant species in both villages was *M. natalensis* (86%) followed by *P. daltoni* (13%).

Other trapped species were *P. rostratus*, *L. striatus*, *Mus* spp., *R. rattus* and *Crocidura* spp.

We found 65 animals with signs of RB (Table 3). The majority of trapped rodents in the RB fields were RB positive, indicating that these animals were willing to eat the dyed bait. In the houses, 18 *M. natalensis* and 7 *P.*

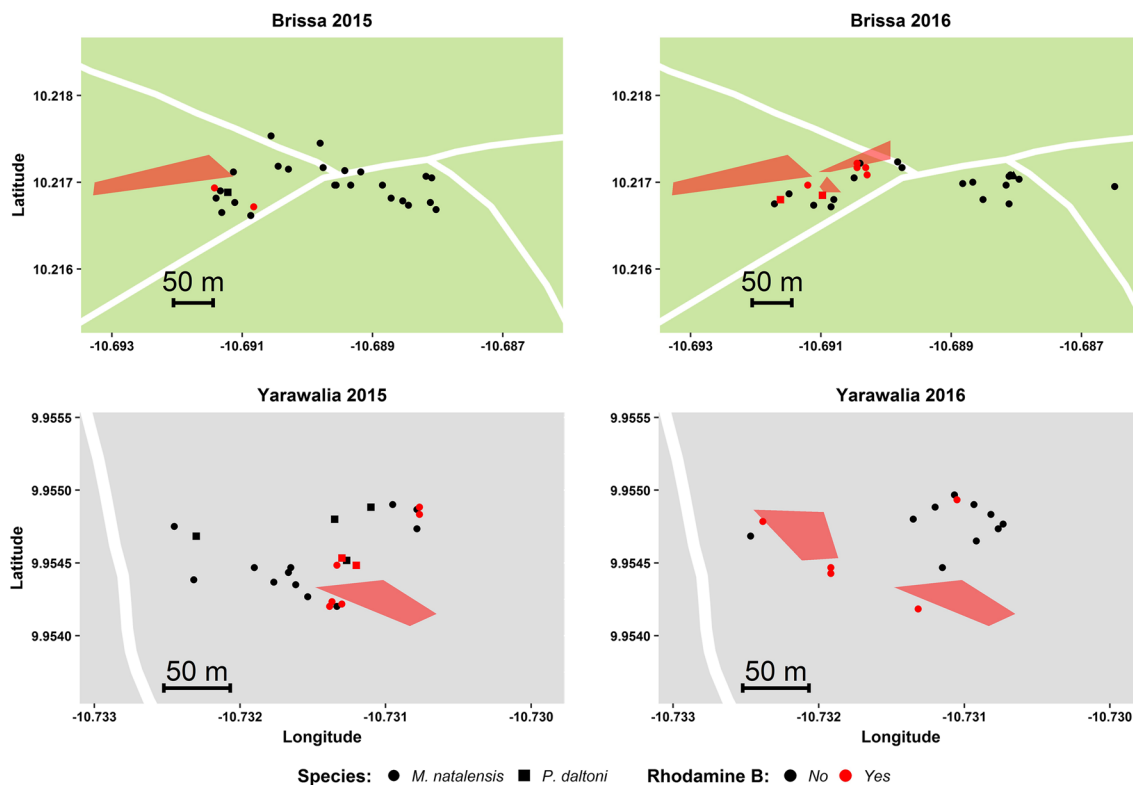


Figure 3. Overview of the villages (Brissa and Yarawalia) where Rhodamine B experiments were performed per year (Google Maps image). Red polygons represent Rhodamine B fields. Points and squares represent houses where rodents were captures (Color: black = Rhodamine B-negative rodents, red = Rhodamine B-positive rodents; symbol: points = *M. natalensis*; squares = *P. daltoni*).

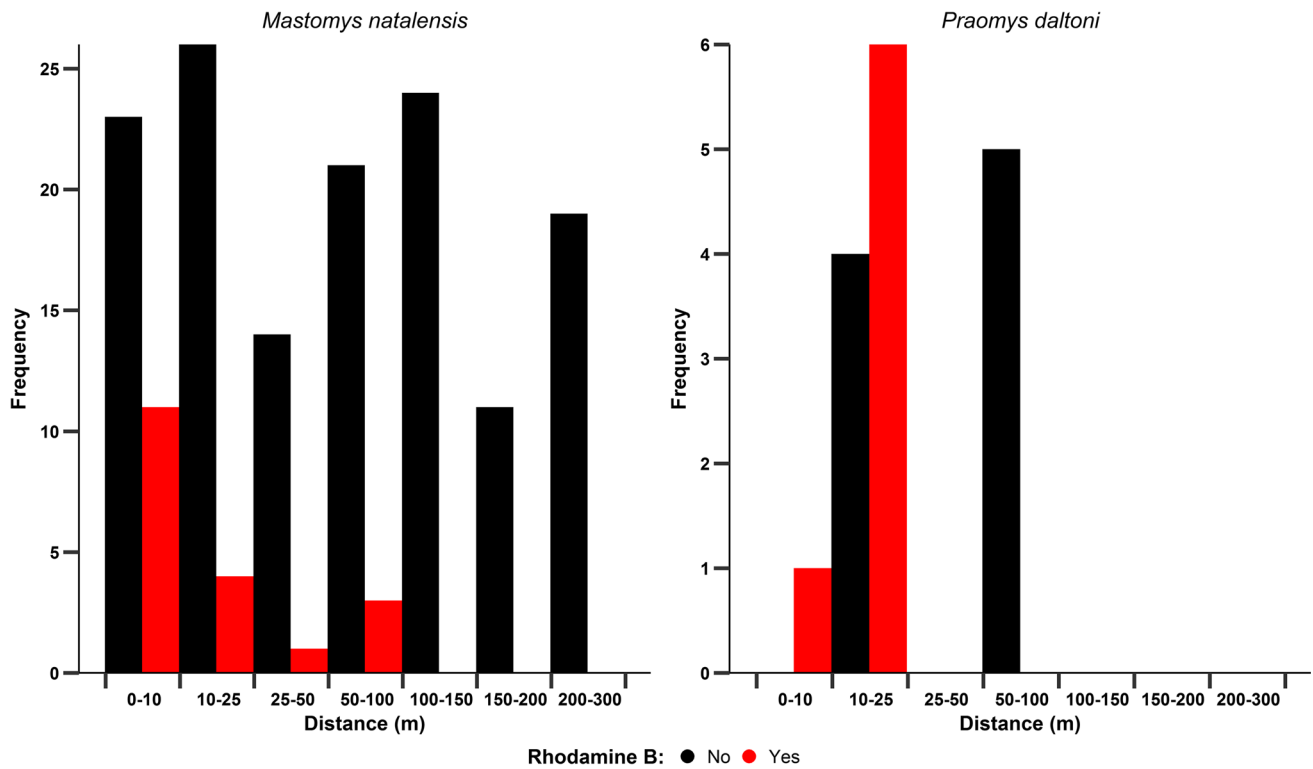


Figure 4. Minimal distances between Rhodamine B fields and houses where rodents (left = *M. natalensis* and right = *P. daltoni*) were trapped. Bars represent the number of trapped individuals per distance interval away from the closest Rhodamine B field (black = rodents without Rhodamine B signs, red = rodents with RB signs).

daltoni were found to be RB positive, which means that these individuals had moved from the fields to the houses during our study (thus within maximally 16 days) (Fig. 3). Most of these RB-positive individuals were found in houses that were close (< 25 m) to a RB field (Fig. 4). The number of RB-positive animals decreased with distance from the RB fields, and no positive individuals were found in houses that were more than 100 m from the closest RB field.

DISCUSSION

We hypothesized that *M. natalensis* moves from the surrounding fields to the houses during the dry season to search for food and shelter, which is abundant inside but scarce outside houses at that time (Fichet-Calvet et al. 2007). While we observed direct movements from the fields to the houses in all experiments, we did not find overall migration in this direction only. In fact, more individuals moved from the houses to the fields during the CMR experiments. The low number of recaptured animals in the

CMR experiments and the fact that we only checked for movements from the fields to the houses in the RB experiments made it impossible to statistically investigate the overall direction in which *M. natalensis* actually migrated.

Although we could not statistically confirm the migration hypothesis, our study shows that *M. natalensis* can easily enter and leave houses, stay for a long time inside the same house or move from one house to another. These results suggest that an individual home range of *M. natalensis* can include both houses and outdoor fields in rural villages. Therefore, it remains likely that *M. natalensis* stays for longer periods inside houses when food availability is limited outdoor, which might explain the increased indoor rodent abundance and LASV transmission risk to humans during the dry season (Bausch et al. 2001; Fichet-Calvet et al. 2007). Similar results were found in other field studies performed in Tanzania and Swaziland, where *M. natalensis* visited houses after which it retreated up to 100 m into the surrounding fields (Monadjem et al. 2011). Our results are also consistent with a telemetry study performed in Namibia in which radio-tracked *M. natalensis*

was found to enter houses regularly during the post-harvest season, but not during the pre-harvest or pre-planting seasons (Monadjem et al. 2011). Half of the radio-tracked individuals remained inside the same house after entering, while the other half returned to the fields. In contrast, radio-tracked *M. natalensis* stayed predominantly in the fields in rural villages in Swaziland, probably due to the abundant presence of competing *Rattus* species in the houses (Monadjem et al. 2011).

Most *M. natalensis* moved little between captures and distances presented here are similar to those observed in other CMR studies performed in agricultural fields in Africa. Since the MDSC was suggested to be a good indicator of *M. natalensis*' home-range size (Monadjem and Perrin 1998; Slade and Russell 1998), we can assume that sizes in Guinea are similar to those observed in South Africa ($\pm 680 \text{ m}^2$) and Tanzania ($\pm 650 \text{ m}^2$) (Borremans et al. 2013; Leirs et al. 1997; Monadjem and Perrin 1998). These sizes could, however, be underestimations as home ranges of radio-tracked *M. natalensis* were considerably larger in agricultural fields in Tanzania ($\pm 1200 \text{ m}^2$), rural villages in Swaziland and Namibia ($\pm 4300 \text{ m}^2$) and natural vegetation in Uganda ($\pm 8400 \text{ m}^2$) (Hoffmann and Klingel 2001; Leirs et al. 1997; Monadjem et al. 2011). Animals with home ranges of this magnitude would indeed be able to move easily between houses and surrounding fields.

The patchy vegetation structure of the fields allowed us to assess microhabitat choice of *M. natalensis* within and close to the villages. Overall, *M. natalensis* seems to move easily among vegetation types without showing clear preferences between grass, bush or cultivations. There were, however, some differences between the two villages. *M. natalensis* was trapped more frequently in cultivations than in bush and grass in Silimi, although the opposite was true in Tambaya. More vegetables were still present on the cultivations in Silimi compared to Tambaya, which might explain this result. In Tambaya, *M. natalensis* was most often trapped in grass, which is also assumed to be its natural habitat (Leirs 1994). In East Africa, abundances are generally lower in grasslands compared to agricultural fields, except during the early breeding season (Leirs 1994). This suggests that *M. natalensis* migrates from agricultural fields to grasslands for reproduction, probably because juveniles are better protected against predators in the denser grass vegetation. Since *M. natalensis* breeds throughout the year in Guinea (Fichet-Calvet et al. 2008),

abundances in grass vegetation might be generally higher here.

We also captured several other rodent and shrew species in this study besides *M. natalensis*. These species were predominantly captured outdoor and assumed not to be reservoirs of LASV. Nevertheless, we included these animals in this study for two reasons. First, antibodies against LASV, or LASV-like arenaviruses, were found previously in some of these species, indicating that spillover infections could occur (Fichet-Calvet et al. 2014). Secondly, according to our knowledge, no other studies investigated the spatial behavior of these animals in rural villages. Although observed habitat choices and distances between captures were not exceptional for most species (Happold 1977), a high proportion of *P. daltoni* trapped in houses close to the RB field ($< 25 \text{ m}$) showed signs of RB consumption. This proportion was considerably higher compared to *M. natalensis* (63 vs 30%, respectively), suggesting that *P. daltoni* visits houses for short periods after which it returns to the fields, where it is trapped most often. In other countries such as Ghana, Senegal or Nigeria, *P. daltoni* can represent a larger proportion of the commensal rodent populations (Bâ et al. 2012; Kronmann et al. 2013; Olayemi et al. 2017). *Praomys daltoni* seems to become the main commensal species when *M. natalensis* is rare or the other way around.

Overall results from this study are rather disappointing for the development of simple rodent control programs. Occasional rodent elimination seems pointless, as *M. natalensis* is likely to reinvade houses or cultivations rapidly from fields (e.g., bush or grass patches) where rodents are not controlled. In support of this reasoning, local villagers in Sierra Leone (a neighboring country) had the impression that rodents returned quickly after they set poison or traps, especially in houses close to the village border (Bonwitt et al. 2017). We therefore recommend that, in Guinea, rodents must be controlled on a permanent basis in order to be effective, at least during the dry season when *M. natalensis* abundances are high in the houses. Similar suggestions were made during experimental studies performed in rural villages in Namibia where contamination and loss of grain were clearly lower in year-round controlled than in non-controlled villages (Taylor et al. 2012). We also recommend combining rodent elimination with other control strategies. Rodent proofing of houses and storing food in airtight containers were found to be highly effective in discouraging rodents from entering houses, while keeping

cats and dogs or attracting wildlife predators (e.g., owls, civets) might scare them away (Hopkins et al. 2002; Labuschagne et al. 2016; Mahlaba et al. 2017; Mdingi et al. 2013). Future research is necessary to see if these ecologically based control strategies can indeed decrease LASV transmission risk to humans in Guinea.

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