ECOLOGY OF MAJOR RODENT PEST SPECIES IN MAIZE AND RICE CROPPING SYSTEMS IN EASTERN UGANDA

ALEX MAYAMBA

A THESIS SUBMITTED IN FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY OF SOKOINE UNIVERSITY OF AGRICULTURE. MOROGORO, TANZANIA.

2020

EXTENDED ABSTRACT

Rodent pests cause significant losses on several cereal crops but more so on maize and rice crops and thus pose a threat to the food security in Uganda and the rest of East Africa. In order to develop an effective management strategy against rodent pests, it is important to understand the diversity, breeding patterns and population dynamics and key demographic and ecological factors that regulate abundance and richness of the major rodent pest species. The above aspects formed the basis of this study's objectives and provide the first detailed ecological information in Uganda's rodent fauna in agro ecosystem environments.

Two studies were conducted; in the first study a 2-year Capture Mark Release (CMR) rodent trapping was carried out in Mayuge district with grids placed in cultivated and fallow field habitats with the aim of establishing the species composition and community structure of small rodents, establish the population fluctuation and breeding patterns of key rodent species and establish the demographic traits including survival and maturation of key small rodent species in agro ecosystem environment. Sherman live traps were used to trap the small rodents on a monthly basis and traps set for 3 consecutive nights at each trapping session. Trapping was done on four permanent grids of 70*70 m^2 measurement, with traps spaced at 10*10m making a total of 49 traps per grid. The second study was a trapping survey conducted across three districts with varying cropping systems and in the different seasons with the aim of establishing geo spatial ecological factors that influence rodent abundance. With the aid of Geological Information System (GIS) and remote sensing 20 sampling grids in each district were randomly identified using a randomization tool in Quantum GIS and were georeferenced and located with Global Position System machine for field rodent trapping. Landsat 8 images were acquired from the United States

Geological Survey (USGS) website for land use land cover characterization of the studied sites with further additional data collection on farm management practices.

A total of 11 identified small rodent species and one insectivorous small mammal were recorded in both fallow and cultivated field habitats with the *Mastomys natalensis* being the most dominant in the following order; *M. natalensis* (60.7%), *Mus triton* (16.1%), *Aethomys hendei* (6.7%), *Lemniscomys zebra* (5.2%), *Lophuromys sikapusi* (4.8%), *Arvicanthis niloticus* (0.9%), *Gerbilliscus kempi* (0.1%), *Graphiurus murinus* (0.1%), *Steatomys parvus* (0.1%), *Dasymys incomtus* (0.1%) and *Grammomys dolichurus* (0.1%). In terms of species turnover, spatially there was a significant difference ($F_{1,6}$ =9, p=0.024) for the studied field habitats with fallow field habitats showing higher species turnover (6±1) compared to cultivated field habitat (4±1). Temporal species turn over (β_T) also showed a significant difference ($F_{5, 44}$ =18.819, p=0.0001) over the three years of the study, with her turnover in first of trapping. In terms of community structure, higher species diversity associated more with fallow field habitats but also with certain rare species found only in cultivated fields.

Higher diversity and species turnover in fallow fields could be explained by the characteristic nature of this habitat having better vegetation ground cover and less human interaction as compared to cultivated fields. On the other hand, the higher abundance ranking of *M. natalensis* in cultivated fields could be associated to its characteristic nature of being a good colonizer of disturbed habitats like farm lands. Based on these findings, management strategies ought to target *M. natalensis* and should be applied in both cultivated and fallow fields to prevent rodent infestation of crops. Further analysis on the population structure of the most dominant species i.e. *M. natalensis* was performed on the basis of seasonal changes in breeding patterns, population density and recruitment.

In terms of breeding, female animals were considered to be actively breeding when they had perforated vagina, enlarged nipples or pregnant whereas males were considered actively breeding in case of a visible scrotum.

Data on recruitment of new individuals in the trappable population was also generated. Data on population density, percentage actively breeding animals and percentage recruitment were subjected to Generalized Linear Mixed Model with a Penalized Quasi Likelihood (PQL) method. Results on the breeding patterns showed continuous breeding of females throughout the year, with significantly higher percentages in second dry season (June-July), which was attributed to the observed availability of drying cereals and legumes from main planting season of the first wet season (March-May). Population density was observed to have peaked in the second wet season (September-November) and recruitment was significantly higher in the second dry season, with the later attributed to the increased animal breeding observed in the same period as reported above. Results have important applications on the timing of management practices, with possible recommendations to apply management options in the first wet season to prevent buildup of populations in subsequent seasons that can result into damaging populations.

The demographic traits of *M. natalensis* in terms of maturation (the probability for a juvenile to become an adult) and survival (the monthly probability for an individual to survive from one month to the next) were also examined. CMR input data were subjected to specialized statistical modelling using software E-SURGE. Best model estimates showed higher survival of animals when rainfall was medium (300ml) to high (500ml) in the past month. The higher survival during periods of higher rainfall was attributed to possible increase in ground vegetation cover which is triggered by rainfall, thus animals are shielded from potential predatory animals. Maturation on the other hand was not affected by rainfall, sex, habitat and population density a condition which could be attributed to the mixed cropping system in the study area thus offering a diversity of food sources for animal normal growth and development. The recapture probability was also modelled and higher recapture probability was observed in male animals compared to females.

In the second study, data on small rodent population abundance and richness as the response variables were subjected to the Boosted Regression Tree (BRT) model analysis with several predictor variables including; Normalized Vegetation Index (NDVI), total monthly rainfall, soil texture class, farm management practices (crop field status, crop type etc.) to determine the relative importance of these variables on predicting small rodent abundance and richness. Overall modelling showed farm management practices (crop field status) was the most important factor for predicting both abundance and richness. This could be attributed to the additive influence of both crop and field states which have influence on food availability and suitable vegetation ground cover for animal habitation. Other important factors including NDVI, crop type and soil texture (in particular soil silt particle proportion) were important in predicting abundance and richness. In conclusion this study has provided important information on several aspects of the ecology of rodents associated with agro ecosystems, knowledge that can help in the development of adaptive pest management strategies such as concentrating efforts on *M. natalensis* species, timing control in the first wet season, promotion of collective control even in non-cereal crops in Uganda and other regions with similar climatic and farming systems.

DECLARATION

I **ALEX MAYAMBA**, do hereby declare to the senate of Sokoine University of Agriculture that this thesis is my own original work done with the period of registration and that it has neither been submitted nor concurrently submitted in any other institution.

______________________ ____________

Alex Mayamba Date

(PhD candidate).

The above declaration is confirmed by:

______________________ ____________

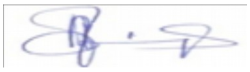
Prof. L.S. Mulungu. Date

(Main supervisor).

______________________ ____________

Dr. R.M. Byamungu Date

(Co-supervisor).



______________________ ____________

Prof. M. Isabirye Date

(Co-supervisor).

______________________ ____________

Prof. D.N. Kimaro Date

(Co-supervisor).

COPYRIGHT

ACKNOWLEDGEMENTS

First and foremost, I thank God for giving me life, ability and strength to keep going even in the hard periods when I felt like giving up. I would also like to thank the Scientific Committee of the Ecologically Based Management of Rodent Pests in Maize and Rice in East Africa, a project granted to Sokoine University of agriculture by Bill and Melinda Gates foundation for offering me a scholarship to further my career with this PhD. In particular, I would like to thank my supervisors; Dr. Robert M. Byamungu, Prof. Moses Isabirye and Prof. D.N. Kimaro for or the mentorship and support they accorded me over the three years period.

Special thanks to Prof. Loth Mulungu; my Principal Promoter, I am honored to have been your PhD student. You have taught me, both consciously and unconsciously, how to appreciate science. The enthusiasm you have for research and education motivated me, even during the tough times in this journey. I am grateful and will always struggle to emulate you.

I also thank Prof. Leirs, H, Dr. Bram, V, Dr. Isabirye, B, Prof. Massawe, A Prof. R.H Makundi, Dr. Kayingo, J, Dr. Mdangi, M, Dr. Nakiyemba, A and Mr. Kifumba, D for all the advice and reviews of my manuscripts. This work would not have been possible without your guidance.

More thanks to the entire team of Sokione Pest Management Center including Dr. Ladslaus Mnyone (Center Director), Dr. Katakweba A, Prof. Machangu, R. Dr. Sabuni to mention but a few, you always encouraged me and accorded me a good atmosphere to finish successful.

Thanks also go out to the team which accompanied in the field; Alex Kisakye, Ramathan Kigunguli, Halid Kibwana, Ouma Namulochi and the farmers who offered their gardens for CMR studies. Also, to my fellow students with whom we have journeyed together: Mlyshimbi and Hamza Kijja, I so much appreciate your courage and enthusiasm for this higher degree.

I also wish to thank my dear wife and soul mate, Ruth N. Mayamba, for your love and encouragement especially in the last phases when I felt like giving up!! I just cannot imagine how life would have been without you. Thank you for believing in me and for your patience during the lonely days when I was away from home and would struggle with the children alone. I also hail the love and support of my children (Rossette, Ellah, Herman, Hepher and untie Winnie) and to you Miriam, Esther and Racheal. Without your support and prayers, this would have been a hectic journey.

To my parents (Mr. Simali Wilson and Rosemary Nambuya (Late)) thank you for giving me the chance to pursue my own interests and for teaching me good values such as honesty and hard work. Lastly great thanks to all my friends, Mutumba, Flavia, Ssebikyu, David, Ramadhan, Kasim, Jean, Sharifah, Catherine, Sarah, Becker, Nasif among others. I thank you for the many years of true friendship, and for the encouragement and belief in me.

May God bless you all!

DEDICATION

I sincerely dedicate this work to my lovely wife Ruth N. Mayamba and my lovely children Rossette, Herman and Hepher for your endless prayers and withstanding the lonely days and hardships when I was away for my studies.

TABLE OF CONTENTS

EXTENDED ABSTRACT......ii

DECLARATION......vi

COPYRIGHT......vii

ACKNOWLEDGEMENTS......viii

TABLE OF CONTENTS......xi

LIST OF PAPERS......xvii

LIST OF TABLES......xviii

LIST OF FIGURES......xx

LIST OF APPENDICES......xxiii

LIST OF ABBREVIATIONS AND SYMBOLS......xxiv

CHAPTER ONE......1

1.0 GENERAL INTRODUCTION......1

1.1 Cereal Crops Production......1

1.2 Constraints to Cereal Crops Production......2

1.3 Rodents Public Health Concern and Ecosystem Health......3

1.4 Classification of Rodents......4

1.5 Distribution, abundance and diversity of Rodents in East African Region..4

1.6 Forecasting Models for Rodents in East African Region......5

1.7 Management of Rodents......7

1.8 Statement of the Problem......7

1.9 Justification of the Study......8

1.10 Objectives......9

1.10.1 Overall objective......9

1.10.2 Specific objectives......10

1.10.3 Research hypotheses..10

1.11 References..10

CHAPTER TWO..20

PAPER I..20

SPECIES COMPOSITION AND COMMUNITY STRUCTURE OF SMALL RODENTS (MURIDAE) IN CULTIVATED AND FALLOW FIELDS IN MAIZE GROWING AREAS IN MAYUGE DISTRICT, EASTERN UGANDA..20

2.1 Introduction..22

2.2 Materials and Methods..23

2.2.1 Study site..23

2.2.2 Sampling procedure..24

2.2.3 Trapping procedure..25

2.2.4 Data processing and analysis..26

2.3 Results..28

2.3.1 Small mammal species composition..28

2.3.2 Small rodent community structure across field trapping habitats..................33

2.4 Discussion..35

2.4.1 Small rodent species composition..35

2.4.2 Spatial patterns in species richness and diversity..39

2.4.3 Temporal patterns in total species richness and abundance...........................40

2.5 Acknowledgments..43

2.6 References..45

CHAPTER THREE..56

PAPER II..56

POPULATION AND BREEDING PATTERNS OF THE PESTIFEROUS RODENT: MASTOMYS NATALENSIS IN A MAIZE DOMINATED AGROECOSYSTEM IN LAKE VICTORIA CRESCENT ZONE, EASTERN UGANDA......56

3.1 Introduction......58

3.2 Materials and Methods......59

3.2.1 Description of study area......59

3.2.2 Rodent field trapping procedure......60

3.2.3 Examination of captured animals......61

3.2.4 Data analysis......62

3.2.4.1 Population size......62

3.2.4.2 Population dynamics......62

3.2.4.3 Sex ratio......62

3.2.4.4 Sexual activity......63

3.2.4.5 Recruitment......63

3.3 Results......64

3.3.1 Population size......64

3.3.2 Population dynamics......64

3.3.3 Breeding patterns......67

3.3.4 Recruitment......68

3.3.5 Sex ratio......68

3.4 Discussion......69

3.4.1 Population dynamics......69

3.4.2 Breeding patterns of *M. natalensis*......71

3.4.3 Sex ratio......72

3.4.4 Recruitment......73

3.5 Conclusions.....73

3.6 References.....74

CHAPTER FOUR.....85

PAPER III.....85

FITNESS OF THE PESTIFEROUS SMALL RODENT (MASTOMYS NATALENSIS) IN AN AGROECOSYSTEM IN LAKE VICTORIA CRESCENTS ZONE, EASTERN UGANDA.....85

Abstract.....86

4.1 Introduction.....86

4.2 Materials and Methods.....88

4.2.1 Study site.....88

4.2.2 Trapping fields/grids.....89

4.2.3 Trapping procedure.....90

4.2.4 Statistical analysis.....90

4.3 Results.....92

4.3.1 Model selection.....92

4.3.2 Maturation estimates.....95

4.3.3 Recapture estimates.....95

4.3.4 Survival estimates.....96

4.4 Discussion.....98

4.4.1 Maturation.....99

4.4.2 Survival.....100

4.4.3 Recapture.....101

4.5 Conclusion.....102

4.6 References.....104

CHAPTER FIVE..114

PAPER V..114

FACTORS INFLUENCING THE DISTRIBUTION AND ABUNDANCE OF SMALL RODENT SPECIES IN AGRICULTURAL LANDSCAPES IN EASTERN UGANDA...114

5.1 Introduction...117

5.2 Materials and Methods...119

5.2.1 Description of study site...119

5.2.2 Acquisition of remote sensing data...121

5.2.3 Mapping of vegetation characteristics...122

5.2.4 Generation of general land cover and land use types...................................123

5.2.5 Determination of NDVI across vegetation habitats.....................................125

5.2.6 Ground truthing and field characterization..128

5.2.7 Rodent trapping...129

5.2.8 Rainfall data acquisition...129

5.2.9 Data analysis...130

5.3 Results..131

5.3.1 Rodents species richness and abundance...131

5.3.2 Influence of landscape ecological factors on small rodent abundance..........133

5.3.2.1 Vegetation characteristics...133

5.3.2.2 Land use/land cover...133

5.3.2.3 Soil physical characteristics..134

5.3.2.4 Climatic variables...135

5.3.3 Influence of landscape ecological factors on small rodent species richness...136

5.3.3.1 Vegetation characteristics...136

5.3.3.2 Land use/land cover characteristics..136

5.3.3.3 Climatic influence..137

5.3.3.4 Soil physical characteristics..138

5.4 Discussions...142

5.4.1 Rodent species richness..142

5.4.2 Rodent abundance...144

5.5 Conclusion...146

5.6 References...148

CHAPTER SIX...158

6.0 GENERAL DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS...158

6.1 General Discussion...158

6.2 General Conclusions...162

6.3 General Recommendations..164

6.4 References..166

APPENDICES...171

LIST OF PAPER

PAPER 1: SPECIES COMPOSITION AND COMMUNITY STRUCTURE OF SMALL RODENTS (MURIDAE) IN CULTIVATED AND FALLOW FIELDS IN MAIZE

GROWING AREAS IN MAYUGE DISTRICT, EASTERN UGANDA..20

PAPER 2: POPULATION AND BREEDING PATTERNS OF THE PESTIFEROUS RODENT: *MASTOMYS NATALENSIS* IN A MAIZE DOMINATED AGROECOSYSTEM IN LAKE VICTORIA CRESCENT ZONE, EASTERN UGANDA............................56

PAPER 3: FITNESS OF THE PESTIFEROUS SMALL RODENT: *MASTOMYS NATALENSIS* IN AN AGROECOSYSTEM IN LAKE VICTORIA CRESCENTS ZONE, EASTERN UGANDA..85

PAPER 4: FACTORS INFLUENCING THE DISTRIBUTION AND ABUNDANCE OF SMALL RODENT SPECIES IN AGRICULTURAL LANDSCAPES IN EASTERN UGANDA 114

Y

LIST OF TABLES

CHAPTER ONE TABLES

Table 1.1: Production Statistics of selected crops; the regional and national production statistics of selected crops from the Uganda Census of Agriculture survey conducted during 2008/09...2

CHAPTER TWO TABLES

Table 2.1: Inventory of small rodent species and an insectivorous mammal recovered in cultivated and fallow field habitats in Mayuge district, Eastern Uganda, during the study period 2016-2018..........29

CHAPTER THREE TABLES

Table 3.1: Common weed species encountered in the study area..........61

Table 3.2: Generalized Linear Mixed Model parameter estimates for fixed effect factors; habitat and seasons on *M. natalensis* population density..........65

Table 3.3: Generalized Linear Mixed Model parameter estimates for fixed effect factors; habitat, seasons and total monthly rainfall on sexually active breeding *M. natalensis*..........67

Table 3.4: Generalized Linear Mixed Model parameter estimates for fixed effect factors; habitat and seasons on newly trappable *M. natalensis* animals (recruitment) in a trappable population..........68

CHAPTER FOUR TABLES

Table 4.1: Modelling of maturation, recapture and survival. Highlighted (bold) models where the best models (with the lowest AICc) and were selected in each step and used as a starting point for the subsequent step..........94

CHAPTER FIVE TABLES

Table 5.1: Detailed description of landscape characteristics of the studied landscape units..121

Table 5.2: Temporal characteristics of Landsat 8 (OLI) data acquisition..122

Table 5.3: Macro and micro land use/land cover classes..124

Table 5.4: Species composition of rodents in the trapping survey conducted in Mayuge, Butalejja and Bulambuli districts during the study period..132

Table 5.5: Mean (±SE) for small rodent population abundance across the studied districts and overall..135

Table 5.6: Mean (±SE) for small rodent species richness for across the studied sites and overall..138

LIST OF FIGURES

CHAPTER TWO FIGURES

Figure 2.1: Map showing the location of the study site, Kigulu parish, Kigandalo subcounty, Mayuge district Eastern Uganda............................24

Figure 2.2: Species accumulation for all samples (A) and (B) for the separate studied fields (Fallow and cultivated fields with ±Standard deviation)..30

Figure 2.3: Mean (±SE) monthly species richness over the two and half years of the study period in fallow and cultivated fields in Mayuge district, Eastern Uganda..32

Figure 2.4: Mean (±SE) monthly small rodent abundance over the two and half years of the study period in fallow and cultivated field habitats in Mayuge district, Eastern Uganda....................................32

Figure 2.5: Mean (±SE) temporal Species Turn Over (β_T) for the different years of study in Mayuge district, Eastern Uganda...33

Figure 2.6: Bray-Curtis similarities in rodent composition among the trapping habitats and species communities in the study............................34

Figure 2.7: Ordination plots for Non-Metric Dimensional Scaling (NMDS) in rodent community composition among trapping habitats...35

CHAPTER THREE FIGURES

Figure 3.1: Box plots with mean, median, 25^{th} and 75^{th} quartile range for *M. natalensis* population density in cultivated and

fallow field habitats for trapped animals in Mayuge district for a period of 2016-2018..65

Figure 3.2: Box plots with mean, median, 25th and 75th quartile range for seasonal *M. natalensis* population density in Mayuge district for the period of 2016-2018..66

Figure 3.3: Relationship between population density for *M. natalensis* and total monthly rainfall in Mayuge district eastern Uganda for the period 2016-2018..66

Figure 3.4: Box plots with mean, median, 25th and 75th quartile range for seasonal percentage sexually active females in Mayuge during the period of 2016-2018..67

Figure 3.5: Box plots with mean, median, 25th and 75th quartile range for seasonal percentage recruitment of *M. natalensis* in a trappable population in Mayuge during the period of 2016-2018..69

CHAPTER FOUR FIGURES

Figure 4.1: Recapture probability of males (blue lines) and females (red lines) for every trapping session. Error bars represent the 95% Confidence intervals of each estimate...97

Figure 4.2: Monthly Survival probability of *Mastomys natalensis* in periods where cumulative rainfall in the last two months was lower than 300mm (Low), between 300-500mm (Medium) or higher than 500mm (high) Within these periods, there were differences in survival probability when current density was low (<10 captured individuals)

or high (>10 captured individuals). The error bars represent the 95% confidence interval..98

CHAPTER FIVE FIGURES

Figure 5.1: Location of study sites..120

Figure 5.2: Land use/land cover (LULC) map representative of A-Kigulu parish, Mayuge district, B-Kapisa parish, Bualeja district and C-Bukhalo parish, Bulambuli district...................................125

Figure 5.3: Normalized Difference vegetation Index (NDVI) maps covering the different seasons across the three study sites: A; Kapisa parish in Butaleja landscape unit, B; Kigulu parish in Mayuge landscape unit and C; Bukhalo parish in Bulambuli landscape unit...128

Figure 5.4: Partial dependence plots showing the relationships/effects of predictor variables with rodent population abundance. (A): Butaleja and (B): Mayuge districts..139

Figure 5.5: Partial dependence plots showing the relationships/effects of predictor variables with rodent population abundance. (C): Bulambuli district and (D): Overall (Pooled data for the three districts..140

Figure 5.6: Partial dependence plots showing the relationships/effects of predictor variables with rodent species richness. (E): Butaleja and (F): Mayuge districts..141

Figure 5.7: Partial dependence plots showing the relationships/effects of predictor variables with rodent species richness. (G):

Bulambuli and (H): Overall (Pooled data for three districts.
....142

LIST OF APPENDICES

Appendix 1: Publishable Paper..171

LIST OF ABBREVIATIONS AND SYMBOLS

%	Percent
ANOVA	Analysis of Variance
BRT	Boosted Regression Tree
CMR	Capture Mark Release
CV	Cross Validation
Df	Degrees of Freedom
EA	East Africa
EBRM	Ecologically Based Rodent Management
E-SURGE	A Software Application for Fitting Multievent Models
FAO	Food and Agriculture Organization
GLMM	Generalized Linear Mixed Model
Ha	Hectare
mm	Millimeter
MVC	Maximum Value Composite
NDVI	Normalized Difference Vegetation Index
NIR	Reflectance in the Near Infra-Red band of the Electromagnetic Spectrum
OLI	Operation Land Imager
P	Probability
PAST	PAleontological Statistics
PQL	Penalized Quasi Likelihood
Q-GIS	Quantum Geological Information System software
R	Surface Reflectance in the Red Portion of the Electromagnetic Spectrum
ROI	Region of Interest
SCP	Semi-automatic Classification Plugin
SRTM	Shutter Radar Topographic Mission
SUA	Sokoine University of Agriculture
UBOS	Uganda Bureau of Statistics
USA	United States of America
USD	United States Dollar
USDA	United States Department of Agriculture
USGS	United States Geological Survey
VIF	Variance Inflation Factor
XLSTAT	An Excel add-in Statistical Analysis Software
χ^2	Chi square

CHAPTER ONE

1.0 GENERAL INTRODUCTION

1.1 Cereal Crops Production

Cereal crops contribute a great part of the staple food crops among many communities in Uganda and are a highly prioritized group of crops for research and development (Shellemiah and Rubaihayo, 2013). Production statistics, over the years for cereals show an increasing trend from about 1.29 million metric tons in 1968 to 3.83 million metric tons in 2017, growing at an average annual rate of 3.01 % (https://knoema.com/atlas/Uganda/Cereal-production).

In terms of importance, maize, sorghum, millet, rice and wheat dominate the cereal crops sector in the whole of Uganda (Uganda Export Promotions Board, 2012). However, maize (*Zea mays*) and rice (*Oryza sativa*) dominate the Eastern region of the country with this region leading in production of these two crops (Table 1.1) (UBOS report, 2010). Further, export earnings from maize is by far the most traded export commodity in Ugandan grains market, with exports worth USD 78.6 million in 2015. Earlier statistics reports during the period of 2010-14, maize exports yielded USD 43.5 million, rice USD 28.7 million and sorghum USD 35.2 million in 2014 (https://knoema.com/atlas/Uganda/Cereal-production). Indeed, the monetary value of cereal crops has been increasing steadily since 2010.

Table 1.1: Production Statistics of selected crops; the regional and national production statistics of selected crops from the Uganda Census of Agriculture survey conducted during 2008/09

Crop	Central	Eastern	Northern	Western	Total
			Acreage [ha]		
Maize	189 135	388762	247780	188583	1 014 260
Finger millet	5832	86911	105656	5588	203 987
Sorghum	2261	101645	249330	46016	399 252
Rice	2637	36033	25912	10504	75 085
Beans	120798	108107	146702	241915	617 521
Banana (Food type)	283472	59783	5059	458312	806 627
Banana (Sweet type)	8596	3039	3932	7556	23 129
Banana (Beer type)	34014	6682	204	45228	86 127
Cassava	127788	342387	269886	131328	871 389
Sweet potatoes	98054	159948	60573	121681	440 256
	Production [Metric tons]				
Maize	449 859	1 108 554	308 798	497 745	2 364 956
Finger millet	13 734	106 838	78 572	77 784	276 928
Sorghum	2 678	133 318	177 088	62 716	375 795
Rice	2 173	128 195	43 719	16 649	190 736
Beans	167 276	98 834	251 221	411 945	927 278
Banana (Food type)	929 534	333 851	26 015	2 728 587	4 017 986
Banana (Sweet type)	11 319	3117	4 630	17 447	36 514
Banana (Beer type)	98 984	5266	981	137 614	242 845
Cassava	409 812	1 061 186	983 124	440 189	2 894 311
Sweet potatoes	312 402	847 140	292 932	366 295	1 818 769

Source: Uganda Bureau of Statistics 2010 Summary Report on Uganda Census of Agriculture 2008/09.

1.2 Constraints to Cereal Crops Production

Unfortunately, potential cereal crops production in Uganda and elsewhere in the region is hampered by multiplicity of constraints including among others; poor soil fertility, poor seed, unreliable rainfall and several pests and diseases (Vivek *et al*., 2010; Waddington *et al*., 2010; Nabbumba, 2003; Makundi *et al*., 1999). Among the cereal crop pests, rodents are globally documented to inflict significant crop damage and loss on production (Myllymäki *et al*., 1987; Fiedler, 1988; Mwanjabe *et al.*, 2002; Brown *et al*., 2017; Mulungu, 2017). Their occurrence results into significant crop losses in normal years and heavy losses in outbreak years (Fiedler, 1988; Shanker, 2001; Mulungu, 2003; Makundi *et al*., 2005; Meheretu *et al*., 2010; Singleton *et al*., 2010a; Mulungu, 2017) and can result into serious food shortages and hunger. Unfortunately, minimal research efforts have been rendered to this group of animals in Africa as crop pests (Singleton, 2003). In East Africa, rodents mainly inflict damage on cereal crops and are ranked as major crop pests, threatening both national and international food security (Mwanjabe *et al*., 2002; Mohammed Kasso, 2013; Mulungu, 2017).

For instance, crop loss estimates ranging between 5-15% of the annual maize production in Tanzania is reported to be lost to rodents (Makundi *et al.,* 1999; Leirs, 1992) but the situation can worsen and losses can reach as high as 80% in certain seasons and locations (Mulungu, 2003; Mulungu *et al*., 2003). In Western Kenya, a range of 20-30% loss and 34-100% loss was realized on maize and wheat crops respectively after an outbreak of rodents (Taylor, 1968).

1.3 Rodents Public Health Concern and Ecosystem Health

Rodents are also listed as important carriers of human and animal diseases such as plague and typhus and can result into serious public health concerns (Kernéis *et al*., 2009; Meerburg *et al*., 2009; Neerinckx *et al*., 2010; Makundi *et al*., 2003). On another note, a number of rodent species are beneficial to the environment as they are regarded as indicators of ecosystem health and play a role in food web of many wild animals (Apline *et al*., 2003) thus caution should be taken when applying any controlling rodents as pests in a given locality.

1.4 Classification of Rodents

Taxonomically, rodents are a group of mammals belonging to order Rodentia (29 families, 468 genera and 2 052 species) and are highly diverse in population size and environmental adaptations (Kingdon, 1974; Nowak, 1999; Happold, 2013). They are reported to constitute approximately 42% of the entire mammalian species (Nowak, 1999;

Aplin *et al*., 2003). It is further estimated that less than 10% of rodent species are major pest species of agricultural and urban areas (Stenseth *et al*., 2003; Singleton *et al*., 2007); and their impact as pests is generally utmost in the poorer developing countries. As crop pests, generalist species tend to cause more harm where certain genera and species have been quantified to be of more significant importance (Singleton, 2003).

1.5 Distribution, abundance and diversity of Rodents in East African Region

Rodents are known to thrive under various ecological conditions (areas with similar combinations of soil, landform, vegetation habitats, elevation and climatic characteristics) and numerous studies on this exist in the East African (EA) region (Delany, 1975; Leirs, 1995; Makundi *et al*., 1999; Clausnitzer and Kityo, 2001; Mulungu *et al*., 2003, 2005; Massawe *et al*., 2005). The ecological conditions govern the distribution and abundance of different species. For instance, *M. natalensis* tends to dominate agricultural landscapes (Massawe *et al*., 2005) and less in forest areas. Furthermore, the abundance of rodents is regulated by availability of food resources both in quantity and quality, which are influenced by onset of rainfall (Leirs, 1992).

In terms of diversity, the measure of the number of different species present in a given locality is also known to vary spatially and is mostly regulated by both climatic and other environmental conditions including food and shelter availability. For example, over 161 rodent species are reported and some were found associated with crop fields in the region, with *M. natalensis* being the most dominant species (Mulungu *et al.*, 2003; Makundi *et al*., 2005; Massawe *et al*., 2005). Other studies have focused on dietary diversity, life history and demographic parameters of some key species of economic importance (Sludyts *et al*., 2007; Mulungu *et al*., 2011; Borremans *et al*., 2013; Marien *et al*., 2018; Mlyashimbi *et al*., 2018).

Rodent population abundance has also received wide consideration in different countries and shows great variability depending on season, locality, crop cover and stage of crop growth (Mulungu *et al*., 2003; Massawe *et al*., 2005; Mulungu *et al*., 2010). For instance, rainfall has been shown to have an indirect influence on rodent population abundance and diversity (Leirs, 1992). Also, the breeding patterns have been studied, for instance breeding patterns of *M. natalensis* in Tanzania were associated with food availability and rainfall patterns (Massawe *et al*., 2012; Mulungu *et al*., 2013) i.e. populations' increase with onset of rains. Elevation is another key factor that has been shown to influence rodent pest species diversity and abundance with higher diversity and abundance reported at high elevation due to the likely increase in availability and quality of food, shelter and rainfall (Bayessa, 2010 and Hamilton, 1998). Similarly, vegetation habitats such as shrubs have been shown to support more small mammals than other habitats (Njaka *et al*., 2014). Other important parameters that regulate distribution of rodents include survival; defined as the monthly probability for an individual to survive from one month to the next and maturation, the probability for a juvenile to become an adult.

1.6 Forecasting Models for Rodents in East African Region

Attempts to develop forecasting models for the most dominant species (*M. natalensis)* have been undertaken in the region in a bimodal rainfall regime in Tanzania (Leirs *et al*., 1997). The model developed mainly considered rainfall as the predictor variable for rodent outbreaks and aimed at improving available control efforts for a sustainable rodent control program. Consequently, detailed studies proceeded to characterize the major demographic processes such as maturation and survival in Tanzania (Juliad *et al*., 1999; Sludyts *et al*., 2007; Marien *et al*., 2018). These have yielded additional information for the development of better forecasting models but they are mostly localized in Tanzania.

Similarly, more scientific advances have incorporated Geographical Information System and remote sensing to establish the influence of landscape ecological factors on rodent abundance in Tanzania (Chidodo, 2017 unpublished) and have revealed that NDVI is a key predictor of rodent population abundance in a given locality. Based on the above information, provisional control strategies have been formulated.

The most recent ones in Africa are the density-dependent, stochastic model (Leirs *et al*., 1997) for the multi-mammate rat *Mastomys natalensis* in Africa and the model used by Pech *et al*. (1997) to assess the value of fertility control for the management of foxes in Australia. The former model suggests that the onset of breeding by mice depends on seasonal environmental triggers. Further reviews suggest that in addition to climatic factors, other factors could be included to fine-tune on the existing models. For instance, Turretfied model (Newsome, 1969) suggest that landscape heterogeneity and the role of refuge habitats appears to be important in the population dynamics of mice in the Victorian Mallee, factors that could improve model accuracy if incorporated in density dependent model. It is clear that all models can offer useful information relevant to pest managers and policy implementers in planning for the implementation of management strategies for rodent control.

1.7 Management of Rodents

Several strategies for control of rodents have been documented (Makundi *et al*., 1991, 1999, 2005, Ngowo *et al*., 2005; Mdangi *et al*., 2013). These can be generally categorized into physical, chemical and biological control with the ultimate aim to reduce the impact (i.e. reduce damage to crops) rather than to kill animals *per se*. These control methods include among others; creation of rodent barriers, especially in storage structures, poisoning using acute and chronic rodenticides, trapping, removal of refugia and other shelter (e.g. through burning). All these have however, had little impact and new developments in recent years have taken into consideration a system which provides early warning of rodent outbreaks (Mulungu *et al*., 2010). This approach is based on the understanding of the biology and ecology of rodent pests and offers more sustainable and environmentally acceptable options (Singleton *et al*., 2010).

1.8 Statement of the Problem

Rodents remain key pests in cereal crops production (Maheretu *et al*., 2010) despite continued efforts to control them. The frustrating performance of control efforts in Sub-Saharan Africa is partially attributed to a limited understanding of rodent pest ecology and biology at small scale level (Tubin and Fall, 2004). Specifically, for Uganda, few studies on rodents exist to provide relevant ecological information to allow development of appropriate rodent pest management (Eisen *et al*., 2013; Basuta and Kasenene, 1987; Cheeseman and Delany, 1979). For instance, the diversity of major rodent pest species associated with farming systems is unknown yet it's the basis for successful pest management. Also, while a predictive model exists for *M. natalensis* in a bimodal rainfall regime in Tanzania (Leirs, 1996), its applicability is limited since it was developed on only rainfall as the predictor variable yet additional findings have shown NDVI to be a very important variable as well an indication that there may be more other important predictor variables that need to be explored. There is therefore a need to generate more ecological information on rodent pests in agro ecosystems in Uganda for further development of accurate models. This information is expected to facilitate development and recommendation of appropriate environmentally and economically potent management protocols that are either less dependent on chemical rodenticides or that can better target their usage.

1.9 Justification of the Study

Despite the above continued efforts in the East African region to manage rodent pest species, the performance of control strategies has largely remained dismal in many localities (Mulungu, 2017). This has been mainly attributed to the limited knowledge on the ecology of major rodent pest species, information which provides clues for development of better sustainable integrated pest management strategies. In Uganda, where rodents continue to surface as pests with a loss estimate of 10-19% on average in maize and rice crop (Project survey report, 2016), there exists no literature on efforts to understand the ecological aspects of major rodent pest species. In addition, with the exception of the earlier efforts that mainly concentrated in conservation areas like Kibale Nation Park (Basuta and Kasene, 1987) Rwenzori National Park (Delany, 1975) and Claustzer and Kitryo (2001) that provided insights into the diversity and habitat suitability of rodents, few efforts have been devoted to the assessment of the ecology and biology of rodents as agricultural crop pests at a detailed scale in any agro ecological zone. The differences in climatic and cropping systems in Uganda with those in the EA region could cause significant differences in the ecology of major rodent pests their damage levels. Ultimately, the differences may lead to variations in faunal composition and hence call for specific control measures. This, therefore, warrants further studies on the diversity, population fluctuation and breeding patterns and influence geo spatial landscape factors on rodent abundance, as a means to formulation of an Ecologically Based Rodent Management (EBRM) strategy for rodent pests in Uganda.

Secondly, while rodents comprise notable pest species, a majority of rodent species are considered beneficial to the ecosystem as environmental engineers (Apline *et al.*, 2003). This aspect thus necessitates that control strategies need to be synchronized to target major pest species for a given locality and save the beneficial species. This study thus provides a list of the main rodent species associated with maize and rice cropping systems and their seasonal population and breeding patterns; information necessary to allow synchrony of management efforts by Agriculture agents to target key stages of key pest species before populations build up to damaging levels. Additionally, it is known that mobile pests do not recognize farm and field boundaries (Schellhorn *et al.*, 2008) and thus control efforts on field-based approach alone have often failed. Further observations have shown that some landscapes are less prone to pest infestation than others (Parry and Schellhorn, 2013), implying that there are features of the landscape that may be managed to create more pest suppressive landscapes. This study provides information on key important environmental factors in the landscape that regulate rodent population distribution and abundance. The information can further be utilized in development of national and regional probabilistic models for predicting potential rodent pest out breaks in maize and rice cropping systems.

1.10 Objectives

1.10.1 Overall objective

To investigate the ecology of major rodent pest species associated with maize and rice cropping systems for development of ecologically based rodent management systems in Eastern Uganda.

1.10.2 Specific objectives

i. To identify the different rodent pest species associated with maize-fallow fields in Eastern Uganda

ii. To determine seasonal population abundance of major rodent pest species in Eastern Uganda

iii. To determine the survival and maturation probabilities of key rodent pest species in agro ecosystem

iv. To establish the influence of geo-spatial landscape factors to rodent pest species abundance.

1.10.3 Research hypotheses

i. The diversity Rodent pest species associated with maize-fallow in Uganda is unknown.

ii. Ecological process such as maturation and survival are not influenced by habitat, rainfall and population density of a particular rodent species in agroecosystem in Uganda.

iii. Rodent pest population abundances in agroecosystem environment is not influenced by seasonal changes in different habitats in Uganda.

iv. Landscape and climatic factors do not influence rodent species abundance and richness in agroecosystem in Uganda.

1.11 References

Addisu, A. and Bekele, A. (2013). Habitat preferences, seasonal abundance and diets of rodents in Alage, Southern Ethiopia. *African Journal of Ecol*ogy 52: 284 - 291.

Aplin, K. P., Brown, P. R., Jacob, J., Krebs, C. J. and Singleton, G. R. (2003). Field Methods for Rodent Studies in Asia and the Indo-Pacific. Australian Centre for International Agricultural Research: Canberra. pp. 223.

Baillie, I. C. (2001). Book Review: Soil Survey Staff 1999, Soil Taxonomy A basic system of soil classi ® cation for making and Agricultural Handbook 436 ; Natural Resources. *Soil Use and Management* 17: 57 - 60.

Chidodo, D. J. (2017). *Evaluation of Normalized Difference Vegetation Index of common vegetation habitats for monitoring rodent population and outbreaks in Ismani, Tanzania* (MSc. Thesis). Morogoro: Sokoine University of Agriculture, Morogoro Tanzania. 117pp.

Clausnitzer, V. and Kityo, R. (2001). Altitudinal distribution of rodents (Muridae and Gliridae) on Mt Elgon, Uganda, *Tropical Zoology* 14 (1): 95 - 118.

Delany, M.J. (1975). *The Rodents of Uganda.* Kettering Northamptonshire: The George Press. 67pp.

Eccard, J.A., Klemme, I., Horne, T.J. and Ylönen, H. (2002). Effects of competition and season on survival and maturation of young bank vole females. *Evolutionary Ecology* 16: 85 - 99.

Fiedler, L.A. (1988). *Rodent problems in Africa*, in I. Prakash (ed.), Rodent Pest Management, Boca Raton: CRC Press Inc., pp. 35 - 64.

Fiedler, L.A. (1994). Rodent Pest Management in East Africa. FAO plant production and protection paper 123, FAO, Rome, Itally. 83pp.

Happold, D.C.D. (ed.). (2013). *Mammals of Africa*, volume III*:* Rodents, Hares and Rabbits. Bloomsbury Publishing, London. 784pp.

Hieronimo, P., Kimaro, D. N., Kihupi, N. I., Gulinck, H., Mulungu, L. S., Msanya, B. M. and Deckers, J. A. (2014). Land use determinants of small mammals abundance and distribution in a plague endemic area of Lushoto district, Tanzania. *Tanzania Journal of Health Research* 16(3): 1 - 12.

Julliard, R., Leirs, H., Stenseth, N. C., Yoccoz, N. G., Prévot-Julliard, A. C., Verhagen, R. and Verheyen, W. (1999). Survival-variation within and between functional categories of the African multimammate rat. *Journal of Animal Ecology* 68: 550 - 561.

Kingdon, J. (1974). *East Africa mammals: an atlas of evolution in Africa.* Volume II Part B (Hares and Rodents). Academic Press, London. 704pp.

Kotler, B.P. (1984). Predation risk and the structure of desert rodent communities. *Journal of Ecology* 165: 689 - 701.

Leirs, H. (1992). Population ecology of *Mastomys natalensis* (Smith, 1834) multimammate rats: possible implications for rodent control in Africa. PhD Thesis, Belgium, University of Antwerp, Belgium. 268pp.

Leirs, H., Verhagen, R. and Verheyen, W. (1994). The basis of reproductive seasonality in Mastomys rats (Rodentia: Muridae). *Journal of Tropical Ecol*ogy 10(1): 55 - 66.

Leirs, H., Verhagen, R., Sabuni, C. A., Mwanjabe, P. and Verheyen, W. N. (1997). Spatial dynamics of Mastomys natalensis in a field-fallow mosaic in Tanzania. *Belgian Journal of Zoology* 127: 29 - 38.

Magige, F. and Senzota, R. (2006). Abundance and diversity of rodents at the human-wildlife interface in Western Serengeti, Tanzania. *African Journal of Ecology* 44: 371 - 375.

Makundi, R.H., Massawe, A.W. and Mulungu, L.S. (2005). Rodent population fluctuations in three ecologically distinct locations in north-east, central and south-west Tanzania. *Belgian Journal of Zoology* 135: 159 - 165.

Makundi, R.H., Massawe, A.W., Mulungu, L.S. and Katakweba, A. (2009). Species diversity andpopulation dynamics of rodents in a farm-fallow field mosaic system in Central Tanzania. *African Journal of Ecology* 48: 313 - 320.

Makundi, R.H., Massawe, A.W., Mulungu, L.S., Katakweba, A., Mbise, T.J. and Mgode, G. (2008). Potential mammalian reservoirs in a bubonic plague outbreak focus in Mbulu District, northern Tanzania. *Mammalia* 72: 253 - 257.

Makundi, R.H., Oguge, N.O. and Mwanjabe, P.S. (1999). Rodent pest management in East Africa. In: Singleton GR, Hinds L, Leirs H, Zhang Z, editors. Ecologically based management of rodent pests. Canberra (Australia): ACIAR. pp. 460 - 476.

Mariën, J., Sluydts, V., Borremans, B., Gryseels, S., Vanden Broecke, B., Sabuni, C. A. and Leirs, H. (2018). Arenavirus infection correlates with lower survival of its natural rodent host in a long-term capture-mark-recapture study. *Parasites and Vectors* 11: 90 - 97.

Massawe, A. W., Rwamugira, W., Leirs, H., Makundi, R. H., Mulungu, L., Ngowo, V. and

Machangu, R. (2008). Soil type limits population abundance of rodents in crop fields: case study of the multimammate rat Mastomys natalensis Smith, 1834 in Tanzania. *Integrative Zoology* 3(1): 27 - 30.

Massawe, A.W., Mulungu, L.S. and Makundi, R.H. (2011). Spatial and Temporal Population Dynamics of Rodents in Three Geographically Different Regions in Africa: Implication for Ecologically-Based Rodent Management. *African Zoology* 46: 393 - 405.

Mdangi, M., Mulungu, L. S., Massawe, A.W., Eiseb, S. J., Tutjavi, V., Kirsten, F., Mahlaba, T., Malebane, P., von Maltitz, E., Monadjem, A., Dlamini, N., Makundi, R. H. and Belmain, S. R. (2013). Assessment of rodent damage to stored maize (*Zea mays* L.) on smallholder farms in Tanzania. *International Journal of Pest Management* 59: 55 - 62.

Meerburg, G. M., Singleton, G. R. and Kijlstra, A. (2009). Rodent-borne diseases and their risks for public health. *Critical Reviews in Microbiology* 35: 221 - 270.

Meheretu, Y., Kiros, W., Seppe, D., Dirk, R., Makundi, R. and Leirs, H. (2010). Farmers' perspectives of rodent damage and management from the highlands of Tigray, Northern Ethiopian," *Crop Protection* 29: 532 - 539.

Meliyo, J., Brabers, L., Massawe, B., Msanya, B., Kimaro, D., Mulungu, L. and Leirs, H. (2015). The Effect of Soil Physical Properties and Soil Microclimate on Rodent Burrows' Abundance and their Characteristics in Western Usambara Mountains, Tanzania. *Journal of Agriculture and Ecology Research International* 2(2): 105 - 119.

Mohammed, K. (2013). Pest rodent species composition, level of damage and mechanism of control in Eastern Ethiopia. *International Journal of Innovation Applied Studies* 3: 502 - 511.

Monadjem, A. and Perrin, M. (2003). Population fluctuations and community structure of small mammals in a Swaziland grassland over a three-year period. *African Zoology* 38(1): 127 - 137.

Mulungu, L.S. (2003). *Assessment of maize (Zea mays L) damage and yield loss due to rodents in the field.* PhD Degree awarded at Sokoine University of Agriculture, Morogoro, Tanzania, 178pp.

Mulungu, L.S. (2017). *Control of rodent pests in maize cultivation: the case of Africa*. pp. 317 - 338.

Mulungu, L.S., Lopa, H. and Mdangi, E.M. (2016). Comparative Study of Population Dynamics and Breeding Patterns of *Mastomys natalensis* in System Rice Intensification (SRI) and Conventional Rice Production in Irrigated Rice Ecosystems in Tanzania. *Journal of Rice Research* 4: 1 - 5.

Mulungu, L.S., Makundi, R.H., Leirs, H., Massawe, A.W., Vibe-Petersen, S. and Stenseth, N.C. (2003). The rodent-density-damage function in maize fields at an early growth stage. In ‘Rats, Mice and People: Rodent Biology and Management’. (Eds G. R. Singleton, L. A. Hinds, C. J. Krebs and D. M. Spratt.) Australian

Centre for International Agricultural Research: Canberra. pp. 301 - 303.

Mulungu, L.S., Ngowo, V., Mdangi, M., Katakweba, A.S., Tesha, P., Mrosso, F.P., Mchomvu, M., Sheyo, P. M. and Kilonzo, B.S. (2013). Population dynamics and breeding patterns of Multimammate mouse, *Mastomys natalensis* (Smith, 1834), in irrigated rice fields in eastern Tanzania. *Pest Management Sciences* 69: 371 - 377.

Mwanjabe, P. S., Sirima, F. B. and Lusingu, J. (2002). Crop losses due to outbreaks of Mastomys natalensis (Smith, 1834) Muridae, Rodentia, in the Lindi region of Tanzania. *International Biodet and Biodeg* 49: 133 - 137.

Myllymäki, A. (1987). Control of rodent problems by the use of rodenticides: rationale and constraints. In: Richards, C. G. J. and Ku, T. Y. (eds), Control of Mammal Pests. Taylor and Francis, London, pp. 83 - 111.

Nabbumba, R. and Bahiigwa, G. (2003). Agricultural productivity constraints in Uganda; implications for investment. Research series No: 31. 42pp.

Neerinckx, S., Bertheratc, E. and Leirs, H. (2010). Human plague occurrences in Africa: an overview from 1877 to 2008. *Transactions of the Royal Society of Tropical Medicine and Hygiene* 104: 97 - 103.

Ngowo, V., Mulungu, L.S., Lodal, J., Leirs, H., Massawe, A.W. and Makundi, R.H. (2005). Evaluation of Thiram and Cinnamamide for Maize Seeds Protection against Multimammate Rat, *Mastomys natalensis*, in Maize Fields in Tanzania. *Belgian Journal of Zoology* 135(Suppl): 179 - 181.

Nowak, R. M. (1999). *Walkers Mammals of the World* Vol. II 6th ed. The John Hopkins University Press, Baltimore and London. 89pp.

Odhiambo, R.O. (2005). *Community structure and diet preference of rodent pests of maize (Zea mays* L.*) in Central and Southwestern Tanzania* (PhD Thesis). Sokoine University of Agriculture, Morogoro, Tanzania. 178pp.

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J. and Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution* 20(9): 503 - 510.

Shanker, K. (2001). The role of competition and habitat in structuring small mammals communities in a tropical montane ecosystem in southern India. *Journal of Zoology* 253: 15 - 24.

Singleton, G. R. (2003). Impacts of rodents on rice production in Asia. IRRI Discussion Paper Series No 45. Los Baños, Philippines: International Rice Research Institute. 12pp.

Singleton, G. R., Belmain, S. R., Brown, P. R. and Hardy, B. (2010). Rodent outbreaks: ecology and impacts. Los Banos (Philipines); International Rice Research Institute. 289pp.

Singleton, G. R., Brown, P. R., Jacob, J. and Aplin, K. P. (2007). Unwanted and unintended effects of culling: A case for ecologically-based rodent management. *Integrative Zoology 2*: 247 - 259.

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

Stenseth, N. C., Leirs, H., Skonhoft, A., Davis, S. A., Pech, R. P., Andreassen, H. P., Lima, M., Machangu, R. M., Makundi, R. H., Zhang, Z., Brown, P. R., Shi, D. and 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, M., Keith, M., Kirsten, F., Leirs, H., Mahlaba, T.A.M., Makundi, R.H., Malebane, P., Maltitz, E.F., Massawe, A.W., Monadjem, A., Mulungu, L. S., Singleton, G.R., Taylor, P. J., Soarimalala, V. and 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(3): 17 - 45.

Taylor, K. D. (1968). An outbreak of rats in agricultural areas of Kenya in 1962. *East African Agricultural and Forestry Journal* 34: 66 - 77.

UBOS (Uganda Bureau of Statistics) (2006). National Household Survey, Agricultural Module, Kampala, Uganda. 87pp.

UBOS (Uganda Bureau of Statistics) (2010). National Household Survey 2009/10 [www.ubos.org/UNHS0910/unhs2009/10.pdf]. Site visited on 2/3/2020.

Vivek, B.S., Odongo, O., Njuguna, J., Imanywoha, J., Bigirwa, G., Diallo, A. and Pixley, K. (2010). Diallel analysis of grain yield and resistance to seven diseases of 12 African maize (*Zea mays* L.) inbred lines. *Euphytical* 172: 329 - 340.

Waddington, S.R., Li, X., Dixon, J., Hyman, G. and de Vicente, M.C. (2010). Getting the focus right: production constraints for six major food crops in Asian and African farming systems. *Food and Security* 2(1): 27- 48.

CHAPTER TWO

PAPER I

SPECIES COMPOSITION AND COMMUNITY STRUCTURE OF SMALL RODENTS (MURIDAE) IN CULTIVATED AND FALLOW FIELDS IN MAIZE GROWING AREAS IN MAYUGE DISTRICT, EASTERN UGANDA

Alex Mayamba[1,2*]; Robert M Byamungu[2]; Rhodes H Makundi[3]; Didas N Kimaro[4]; Moses Isabirye[1]; Apia W Massawe[3]; David Kifumba[1], Alice Nakiyemba[1]; Herwig Leirs[5]; Mshaka E Mdangi[6]; Brian E Isabirye[7] and Loth S Mulungu[3]

[1]Faculty of Natural Resources and Environment, Busitema University, P. o. Box 236, Tororo, Uganda, [2]Department of Wildlife Management, Sokoine University of Agriculture, P.o. Box 3073, Morogoro, Tanzania, [3]Pest Management Centre, Sokoine University of Agriculture, P. o. Box 3110, Morogoro, Tanzania, [4]Department of Engineering Sciences and Technology, Sokoine University of Agriculture, P.o. Box 3003, Morogoro, Tanzania, [5]Evolutionary Ecology Group, Universiteit Antwerpen, Groenenborgerlaan 171, B-2020 Antwerpen, Belgium, [6]Ministry of Agriculture Training Institute (MATI) Ilonga, P. o. B0x 66, Kilosa, Tanzania, [7]International Center of Insect Physiology and Ecology (ICIPE), Kasarani, Nairobi, Kenya.

Email: alex.mayamba@gmail.com

Published: Ecology and Evolution, Vol 9, 7849-7860

Available online at DOI: https://doi.org/10.1002/ece3.5371

Abstract

Pest rodents remain key biotic constraints to cereal crops production in the East African region where they occur, especially in seasons of outbreaks. Despite that, Uganda has scant information on rodents as crop pests to guide effective management strategies. A Capture-Mark-Recapture (CMR) technique was employed to study the ecology of small rodents, specifically to establish the species composition and community structure in a maize-based agro ecosystem. Trapping of small rodents was conducted in permanent fallow land and cultivated fields, with each category replicated twice making four study grids. At each field, a 70*70 m^2 grid was measured and marked with permanent trapping points spaced at 10*10 m^2, making a total of 49 trapping points/grids. Trapping was conducted monthly at 4 weeks interval for three consecutive days for two and half years using Sherman Live traps. Eleven identified small rodent species and one insectivorous small mammal were recorded with *Mastomys natalensis* being the most dominant species (over 60.7%). Other species were *Mus triton* (16.1%), *Aethomys hendei* (6.7%), *Lemniscomys zebra* (5.2%), *Lophuromys sikapusi* (4.8%), *Arvicanthis niloticus* (0.9%), *Gerbilliscus kempi* (0.1%), *Graphiurus murinus* (0.1%), *Steatomys parvus* (0.1%), *Dasymys incomtus* (0.1%) and *Grammomys dolichurus* (0.1%). Spatially, species richness differed significantly (p = 0.0001) between the studied field habitats with significantly higher richness in fallow land compared to cultivated fields. Temporally, total species richness and abundance showed a significant interaction effect over the months, years and fields of trapping with significantly (p = 0.001) higher abundances during months of wet seasons and in the first and third year of trapping. In terms of community structure, higher species diversity associated more with fallow field habitats but also with certain rare species found only in cultivated fields. Synthesis and application: Based on these findings, management strategies can be designed to target the key pest species and the most vulnerable habitats thus reducing the impact they can inflict on field crops.

Key words: Species diversity, Richness, Composition, Community Structure, Fallow land, Cultivated fields

2.1 Introduction

Rodents exhibit irregular population dynamics with occasional outbreaks, typically occurring over extensive areas (Fiedler, 1988; Leirs *et al*., 1996). Globally, they are among the most destructive vertebrate pests to cereal crops (Singleton *et al*., 1999a, Leirs, 2003; Stenseth *et al*., 2003), with profound crop damage impact in the low developing countries in Africa (Mdangi *et al*., 2013; Makundi *et al*., 1999), Asia (Singleton, 2003) and Indonesia (Geddes, 1992). Particularly, studies in the East African region (e.g. Mulungu *et al.*, 2003; Makundi *et al*., 1999; Leirs *et al*., 1999; Mwanjabe, 1990) have identified several rodent species that are important and responsible for crop yield loss and in lowering of crop qualities. In this region, rodents commonly cause 5 - 15% damage on maize crop (Mwanjabe and Leirs, 1997), but projections indicate that it can reach over 80% in seasons of outbreaks (Mulungu *et al*., 2003). Largely, Multimammate rats (*Mastomys natalensis*) are pointed out as the most important rodent pests involved in crop damage in the sub Saharan Africa (Fiedler, 1988) though other groups such as *Gerbiliscus* spp and *Arvicanthis* spp are also involved (Makundi *et al.*, 1999). These rodent groups are known for their damages on a diversity of cereal crops with preponderant impact on maize and rice, the crops which are important in food security across the east African region.

In Uganda, cereal crops form a key component of the crop production sector and contribute significantly to the dietary diversity of many rural and urban communities (Shellemiah and Rubaihayo, 2013). However, production of diverse cereals is still low due to several production constraints including massive loss due to rodent pest damages (Waddington *et al*., 2010; Nabbumba, 2003). Currently, rodent management strategies in the country are minimal due to the scant information available on rodents as pests to guide management (Moore *et al.*, 2015; Eisen *et al.*, 2013). Specifically, knowledge on the species composition and community structure are known fundamental facts for a successful and acceptable pest control strategy (Parsons *et al.,* 2017; Simberlof 2014; Hoare and Hare, 2006). Presently, literature available in the country focuses on rodents as potential disease vectors to human and livestock (Bochert *et al*., 2010; Eisen *et al*., 2010; Amatre *et al*., 2009) but less so as crop pests. No detailed studies exist in the country on rodents as field crop pests and little is known about rodent communities in agriculture cropping systems. This study thus aimed at determining the species composition and community structure of small pest rodents in cultivated and fallow land fields in maize growing areas in Eastern Uganda, a step towards developing a successful pest management strategy in the country. The knowledge on rodent diversity of rodents and their distribution in the environment will enable design of appropriate management strategies that will target harmful species while sparing the beneficial ones (Singleton *et al*., 2005).

2.2 Materials and Methods

2.2.1 Study site

The study was conducted in Kigulu parish, Kigandalo sub-county, Mayuge district in Eastern Uganda (06°16′S, 37° 31′E), approximately 1020 m above sea level (Fig. 1). The study area experiences a bimodal rainfall pattern, characteristic of Eastern Uganda in the Lake Victoria Crescents agro-ecological zone. There are two rainy seasons in the year; first rainy season normally occurs between March and end of May with a short dry period (June-August). The second rainy season occurs between August and end of November, then a dry spell from December to February of the following year. Due to the intense demand for agricultural and pasture land in this region, land is highly fragmentated and natural forests are very scarce and in small patches.

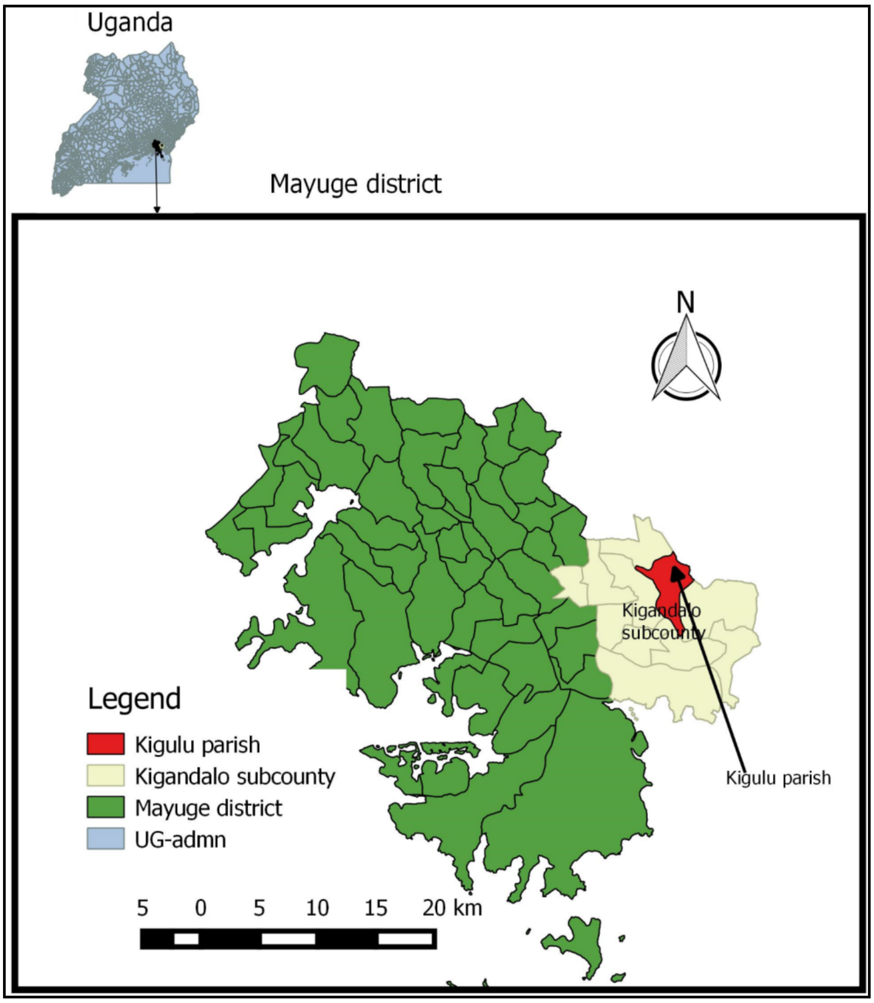


Figure 2.1: Map showing the location of the study site, Kigulu parish, Kigandalo subcounty, Mayuge district Eastern Uganda.

2.2.2 Sampling procedure

Permanent trapping fields for the experiment were obtained through negotiation with landowners and agreements formally made. A purposive sampling technique, where study plots where identified and selected on the basis of availability of the required size (70 m x 70 m) and acceptability by the land owner to offer this area for the study and targeted both cultivated field and fallow land habitats. In this area, land use is highly fragmented and thus we targeted fields that could measure about 70m*70m and the permanent trapping grids were measured off starting at 10 meters from the boundary line.

In each of the two habitat types, two replicate grids were obtained making a total of four trapping fields at a minimum distance of 500m from each other. At each of the identified field sites, a 70 m x 70 m^2 grid was marked and permanent trapping points set. The fallow land fields were initially dominated with heavy thick patches of tick berry (*Lantana camara)* but were subsequently reduced due to animal grazing. Other weedy species noted were perennial and annual grasses (Gramineae) of several species, which are common in disturbed soils and uncultivated fallow lands. They included guinea grass (*Panicum maximuma*) couch grass (*Digitaria scalarum*), black jack (*Bidens pilosa*), Star grass (*Cynodon dactylon)* wondering jew (*Commellina bengelensis*) among others. The fallow lands were surrounded by cultivated fields, which, during the wet season, were planted with maize, beans, cassava and sweet potatoes. After crop harvest, these fields were left with standing stubble and often slash and ox-plough were the main land preparation methods before the next wet/planting season started.

Cultivated fields were planted with maize intercropped with beans in the first year of the study (2016) but in the subsequent seasons, cassava was introduced as a way of crop rotation due to the parasitic witch weed (*Striga* sp.) in the area, which deprives the maize crop from water and other mineral nutrients. Other commonly encountered weeds in the cultivated fields included; Star grass (*Cynodon dactylon*), couch grass (*Digitaria scalarum*), black jack (*Bidens pilosa*), guinea grass, wondering jew (*Commellina bengelensis*) etc. Fragments of mixed crop gardens comprising of coffee, beans, bananas, sweet potato and cassava also surrounded these cultivated study fields.

2.2.3 Trapping procedure

Using Sherman live traps (H.B. Sherman Traps, Inc., Tallahassee, FL, USA) a Capture Mark Release trapping technique was applied following the procedure described in Aplin *et al*. (2003). For each trapping grid, 49 Sherman live traps were set in a 70 m x 70 m^2 configuration (seven trapping lines with seven trapping stations, 10m apart). Trapping was conducted monthly at 4-week intervals. A single Sherman trap baited with peanut butter mixed with maize flour was placed at each trapping station for three consecutive days. Traps were inspected every morning during the three days and captured animals were checked for sexual maturity status, weighed, toe clip coded and released at the points of capture. Both traps with and without animals were re-baited with fresh bait for the following day trapping. The study lasted for 2 and half years from January 2016 to May 2018. The nomenclature by Wilson and Reeder (2005) was used as the main reference to identify the rodent species captured in the study areas. The community structure in this study was described as relative composition based on the trappable rodent species in the study sites. The proportional species composition was presented as percentage based on the relative abundance of each species over the study period. The density of animals per/0.5 hectare was estimated for each three-day trapping session using the M(h) estimator of the programme CAPTURE for a closed population, which allows for individual variations in trapping probability (White *et al*., 1982) and is the most commonly used test in other studies thus allows better comparison with those studies.

2.2.4 Data processing and analysis

Data from the four grids were pooled and formed two data sets: Cultivated field and fallow land field to obtain total small rodent diversity per habitat. Species richness and abundance was calculated using the pooled data for cultivated fields and fallow land fields. All variables were tested for normality using Shapiro -Wilk test and the strongly skewed variables were transformed prior to analyses if necessary, to meet the assumption of normality and homogeneity of variances. Paleontological Statistics software (PAST) (Hammer *et al.*, 2002) was used to calculate diversity measures: species richness, Simpson Diversity Index, evenness and dominance. Species accumulation curves and rank abundance curves were obtained for the two field categories using R software Vegan package (R-software version 3.3.2). The monthly differences in small rodent richness and abundance between cultivated and fallow habitats were tested with Analysis of variance (ANOVA) in XLSTAT (Addinsoft, 2018). Where the ANOVA test indicated significant differences, posthoc Tukey (HSD) test was used. Richness was used as a measure of the number of species in the two field habitats. Species diversity estimations were made by the Simpson's Diversity Index to consider both the richness and evenness. The index was calculated using the formula:

$$D = 1 - \frac{\sum n(n-1)}{N(N-1)}$$

where:

D=Simpson Diversity (D')

n = number of individuals of each species and

N = total number of individuals of all species

A t-test was used to compare the Simpson's Diversity Indices between trapping grids. Species turnover was computed to determine the rate of species change in time and space; temporal turnover (β_T) in species richness between years was calculated for each site as the total number of species found within that site (over the two and half years) minus the mean number of species per year for that site (**α**). Spatial turnover (β_S) was calculated as the total number of species found within a habitat type (over the two and half years) minus the mean number of species per site for that habitat type (over the two and half years). The Bray-Curtis similarity index (Hammer *et al.,* 2002) was used to compare similarities among zones and to construct a species composition similarity dendrogram for the three zones. The Non-Metric Multidimensional Scaling ordination was used to plot species association with habitat type.

2.3 Results

2.3.1 Small mammal species composition

Out of the 17 052 trap nights made, 1 061 and 1 355 small mammal individuals were trapped in cultivated and fallow land fields respectively. These comprised of 11 small rodent species and one insectivorous small mammal species making a total of 12 small mammals (Table 2.1). *Mastomys natalensis* was the most abundant rodent species with 727 (68.5%) individuals in cultivated fields and 740 (54.6%) individuals in fallow land fields, while the least was *Gerbilisicus kempi*, *Gramommys dolichurus*, *Dasmys incomtus* and *Steatomys parvus*. The former four rodent species were very scarce as only one individual each was captured for the whole study period (Table 2.1). The results also showed that fallow fields were species richer (10 small rodent species) compared to cultivated fields (9 small rodent species) (Table 2.1).

Table 2.1: Inventory of small rodent species and an insectivorous mammal recovered in cultivated and fallow field habitats in Mayuge district, Eastern Uganda, during the study period 2016-2018

Species	Total number of individuals (% contribution) in Cultivated field	Total number of individuals (% contribution) in Fallow field	Overall number (% contribution)
Small rodent species			
1.*Mastomys natalensis*	727(68.5)	740(54.6)	1467(60.7)
2.*Mus triton*	210(19.8)	180(13.3)	390 (16.1)
3.*Aethomys hindei*	35(3.3)	128(9.4)	163(6.7)
4.*Lemniscomys zebra*	15(1.4)	102(7.5)	117(4.8)
5.*Lophuromys sikapusi*	6(0.6)	67(4.8)	73(3.3)
6.*Arvicanthis niloticus*	1	25	26
7.*Graphiurus murinus*	0	15	15
8.*Gerbilliscus kempi*	1	0	1
9.*Gramommys dolichurus*	0	1	1
10.*Steatomys parvus*	0	1	1
11.*Dasmys incomtus*	1	0	1
Insectivorous species			
1. *Crocidura* spp.	65(6.1)	80(5.9)	145(6.0)
Total captured	1061(100)	1352(100)	2413(100)
Total trap nights	8820	8232	17052
Species Richness	9	10	12
Simpson's Diversity Index	0.467	0.617	

The species accumulation curve plotted (Fig. 2.2A) showed a good sampling effort as it tended to level off after the 20th trapping session, with minimal encounters of new species after, but also indicates that a few more species can be trapped with more years of trapping. Additionally, separate curves for the habitats were plotted and fallow fields displayed a slightly higher accumulation curve compared to cultivated fields (Fig. 2.2B), implying a higher probability of encountering more species in fallow field habitat with sampling.

The overall maximum species estimated by Chao 2, Jacknife 1 and Bootstrap richness estimators in the study area for the two and half years of the study was 13 species.

Simpson species diversity index showed relatively higher diversity for fallow field (0.617) compared to cultivated field (0.467) but was not significantly different ($p > 0.05$). Species evenness was higher in fallow field (42.04%) compared to cultivated field (34.17%).

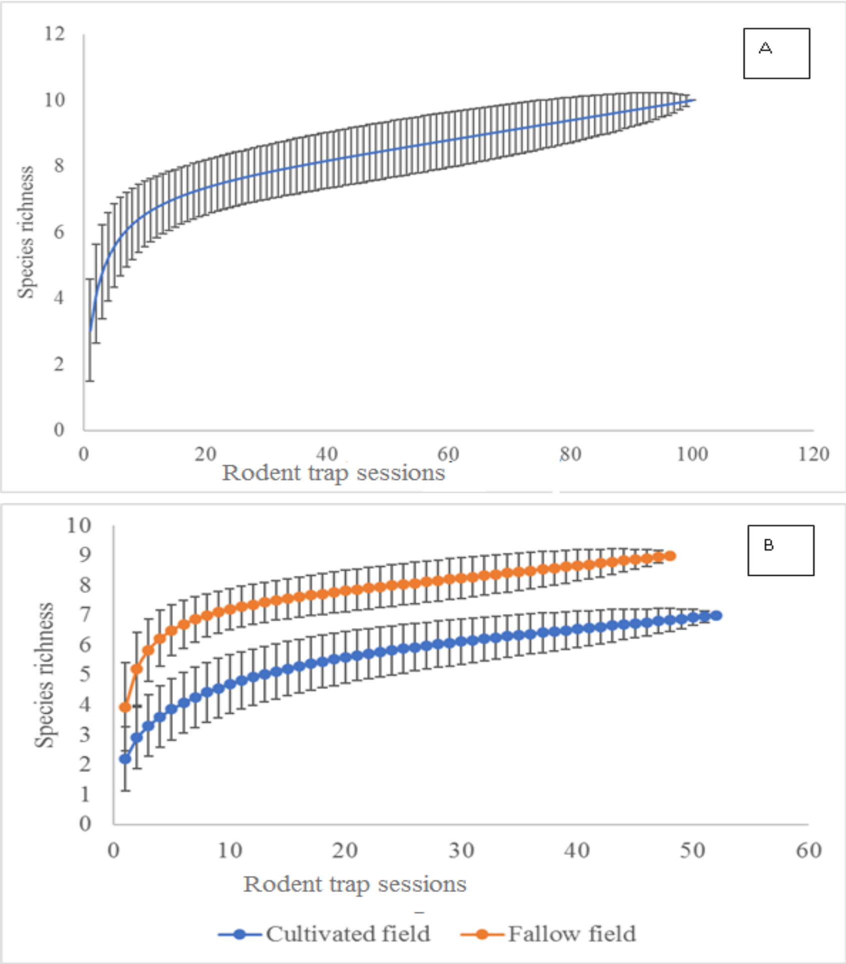


Figure 2.2: Species accumulation for all samples (A) and (B) for the separate studied fields (Fallow and cultivated fields with ±Standard deviation).

In terms of temporal variations in species richness and abundance, there was a significant ($F_{28,29}$ =2.819, p=0.004) interaction effect between months and years of the study for richness within fallow land habitat.

Significantly more species were observed in the first year of trapping (2016) in June, July and August and then November (Fig. 2.3). Lowest species recovery was noted to have occurred in the second year of trapping (2017), specifically in the month of May (Fig. 2.3). Within cultivated field habitat, there was also significant interaction effect between months and years of the study for species richness ($F_{28,29}$ =1.857, p=0.054). Significantly fewer species recovery was observed in the second year of trapping, in January, May and June which differed from the rest. Generally, there was almost consistence in the number of species recovered monthly over the study period (Fig. 2.3).

The interaction effect between years and months on total small rodent species abundance also showed a significant effect for fallow land ($F_{28,29}$ =2.334, p=0.001). Significantly higher abundances were obtained in the months of June (38±2/0.5ha), July (41±8/0.5ha), August (38±2/0.5ha) for 2016 and March (41±26/0.5ha) in 2018. In cultivated field habitats, the interaction effect of year and month of trapping on small rodent abundance was also significant ($F_{28, 29}$ = 2.612, p = 0.007).

Significantly higher abundance was recorded in the last year of trapping (2018) in the month of April (46±19/0.5ha) (Fig. 2.4). Generally, there a was synchrony in temporal changes in rodent abundance over the years in the studied field habitats, with higher abundance in the first year of trapping, then a decline in year two and a steady rise in the third year of trapping.

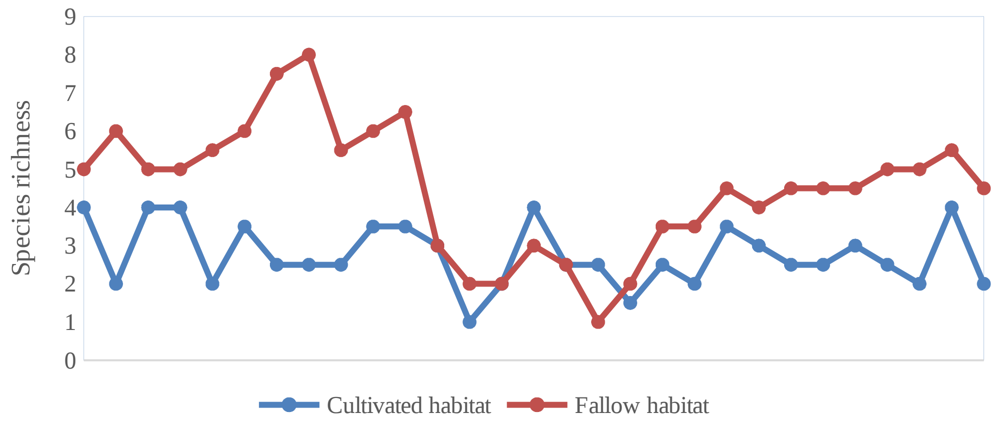


Figure 2.3: Mean (±SE) monthly species richness over the two and half years of the study period in fallow and cultivated fields in Mayuge district, Eastern Uganda.

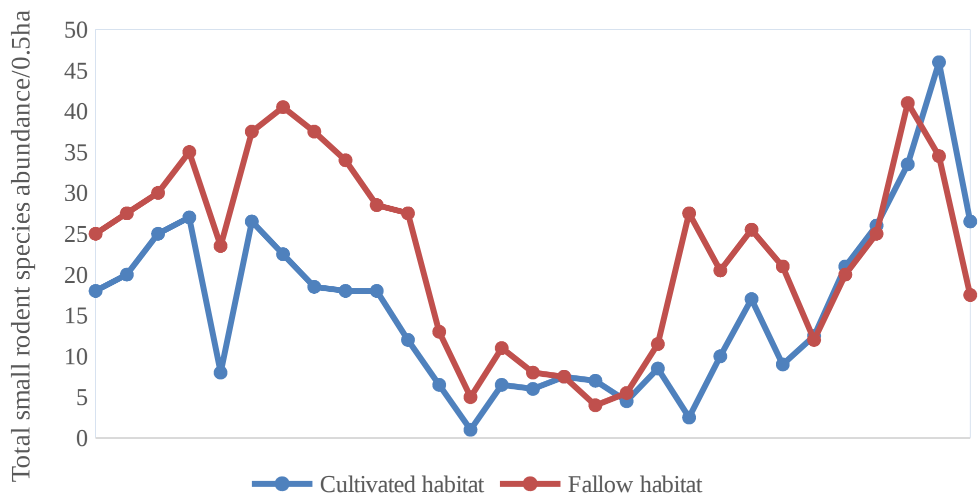


Figure 2.4: Mean (±SE) monthly small rodent abundance over the two and half years of the study period in fallow and cultivated field habitats in Mayuge district, Eastern Uganda.

In terms of species turnover, spatially there was a significant difference ($F_{1, 6} = 9$, $p = 0.024$) for the studied field habitats. Fallow field habitats showed significantly higher species turnover (6±1) species compared to cultivated field habitat (4±1).

Temporal species turn over (β_T) also showed a significant difference ($F_{5, 44}$ =18.819, p = 0.0001) over the three years of the study. The first year of trapping showed a higher species turn over followed by a decline in the second year of trapping and then a rise in the third year of trapping in both habitats (Fig. 2.5).

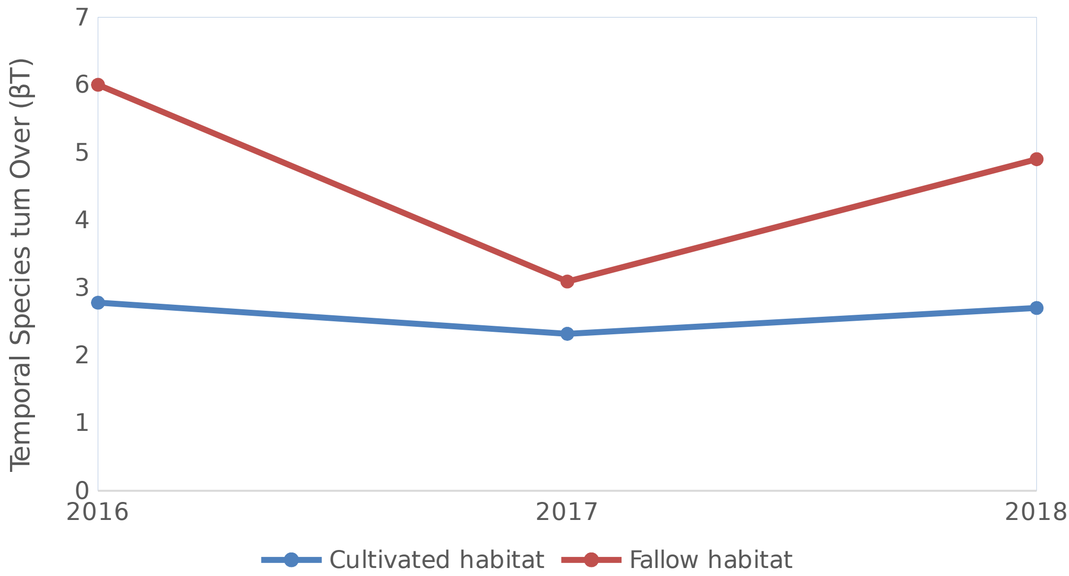


Figure 2.5: Mean (±SE) temporal Species Turn Over (β_T) for the different years of study in Mayuge district, Eastern Uganda.

2.3.2 Small rodent community structure across field trapping habitats

The trapping habitats were generally similar in composition with respect to rodent species. The Bray-Curtis similarity index generated three clusters; one for the cultivated fields, then separate clusters for fallow fields, with an overall cophenation correlation or cluster accuracy of 97.97% (Fig. 2.6).

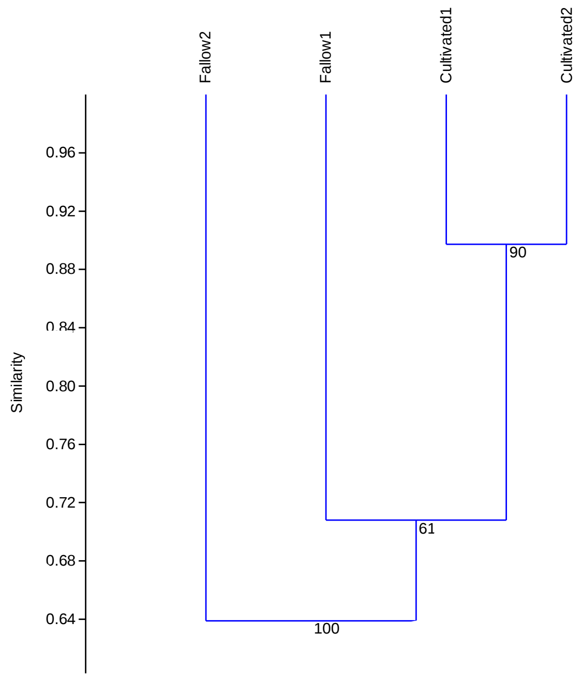


Figure 2.6: Bray-Curtis similarities in rodent composition among the trapping habitats and species communities in the study.

A non-metric multidimensional scaling analysis was conducted and ordination plots were generated with a correlation method. Rodent communities were very distinct between habitats. Some species associated only with certain communities such as *G. kempi* sp and *D. incomtus,* these only associated with cultivated habitats. The ordination plots also revealed that several of the recorded rodent species in the study associated more with fallow habitats. There was one rodent species, *M. natalensis* which exhibited unique characters as it plotted almost at zero implying it's a generalist species. It associated equally in both fallow land and cultivated field habitats (Fig. 2.7).

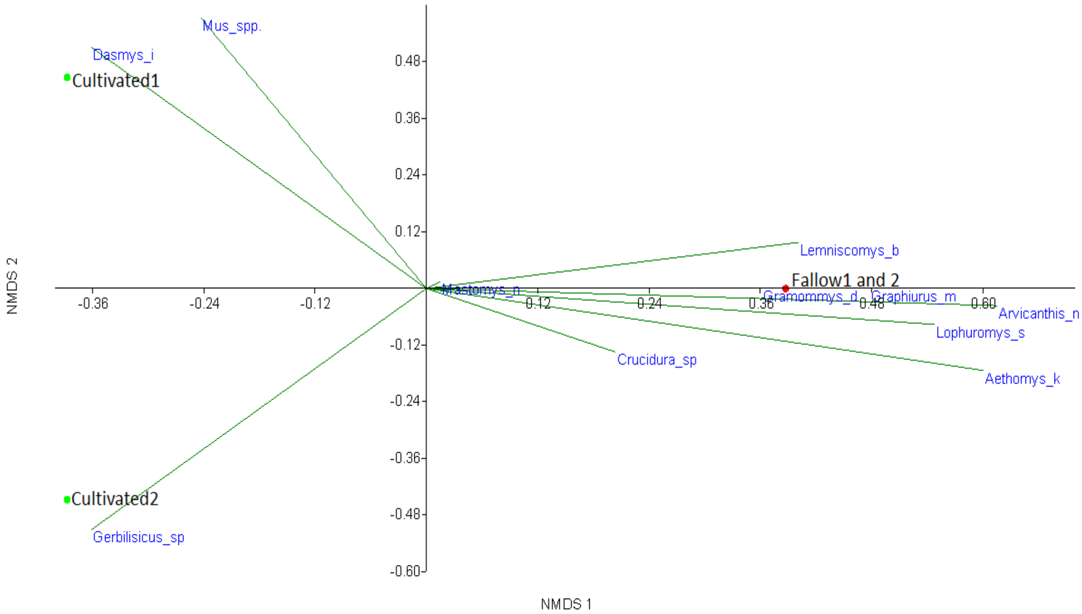


Figure **2.7**: Ordination plots for Non-Metric Dimensional Scaling (NMDS) in rodent community composition among trapping habitats

2.4 Discussion

2.4.1 Small rodent species composition

This study presents the first comprehensive inventory of small rodent species in agricultural environmental setting in Uganda. Eleven small rodent species and one insectivorous mammal were recorded from both fallow land and cultivated fields. Earlier studies in the country report up to maximum of 34 small mammal species (Eisen *et al*., 2013; Amatre *et al.*, 2009; Clausnitzer and Kityo, 2001; Basuta and Kasene, 1987; Delany, 1975). These, report much higher species richness compared to the current study and this was because they targeted all small mammals and their study environments (habitats) were different. For example, Eisen *et al*. (2013) concentrated around homesteads and within huts, where certain species almost permanently dwell such as the roof rat (*Rattus rattus*), but also migratory rodent species could be trapped in localities closer to homesteads as they search for food and escape from adverse weather conditions (Amatre *et al*., 2009). Particularly, some rodent species have been reported to be habitat specific e.g. *Proamys* spp are closed forest dwellers (Basuta and Kasene, 1987) and thus could not be trapped in this study. Elsewhere in the region where studies have been conducted with similar study designs involving fallow land and maize field habitats with the Capture Mark Recapture procedure, a range of between 4 to 11 species of small rodents have been reported (Mulungu *et al*., 2012; Makundi *et al*., 2009; Massawe *et al*., 2006; Mares and Ernest, 1995; August, 1984; Fleming, 1975). Secondly, while the study reports eleven small rodent species, four of them which included*; G. dolichurus, D. incomtus, G. kempi and S. parvus* were very rarely encountered with less than three individuals in the whole study period. The low numbers of the later could suggest possibly unsuitable habitats for these species' settlement, breeding and survival (Taylor, 2016; Delany, 1975; Missone, 1963). The study showed differences in species composition between fallow land and maize field habitats with higher diversity index value (0.617) for fallow land compared to cultivated fields (0.467). In Tanzania, Makundi *et al.* (2009) observed a similar result with a higher diversity index value in fallow land habitat compared to maize habitat. This phenomenon could be explained by land use patterns; where, human activities alter habitat characteristics, which may result in a positive or negative impact on rodent communities (Hoffman and Zeller, 2005). In this study, the authors attribute human activities including land preparation, weeding and harvesting, which normally take place in cultivated fields and are believed to have likely resulted into lower species richness in this habitat.

The study also showed dominance of *M. natalensis,* with over 60% contribution of the total trap catches in both habitats This particular species is reported by several authors in the East African region as an important member of the rodent community, occurring in various habitats both disturbed and undisturbed (Hubard, 1972; Leirs, 1995; Makundi *et al*., 1999; Massawe *et al*., 2005; Mulungu *et al*., 2003; Makundi *et al.,* 2010). The higher abundance of *M. natalensis* in cultivated fields compared to fallow land further affirm the theory that this species highly adapts to new environments and is a good colonizer of disturbed areas including cultivated agricultural fields (Leirs, 1992; Odhiambo, 2005; Massawe *et al.,* 2005; Makundi *et al.,* 2010).

Mus spp were second in abundance, which occurred equally in fallow land, and cultivated fields but more numbers in cultivated fields. This species is reported to be widely distributed across sub-Saharan Africa where it occurs in a variety of savannah and grassland habitats (Monadjem *et al*., 2015). *Mus triton* records in this study are in total agreement with earlier taxonomic records reported in the Kenya and Tanzania (Happold, 2013, Veyrunes *et al*., 2004, 2005; Monadjem *et al*., 2015) that it occurs across the East African countries. The relatively higher numbers of *M. triton* in cultivated fields suggest that they are also good colonizers of disturbed habitats. Earlier findings by Fuller and Perrin (2001) report related results as they recovered higher numbers of Mus spp in a disturbed habitat that was exposed to fire. Similarly, Demeke *et al.* (2007) in Ethiopia, described that Mus spp were more abundant in agricultural farmland than bush habitats. *Aethomys hendei* commonly known as bush rat, is a generalist herbivorous species, and often found in woodlands although it can be found inhabiting fields that have been under cultivation (Kingdon, 1974). In the current study, more trap catches for *A. hendeii* were recovered in fallow land as opposed to cultivation field. This is typically a bush rat, which dwells in bush thickets thus the higher abundances in fallow fields signifies habitat suitability for undisturbed habitats preferably forests (Happold, 2013, Kingdon, 1974). In the current study, *Lophuromys sikapusi* was captured at relatively low numbers. An earlier study which was conducted in a national forest in the country reported relatively higher numbers compared to this study (Basuta and Kasenene, 1987). The difference can be attributed to the habitat type as this species prefers cool mist environments (Happold, 2013; Kingdon, 1974). Its preference for cooler environments was further evidenced by more trap captures in fallow than cultivated fields, which fallow exhibited micro-climatic conditions (cooler undercover temperatures) that could have been enhanced by thickets of tick berry plants that were initially dominant in fallow fields. Similarly, in Tanzania, higher numbers of *Lophuromys* spp were trapped in forest habitats particularly when vegetation was dense and humid (Makundi *et al*., 2015).

Other species captured included; *A. niloticus* commonly known as African grass rat, *G. murinus* (arboreal species), *G. kempi* and *D. incomtus* (African Marsh rat) were recorded in relatively low numbers in the study and were mostly encountered in first year of trapping. These species were mostly captured in fallow land, a habitat which is closely related to natural forests, with relatively high weedy grasses, shrubs, trees and form relatively dense vegetation ground cover. Such a habitat is believed to have offered favourable conditions for settlement of the above species. The results are closely related to earlier findings; that reported higher numbers of *A. niloticus* during the rainy season when resources from grasses are rich with dense vegetation cover to provide shelter from predators (Massawe *et al.*, 2005 and Senzonta, 1982). *G. murinus* was captured in fallow land only and encountered in the first year of trapping with no captures in the following years. Observations made during the study showed that vegetation cover reduced drastically in the subsequent years' in the fallow fields due to disturbances in these fields by livestock grazing. Additionally, *G. murinus* low numbers could also be attributed to its arboreal nature as it nests on trees and routinely visits the ground thus chances of being trapped with the live Sherman traps are minimal.

2.4.2 Spatial patterns in species richness and diversity

Spatial variations in total small rodent species richness and diversity were observed, with fallow land displaying higher species richness and diversity. Similarly, spatial species turn over (β_S) was significantly higher in fallow land habitat. The results are not surprising, as it has already been reported that habitat characteristics/patterns play a significant role in the ecology of rodents (Delany, 1975). This study further showed that while cultivated fields are less species rich, they are still very prone to infestation by rodents of different species. Specifically, *M. natalensis*, one of the notorious rodent pest species exhibited higher rank abundance in cultivated field as opposed to fallow. This phenomenon confirms the importance of this species as an agricultural pest that calls for more attention as already reported (Makundi *et al*., 2005; Mulungu *et al*., 2003). Furthermore, Isabirye-Basuta and Kasenene (1987) reported that the abundance and distribution of the small mammals depend mainly upon the nature and density of vegetation, which in turn, influence food and shelter availability. The higher species abundances and richness in fallow fields in this study was linked to the characteristic nature of fallow land habitat which offered more vegetation for food as well as offering shelter for breeding and protection of the small rodents from possible predation as compared to cultivated fields.

Generally, habitat complexity may provide more niches that could be exploited by several species of rodents (Rosenzweig and Winakur, 1969). Niche partitioning (temporally, spatially and trophically) (Pianka, 1973) is an important factor in species co-existence in both stable and disturbed habitats. Human activities have also been reported to significantly influence the species richness and diversity at a small scale (Massawe *et al*., 2005). Additionally, Getachew and Afework (2015) recovered more individuals of small rodents in bushland habitat as compared to the other habitats. This was attributed to habitat's plant composition, which included *Pterolobium stellatum, Capparis tomentosa and Urtica simensis*, which are thorny and prevented movement of humans and livestock, thus offering a safe environment for small mammal breeding and survival. Additionally, wild animals respond to human disturbance in the same way they respond to predation, by avoiding highly disturbed areas or underutilizing them (Gill *et al.*, 1996; Beale and Monaghan, 2004), but the strength of this response is different for different species (Gill *et al.*, 2001). In this study species richness and abundance were high in fallow land habitat, which could possibly be due to the low levels of human activities /disturbance as compared to cultivated field.

2.4.3 Temporal patterns in total species richness and abundance

In the current study, temporal variations were an important factor that influenced the species richness and relative abundance of the species across the fields. The monthly year to year changes in small rodent species richness and abundance was also obvious, with higher richness and abundance in the first year of trapping compared to the proceeding years of trapping**.** There were significant variations in monthly rodent species richness and abundances over the two and half years of the study period with generally higher richness and abundance in the months of June, July and august in 2016 and March and April in 2018 trapping. These results are similar with earlier studies by Makundi *et al.* 2009) and Mulungu *et al.* (2003), when they recovered more species and higher trap catches in the first year of the study. The monthly changes in small rodent abundance reported here only affirm earlier theories that suggest that rodent populations are highly dynamic and are driven by several environmental factors, but more particularly by rainfall, which influences vegetation and human activities (Leirs, 1992). It was noted that vegetation cover and human activities changed with months and this is believed to have played a role in regulating rodent populations in both habitats. For example, due to constant human activities in cultivated fields, the rodent populations fluctuated more highly as opposed to fallow land where it was observed to have had minimal human interaction. Similar observations are reported by Addisu and Bekele (2013) who report that crop harvesting and grazing were perhaps the considerable factors for the reduction in rodent's abundance in maize fields during the dry season in their study in Ethiopia. Specifically, increased animal grazing has been widely shown to affect rodent species composition and abundance (Cao *et al.,* 2016; La Morgia *et al*., 2015; Yihune and Bekele, 2012). Additionally, habitat fragmentation and anthropogenic activity can make areas inviable for certain fauna, and can therefore alter their distribution (Markovchick-Nicholls *et al*., 2008).

Nevertheless, several publications report temporal rodent abundances in terms of months and years various explanations are given. For example, Mulungu *et al.* (2013) reported lower rodent abundances but with more female individuals breeding during the rainy season. Similarly, Massawe *et al.* (2012) reports breeding patterns of some rodent species in Central Tanzania to be seasonal and correlated well with rainfall patterns. Other studies on ecology of rodents in East Africa have associated population dynamics with the indirect influence of rainfall on reproduction patterns and habitat characteristics, including vegetation structure and cover (Delany, 1972; Taylor and Green, 1976; Leirs *et al*., 1989; Telford, 1989; Leirs, 1992; Makundi *et al*., 2005, 2006). Precipitation has been reported to result into increased primary vegetation production, which in turn leads to increased rodent abundance (Gage and Kosoy, 2005).

The temporal differences observed in the current study are likely attributed to several factors already reported on in earlier studies but were not quantitively analysed in this study, which include among others, vegetation ground cover, quality food supply and human activities which are all governed by rainfall. Already, existing theories show that human activity can have negative impacts on many wildlife species, leading to changes in distribution (moving away from human activity), abundance and activity patterns (Griffiths and Schaik, 1993). This type of scenario indeed was observed in fallow fields where species richness and abundance were high in the first year of the study but declined with time due to increased pressure as a result of human activities on this reserved piece of land. Human activities such as animal grazing have thus been observed to have an impact on rodent species distribution and abundance and can be used as a means of modifying environment as a rodent management technique in a localized setting (La Morgia *et al*., 2015).

Consequently, although there were no clear trends in the population dynamics from one year to another, a less similar pattern of increased rodent abundance in the second part of year from May through to November was noted throughout the two and half years of the study.

Synthesis and Applications: Long term studies that provide description of rodent species composition and community structure in agriculture settings contribute to state of the pest management reports, environmental risk assessments and offer options for harmonizing the benefits of rodents in the ecosystem and protection from pest damage. Currently, most descriptions focus on rodents as forest dwellers as indicators of habitat quality and, as vectors of human and livestock diseases (e.g Clausnitzer and Kityo, 2001; Eisen *et al*., 2013). On the contrary, this study focused on understanding rodents as pests in a crop farming system to establish the common species and how they are distributed between cultivated fields and fallow land in such an agricultural setting. Understanding rodent species composition of a given locality is particularly valuable; for conservation and management agencies because it avails a list of species present where management decision can be based to spare the beneficial species. Our approach identifies the most abundant species in cropped fields and relates with other studies in the region on potential impacts these species can have on crops in an agricultural system.

Authors' Contributions: Mayamba. A, Mulungu. L. S, Makundi. R. H and Massawe. Conceived the ideas and designed methodology. Mayamba A, Mulungu. L.S. and Isabirye. B analyzed the data and led the writing of the manuscript. All authors critically reviewed the drafts and gave final approval for publication.

2.5 Acknowledgments

We are extremely grateful to the Ecologically Based Management of Rodent Pests in Maize and Rice in East Africa to Sokoine University of agriculture project (Grant number OPP1112579) supported by Bill and Melinda Gates foundation for the financial support of this research. We are also greateful for the tireless efforts from Kisakye Alex, Ouma Namulochi and Ramadhani Kigunguli from Busitema University, Namasagali campus, Uganda and Pest Management Centre, Sokoine University of Agriculture, Morogoro, Tanzania respectively.

Funding

This work was supported by the Bill and Melinda Gates Foundation through Sokoine University of Agriculture (Project number OPP1112579) that funded Alex Mayamba's PhD studies, of which this paper was part.

Data accessibility statement

We the authors of this manuscript have collectively agreed to have the data used in the results section to publicly avail that information to a public domain Dryad once this paper has been accepted for publication under the journal of Ecology and Evolution. **DOI:** doi:10.5061/dryad.qv9471s

Yours sincerely,

Alex Mayamba, on behalf of the authorship team

2.6 References

Addisu, A. and Bekele, A. (2013). Habitat preferences, seasonal abundance and diets of rodents in Alage, Southern Ethiopia. *African Journal of Ecology* 52: 284–291.

Amatre, G., Babi, N., Russell, E., Ogen-Odoi, A., Atiku, L.A., Akol, A., Gage, K.L. and Eisen, R.J. (2009). Flea Diversity and Infestation Prevalence on Rodents in a Plague-Endemic Region of Uganda. *Journal of Tropical Medicine Hygene* 81(4): 718 – 724.

Aplin, K. P., Brown, P. R., Jacob, J., Krebs, C. J. and Singleton, G. R. (2003). *Field Methods for Rodent Studies in Asia and the Indo-Pacific.* (CSIRO: Canberra). pp. 78.

Basuta, G. and Kasene, J.M. (1987). Small rodent populations in selectively felled and mature tracks of Kibale forest, Uganda. *Biotropica* 19(3): 260 - 266.

Beale, C. M. and Monaghan, P. (2004). Human disturbance: people as predation-free predators? *Journal of Applied Ecology* 41: 335–343.

Borchert, J.N., Enscore, R.E., Eisen, R.J., Atiku, L.A., Owor, N., Acayo, S., Babi, N., Montenieri, J.A. and Gage, K.L. (2010). Evaluation of rodent bait containing imidacloprid for the control of fleas on commensal rodents in a plague-endemic region of northwest Uganda. *Journal of Medical Entomology* 47: 842 – 850.

Cao, C., Shuai, L.Y., Xin, X.P., Lui, Z.T., Song, Y.L. and Zeng, Z.G. (2016). Effects of cattle grazing on small mammal communities in the Hulunber meadow steppe. *Peer Journal* 4: 23 – 49.

Clausnitzer, V. and Kityo, R. (2001). Altitudinal distribution of rodents (Muridae and Gliridae) on Mt Elgon, Uganda, *Tropical Zoology* 14: 95 – 118.

Clausnitzer, V., Church, S. and Hutterer, R. (2003). Habitat occurrence and feeding ecology of *Crocidura montis* and *Lophuromys flavopunctatus* on Mt. Elgon, Uganda. *African Journal of Ecology* 41: 1- 8.

Delany, M.J. (1972). The ecology of small rodents in tropical Africa. *Mammal Rev*iew 2: 1- 42.

Delany, M.J. (1975). *The Rodents of Uganda.* Kettering Northamptonshire: The George Press. 98pp.

Demeke, D., Afework, B. and Gurja, B. (2007). Feeding ecology of pest rodents from Arbaminch forest and farmlands, Ethiopia. *Ethiop. Journal of Sciences* 30: 127 - 134.

Eisen, R. J., Enscore, R.E., Atiku, L.A., Zielinski-Gutierrez, E., Mpanga, J.T., Kajik, E., Andama, V., Mungujakisa, C., Tibo, E., MacMillan, K., Borchert, J.N. and Gage, K.L. (2013). Evidence that rodent control strategies ought to be improved to enhance food security and reduce the risk of rodent-borne illnesses within subsistence farming villages in the plague-endemic West Nile region, Uganda. *International Journal of Pest Management* 59(4): 259 - 270.

Eisen, R.J., Griffith, K.S., Borchert, J.N., MacMillan, K., Apangu, T., Owor, N., Acayo, S., Acidri, R., Zielinski-Gutierrez, E., Winters, A.M. (2010). Assessing human risk of exposure to plague bacteria in northwestern Uganda based on remotely sensed predictors. *American journal of Tropical Medical Hygene* 82: 904 – 911.

Fiedler, L.A. (1988). *Rodent problems in Africa*. *Rodent Pest Management* (ed. I. Prakash), CRC, Boca Raton, FL. pp. 35 - 65.

Fuller, J.A. and Perrin, M.R. (2001). Habitat assessment of small mammals in the Umvoti Vlei Conservancy, KwaZulu-Natal, South Africa. *South African Journal of Wildlife Research* 31: 1 - 12.

Gage, K.L. and Kosoy, M.Y. (2005). Natural history of plague: perspectives from more than a century of research. *Annual Review Entomol*ogy 50: 505 - 528.

Geddes, A.W.M. (1992). *The relative importance of pre-harvest crop pests in Indonesia*. Chatham, UK: Bulletin of the Natural Resources Institute. 70 pp.

Getachew, B. and Afework, B. (2015). Diversity and habitat association of small mammals in Aridtsy forest, Awi Zone, Ethiopia. *Zoological Research* 36(2): 88 - 94.

Gill, J. A., Norris, K. and Sutherland, W. J. (2001). Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation* 97: 265 – 226.

Gill, J. A., Sutherland, W. J. and Watkinson, A. R. (1996). A method to quantify the effects of human disturbance on animal populations. *Journal of Applied Ecology* 33: 786–792.

Griffiths, M. and Van Schaik, C.P. (1993). The impact of human traffic on the abundance and activity periods of sumatran rain forest wildlife. *Conserv Biology* 7(3): 623–626.

Happold, D.C.D. (ed.) (2013). *Mammals of Africa. Volume III: Rodents, Hares and Rabbits*. Bloomsbury Publishing, London. 784pp.

Hoare, J.M. and Hare, K.M. (2006). 'The impact of brodifacoum on non-target wildlife: gaps in knowledge', *New Zealand Journal of Ecology* 30: 157 – 67.

Kingdon, J. (1974). *East Africa mammals: an atlas of evolution in Africa.* Volume II Part B (Hares and Rodents). Academic Press, London. pp. 704.

La Morgia, V., Balbo, C., Memoli, S. and Isaia, M. (2015). Rodents in grassland habitats: does livestock grazing matter? A comparison of two Alpine sites with different grazing histories, *in* Daugeron C., Deharveng L., Isaia M., Villemant C. and Judson M. (eds), Mercantour/Alpi Marittime All Taxa Biodiversity Inventory. *Zoosystema* 37 (4): 571- 580.

Leirs, H. (1992). *Population ecology of Mastomys natalensis (Smith, 1834) multimammate rats: possible implications for rodent control in Africa*. PhD Thesis, University of Antwerp, Belgium. 198pp.

Leirs, H. (1995). Population Ecology of *Mastomys natalensis* (Smith, 1834). Possible Implication for Rodent Control in Africa. Agricultural Edition No. 35. Belgium Administration for Development Cooperation, Brussels. 87pp.

Leirs, H. (2003). Management of rodents in crops: The Pied Piper and his orchestra. In: Singleton GR, Hinds LA, Krebs CJ and Spratt DM (Eds). Rats, mice and people: rodent biology and management. Canberra, Australia: ACIAR. pp. 183 – 90.

Leirs, H., Singleton, G. and Hinds, L. (1999). *Ecologically-based rodent management in developing countries: where to now? Ecologically-Based Management of Rodent Pests* (eds G. Singleton, L. Hinds, H. Leirs and Z.B. Zhang), ACIAR, Canberra, Australia. pp. 477 – 484.

Leirs, H., Verhagen, R., Verheyen, W., Mwanjabe, P. and Mbise, T. (1996). Forecasting rodent outbreaks in Africa: an ecological basis for Mastomys control in Tanzania. *Journal of Applied Ecology* 33: 937 – 943.

Leirs, H., Verheyen, W., Michiels, M., Verhagen, R. and Stuyck, J. (1989). The relationship between rainfall and breeding season of *Mastomys natalensis* (Smith 1834) in Morogoro, Tanzania. *Annales de la Socie´te´ Royale Zoologique de Belgique* 119: 59–64.

Magurran, A.E. (1988). *Ecological Diversity and its Measurement.* Cambridge University Press, Cambridge, 179pp.

Makundi, R.H., Massawe, A.W. and Mulungu, L.S. (2005). Rodent population fluctuations in three ecologically distinct locations in north-east, central and south-west Tanzania. *Belgium Journal of Zoology* 13: 159–165.

Makundi, R.H., Massawe, A.W. and Mulungu, L.S. (2006). Breeding seasonality and population dynamics of three rodent species in the Magamba Forest Reserve in the Western Usambara Mountains, north-east Tanzania. *African Journal of Ecology* 44: 1 – 6.

Makundi, R.H., Massawe, A.W., Borremans, B., Laudisoit, A. and Katakweba, A. (2015). We are connected: flea–host association networks in the plague outbreak focus in the Rift Valley, northern Tanzania. *Wildlife Research* 42(2): 196.

Makundi, R.H., Massawe, A.W., Mulungu, L.S. and Katakweba, A. (2009). Species diversity and population dynamics of rodents in a farm-fallow field mosaic system in Central Tanzania. *African Journal of Ecology* 48: 313–320.

Makundi, R.H., Oguge, N.O. and Mwanjabe, P.S. (1999). *Rodent Pest Management in East Africa – an ecological approach. In: Ecologically-Based Rodent Management* (Eds G. R. Singleton, L. Hinds, H. Leirs and Z. Zhang), pp. 460–476. For International Agri- cultural Research, Canberra, Australia. 97pp.

Markovchick-Nicholls, L., Helen, M. R., Deutschman, D.H., Widyanata, A., Martin B., Noreke, L. and Hunt, T. A. (2008). Relationships between Human Disturbance and Wildlife Land Use in Urban Habitat Fragments. *Conservation Biology* 22(1): 99 –109.

Massawe, A.W., Rwamugira, W., Leirs, H., Makundi, R.H. and Mulungu, L.S. (2005). Influence of land preparation methods and vegetation cover on population abundance of *Mastomys natalensis* in Morogoro, Tanzania. *Belgian Journal of Zoology* 135: 187–90.

Massawe, A.W., Rwamugira, W., Leir, H., Makundi, R.H. and 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.

Monadjem, A., Taylor, P. J., Denys, C. and Cotterill, F.P (2015). *Rodents of Sub-Saharan Africa*: A Biogeographic and Taxonomic Synthesis. *De Gruyter*, Berlin, Germany. 117pp.

Moore, S.M., Monaghan, A., Borchert, J.N., Mpanga, J.T., Atiku, L.A., Boegler, K.A., Montenieri, J., MacMillan, K., Gage, K.L. and Eisen, R.J (2015). Seasonal fluctuations of small mammal and flea communities in a Ugandan plague focus: evidence to implicate *Arvicanthis niloticus* and *Crocidura* spp. as key hosts in Yersinia pestis transmission. *Parasites and Vectors* 8: 11.

Mulungu, L.S. (2017). *Control of rodent pests in maize cultivation: the case of Africa*. Burleigh Dodds Science Publishing Limited 82 High Street Sawston Cambridge UK. pp. 317 - 337.

Mulungu, L.S., Makundi, R.H., Leirs, H., Massawe, A.W., Vibe-Petersen, S. and Stenseth, N.C. (2003). The rodent-density-damage function in maize fields at an early growth stage. In ‘Rats, Mice and People: Rodent Biology and Management’. (Eds G. R. Singleton, L. A. Hinds, C. J. Krebs and D. M. Spratt.) pp. 301 – 303.

Mulungu, L.S., Makundi, R.H., Massawe, A.W., Machangu, R.S. and Mbije, N.E. (2008). Diversity and distribution of rodent and shrew species associated with variations in altitude on Mount Kilimnjaro, Tanzania. *Mammalian* 72: 178 –185.

Mulungu, L.S., Ngowo, V.B., Mdangi, M., Katakweba, A.S., Tesha, P., Furaha, G. and Kilonzoa, B.S. (2013). Population dynamics and breeding patterns of Multi-mammate mouse, *Mastomys natalensis* (Smith 1834) in irrigated rice field in Eastern Tanzania. *Pest Management Science* 69(3): 371 - 377.

Mwanjabe, P. S. (1990). Outbreak of *Mastomys natalensis* in Tanzania. *African Small Mammal Newsletter* 11: 1 - 6.

Mwanjabe, P.S. and Leirs, H. (1997). An early warning system for IPM-Based rodent control in smallholder farming systems in Tanzania. *Belgian Journal of Zoology* 127: 49 - 58.

Nabbumba, R. and Bahiigwa, G. (2003). Agricultural productivity constraints in Uganda; implications for investment. Research series No: 31. 42pp.

Parsons, M.H., Banks, P. B., Deutsch, M.A., Robert, F. C. and Munshi-South, J. (2017). Trends in urban rat ecology: a framework to define the prevailing knowledge gaps and on incentives for academia, pest management professionals (PMPs) and public health agencies to participate. *Journal of urban Ecology* 3: 1 - 8.

Senzota, R.B.M. (1982). The habitat and food habits of the grass rats (*Arvicanthis niloticus*) in the Serengeti National Park, Tanzania. *African Journal of Ecology* 20: 241 - 252.

Shellemiah, K. and Rubaihayo, P. (2013). Progress in On-Farm Production and Productivity in the East African Community: 50 Years after Independence. *Kilimo Trust Technical paper* N0. 8, International Symposium on Agriculture; EAC partner states at 50 years, 5-7 November 2013.

Simberloff, D. (2014). ‘Biological Invasions: Much Progress Plus Several Controversies’, *Contributions to Science* 9: 7–16.

Singleton, G.R., Belmain, S.R., Brown, P.R. and Hardy, B. (2010). *Rodent outbreaks: ecology and impacts. Los Banos (Philipines)*; *International Rice Research Institute*. 289pp.

Singleton, G.R., Hinds, L.A., Leirs, H. and Zhang, Z. (1999). *Ecologically-based rodent management.* Canberra, Australia ACIAR. 78pp.

Stenseth, N. C., Leirs, H., Skonhoft, A., Davis, S. A., Pech, R. P., Andreassen, H. P. and Wan, X. (2003). Mice, rats and people: the bio-economics of agricultural rodent pests. *Frontiers in Ecology and the Environment* 1(7): 367–375.

Taylor, K.D. and Green, M.G. (1976). The influence of rainfall on diet and reproduction in four African rodent species. *Belgian Journal of Zoology* 180: 367–389.

Telford, S.R.J.R. (1989). Population biology of the multimammate rat, (*Mastomys natalensis*) at Morogoro, Tanzania 1981–1985. Bull. Flor. *State Museum Biology Series* 34(6): 249–287.

Veyrunes, F., Britton-Davidian, J., Robinson, T.J., Calvet, E., Denys, C. and Chevret, P. (2005). Molecular phylogeny of the African pygmy mice, subgenus Nannomys (Rodentia, Murinae, Mus): implications for chromosomal evolution. *Molecular Phylogenetics and Evolution* 36: 358–369.

Veyrunes, F., Catalan, J., Sicard, B., Robinson, T.J., Duplantier, J.M., Granjon, L., Dobigny, G. and Britton-Davidian, J. (2004). Autosome and sex chromosome diversity among the African pygmy mice, subgenus Nannomys (*Murinae; Mus*). *Chromosome Research* 12: 369 – 382.

Waddington, S.R., Li, X., Dixon, J., Hyman, G. and de Vicente, M.C. (2010). Getting the focus right: production constraints for six major food crops in Asian and African farming systems. *Food and Security* 2(1): 27 - 48.

White, G.C., Anderson, D.R., Burnham, K.P. and Otis, D.C. (1982). *Capture-Recapture and Removal Methods for Sampling Closed Populations Los Alamos National Laboratory*. Los Alamos, New Mexico, USA. 112pp.

Wilcoxon, F. (1945). *Individual comparisons by ranking methods*. *Biometrics* 1: 80 – 83.

Wilson, D.E. and Reeder, D.M. (2005). *Mammal Species of the World: A Taxonomic and Geographic Reference*. JHU Press, Baltimore, MD, USA. 214 pp..

XLSTAT (2017). *Data Analysis and Statistical Solution for Microsoft Excel*. Addinsoft, Paris, France (2017). [http://www.addinsoft.com]. Site visited on 3/2/2020.

Yihune, M. and Bekele, A. (2012). Diversity, distribution and abundance of rodent community in the Afro-alpine habitats of the Simien mountains national park, Ethiopia. *International Journal of Zoological Research* 8(4): 137 - 149.

CHAPTER THREE

PAPER II

POPULATION AND BREEDING PATTERNS OF THE PESTIFEROUS RODENT: MASTOMYS NATALENSIS IN A MAIZE DOMINATED AGROECOSYSTEM IN LAKE VICTORIA CRESCENT ZONE, EASTERN UGANDA

Mayamba Alex[1*]; Robert Modest Byamungu[2]; Herwig Leirs[3]; Isabirye Moses[1]; Rhodes. H. Makundi[3]; Didas. N. Kimaro[4]; Apia. W. Massawe[3]; David Kifumba[1], Alice Nakiyemba[1]; Mshaka. E. Mdangi[6]; Brian. E Isabirye[7] and Loth. S. Mulungu[3]

[1]Faculty of Natural Resources and Environment, Busitema University, P. o. Box 236, Tororo, Uganda, [2]Department of Wildlife Management, Sokoine University of Agriculture, P. o. Box 3073, Morogoro, Tanzania, [3]Evolutionary Ecology Group, Universiteit Antwerpen, Groenenborgerlaan 171, B-2020 Antwerpen, Belgium, [4]Pest Management Centre, Sokoine University of Agriculture, P. o. Box 3110, Morogoro, Tanzania, [5]Department of Engineering Sciences and Technology, Sokoine University of Agriculture, P.o. Box 3003, Morogoro, Tanzania, [6]Ministry of Agriculture Training Institute (MATI) llonga, P. o. B0x 66, Kilosa, Tanzania, [7]International Center of Insect Physiology and Ecology (ICIPE), Kasarani, Nairobi, Kenya.

Email: alexmayamba@gmail.com

Accepted: Journal of African Zoology

Manuscript ID: TAFZ-2019-0135

Abstract

Multimammate mice (*Mastomys natalensis*) persist as a key rodent pest species to cereal crops production in Sub-Saharan Africa. To develop effective management plans knowledge on the population changes and breeding patterns of this species in agro ecosystems is required. This study thus aimed at generating information on the population fluctuations and breeding patterns of *M. natalensis* in a maize dominated agro ecosystem in a Lake Victoria crescents zone in Uganda. A Capture Mark Recapture study was established in cultivated and fallow field habitats in Mayuge district, Eastern Uganda. The area is characterized by a bimodal rainfall pattern (Wet 1 and Wet 2). In each habitat, two plots of 70 m by 70 meters were set with 49 permanent trapping points spaced in parallel lines at 10m x 10m spacing for monthly rodent live-trapping. Trapping was conducted for three consecutive nights on a monthly basis, with three days daily inspection of the traps, and the study lasted two and a half years. The Generalized Linear Mixed Model analysis showed higher model estimates for population density in fallow compared to cultivated fields. Also, there were higher model estimates for population density in wet season 2 and lowest in dry season 1. The percentage reproductively active breeding females were present throughout the year but with significantly higher model estimations in Dry season 2. In conclusion, the high population density in wet 2 was observed to have resulted from the relatively higher percentage of actively breeding females from Dry season 2. The study results have important application on the timing of control efforts and recommends that control should be initiated during the wet season 1 through dry season 2 to counteract potential damaging population build up in later seasons.

Keywords: Generalized Linear Mixed Model, Seasons, sexual activity, habitat type, population density, multimammate

3.1 Introduction

Rodents (Muridae) are increasingly becoming serious agricultural pests due to the increasing conversion of wild areas into intensive agricultural and settlement land (Makundi *et al*., 2007; Swanepoel *et al.*, 2017; Mylashimbi *et al*., 2018). This is a result of the human population growth which demands more space for settlement and production of food. In Uganda, several small rodent species including *Mus triton, Aethomys hindei, Lemniscomys zebra, Lophuromys sikapusi*, *Graphiurus murinus e.t.c.* are documented in and around crop fields and forests (Basuta and Kasene, 1987, Amatre *et al.*, 2009) with *Mastomys natalensis* (Smith 1834), being the most dominant species associated within agricultural areas (Mayamba *et al.*, 2019). Elsewhere in the region, this species has been observed to dominate agricultural fields and has received considerable research attention (Leirs 1994; Mulungu *et al*., 2013; Makundi *et al*., 2015) due to its economic importance. It is described as one of the key rodent pest species of significant agricultural importance and also a vector of endemic diseases such as plague (Bonwitt *et al*., 2017; Mulungu, 2017; Olayemi *et al.*, 2018). It is characterized by high reproductive rates, high movement patterns and ability to easily colonize new areas (Leirs, 1994; Makundi *et al.*, 2006; Massawe *et al.*, 2006). Further, *M. natalensis* is reported to have a wide distribution; found inhabiting different kinds of habitats (Mulungu *et al*., 2011a) including savannahs, woodland, secondary growth, forest clearings, houses and cultivated fields (Kingdon, 1974). The broad habitat tolerance makes it a pioneer species in the colonization of disturbed (e.g. by agriculture) habitats (Massawe *et al.*, 2003). Consequently, in many localities of the Sub-Saharan Africa, normal rodent population cycles are known to result into substantial crop damage (Fidler *et al.*, 1988), with occasional outbreaks of large numbers resulting into significant crop damage and harvest losses leading to food insecurity (Leirs, 1994; Leirs *et al.*, 1996; Mwanjabe and Leirs, 1997; Mulungu *et al*., 2003). The amount and duration of rainfall have been linked to rodent population cycle, which is believed to be a result of the emerging abundant primary productivity of nutritious seeds and vegetation cover, which support large numbers of rodents (Delany, 1974; Leirs, 1994).

Unfortunately, limited information exists on basic ecology of the above mentioned species in Uganda and thus management efforts cannot be appropriately employed (Mayamba *et al.*, 2019; Makundi *et al.*, 2007). While considerable information exists on the ecology of *M. natalensis* in neigbouring Tanzania, several ecological factors may differ between these two countries including; the farming systems and weather patterns, attributes that have been shown to significantly influence the population and breeding patterns of this important pest species (Massawe *et al*., 2006; Mulungu *et al*., 2015). It is expected that Knowledge on the above enhances development of an effective ecologically sound rodent management strategy (Singleton *et al*., 2008). Understanding the relationship between rainfall seasons and habitats with rodent population abundance and breeding cycles in an agroecosystem will aid selection and timing of appropriate management strategies for effective rodent control in a given locality (Mulungu *et al.*, 2013). This study therefore set out to generate information on how *M. natalensis* population density and breeding patterns fluctuate over the year with rainfall seasons and across maize/fallow habitats in a typical tropical bimodal rainfall characteristic environment in an agroecosystem.

3.2 Materials and Methods

3.2.1 Description of study area

This study was conducted at Kigulu village (06°16′S, 37° 31′E) in Kigandalo subcounty, Mayuge district, Eastern Uganda (Fig. 2.1). The area has a bimodal rainfall pattern in which rains are received from March to end of May (Wet-1) and then August to end of

November (Wet-2). Farmers in the study area produce maize and other annual crops twice per year. The first cropping calendar season is from March to June and the second is from September to December. Land preparation is done in the dry months of January/February for first season planting and then July/August for second season planting. The maize crop reaches physiological maturity in May and November and farmers harvest in June/July and December/January for cropping season one and two, respectively. The vegetative stage is in April and October for season one and two, respectively.

3.2.2 Rodent field trapping procedure

A Capture–Mark–Recapture study was carried out from January 2016 to May 2018. Four 70 × 70 m^2 permanent trapping plots (two cultivated fields initially with maize crop and two fallow fields) were purposively identified (on the basis of availability and acceptability of the land owner to offer the land in that particular area) and agreements made with the land owners. Fallow fields were grids that were previously under annual crops production but the farmer had rested these grids (for more than two years without a crop. Both cultivated fields and fallow fields were characterized by a diversity of vegetation plant species (Table 3.1**)**. The four trapping areas (two replicates of each kind of field) were separated by a minimum distance of 500m, to limit rodent movements from one grid to another (Borremans *et al.,* 2014). Due to witch weed (*Striga* sp) invasion in the area, farmers practice crop rotation and thus in the second year of the study cassava was introduced in the cultivated fields, but always intercropped with common beans/soya beans. Each field consisted of seven parallel lines, 10 m apart, and seven trapping stations per line, also 10 m apart (making a total of 49 trapping stations per field). One Sherman LFA live trap (8×9×23 cm; H.B. Sherman Traps Inc., Tallahassee, FL) was placed at each trapping station and all were set for three consecutive nights per month at intervals of 4 weeks. These Live traps were baited with peanut butter mixed with maize bran/maize flour and were placed in the afternoon and inspected in the morning.

Table 3.1: Common weed species encountered in the study area

Common name	Scientific name	Family name	Distribution
Fallow land			
Tick berry	*Lantana camara*	Verbenaceae	Most abundant and patchy
Star grass	*Cynodon dactylon*	Gramineae	Abundant and scattered
Sodom apple	*Solanum incanum*	Solanaceae	scattered
Black jack	*Bidens pilosa*	Compositae	scattered
Guinea grass	*Panicum maximum*	Gramineae	scattered
Couch grass	*Digitaria scalarum*	Gramineae	scattered
Spear grass	*Imperata cylindrica*	Gramineae	Rare and patchy
Maize field			
Black jack	*Bidens pilosa*	Compositae	Most abundant
Oxalis	*Oxalis latifolia*	Oxalidaceae	abundant
Goat weed	*Ageratum conynzoides*	Compositae	abundant
Tridax	*Tridax procumbens*	Asteraceae	scattered
Star grass	*Cynodon dactylon*	Gramineae	scattered
Couch grass	*Digitaria scalarum*	Gramineae	scattered
Wild finger millet	*Eliusine indica*	Gramineae	Abundant and patchy
Witch weed	*Striga* sp	Orobanchaceae	scattered

3.2.3 Examination of captured animals

All the captured animals were field examined and identified to species level. On the first day of capture, all the captured animals were individually marked by toe clipping and wounds sterilized with alcohol. Their body weight, trapping station, sex and reproductive status were recorded. The sex and reproductive conditions considered included both males and females (either a perforated or closed vagina, nipples swollen on account of lactation or when pregnant in females and scrotal or non-scrotal testes in males). The animals were then released at the same point of capture. In the subsequent trappings, newly trapped animals were toe clipped while the already toe clipped animals (old animals) were examined for weight and reproductive status.

3.2.4 Data analysis

3.2.4.1 Population size

The data were recorded and entered into a CMR data input program for analysis. Population size was estimated for each 3 - day trapping session using the *M*(*h*) estimator of the program CAPTURE for a closed population, which allows for individual heterogeneity in trapping probability for the most abundant species (White *et al*., 1982). Overall population density was subjected to One Way Anova to test for overall effect of habitat on population density. Data were log 10 transformed before they were subjected to Anova as they were not normally distributed.

3.2.4.2 Population dynamics

A Generalized Linear Mixed Model with the Penalized Quasi Likelihood (PQL) method, package 'glmmPQL' (Karim and Zeger, 1992, Knudson, 2018) was run using base R (R-Core-Team, 2013), in order to assess changes in *M. natalensis* population density across habitat and season. We applied a. Poisson distribution family to density, with rainfall seasons (Dry 1, Dry 2, Wet1 and Wet 2) and habitats (cultivated and fallow) as the fixed effects factors, while years and months were considered as random effects. Additional box plots with mean, medians 25th and 75th quantile and standard error bars were plotted to indicate the mean value differences for the fixed factors.

3.2.4.3 Sex ratio

Numbers of trapped animals were sexed (male and female). The ratio was computed as percentage of males out of the total trapped animals. The following formula was used:

$$of\, males = \left(\frac{Number\ of\ male\ animals}{Total\, number\ of\ trapped\ animals} \right) \times 100$$

The percentage data were subjected to arcsine transformation to normalize their distribution before they were subjected to repeated measures ANOVA.

3.2.4.4 Sexual activity

Breeding patterns were determined by establishing the proportion of reproductively active and non-active individuals of both male and female mice in both habitats and month. The definition of sexual activity followed that of Leirs (1995) who defined sexual activity as a physiological condition and not as a typical behavior. Thus, females were considered to be sexually active when the vagina was perforated, when their nipples were swollen on account of lactation or when they were pregnant. Males were considered sexually active when the scrotum was visible and enlarged. For purposes of data analysis only females were used. Similarly, a Generalized Linear Mixed Model with the PQLmethod, package 'glmmPQL' was run to assess changes in *M. natalensis* percentage of sexually active female animals across habitat and season. We applied a. Poisson distribution family to percentage active females, with and habitats (cultivated and fallow) and rainfall seasons (Dry 1, Dry 2, Wet1, Wet 2) as the fixed effects factors, while years and months where considered as random effects. Additional box plots with mean, medians 25^{th} and 75the quantile and standard error bars were plotted to indicate the mean value differences for the fixed factors.

3.2.4.5 Recruitment

Recruitment data was taken as count data on number of newly trapped animals in the Capture Mark Recapture trappable population per trapping session. This was then computed as a percentage per trapping session following the formula below;

$$recruitment = \left(\frac{Number\ of\ new\ inividual\ animals \in a\ trappable\ population}{Total\ number\ of\ trapped\ animals} \right) \times 100$$

Here still we applied a Generalized Linear Mixed Model with the Penalized Quasi Likelihood (PQL) method, package ‘glmmPQL’ in order to assess changes in *M. natalensis* percentage recruitment across habitat and season with a. Poisson distribution family. The response variable was the percentage recruitments while habitats (cultivated and fallow) and rainfall seasons (Dry 1, Dry 2, Wet1, Wet 2) as the fixed effects factors. Years and months where considered as random effects. Box plots with mean, medians 25th and 75th quantile and standard error bars were also plotted to indicate the mean value differences for the fixed factors where there were significant differences.

3.3 Results

3.3.1 Population size

A total of 14 112 trap nights were undertaken with an overall 17.1% trap success and this yielded eleven identified small rodent species with *Mastomys natalensis* being the most dominant species with over 60 % composition. Other species were *Mus triton* (16.1%), *Aethomys hindei* (6.7%), *Lemniscomys zebra* (5.2%), *Lophuromys sikapusi* (4.8%), *Arvicanthis niloticus* (0.9%), *Gerbilliscus kempi* (0.1%), *Graphiurus murinus* (0.1%), *Steatomys parvus* (0.1%), *Dasymys incomtus* (0.1%) and *Grammomys dolichurus* (0.1%). *M. natalensis* composed of 550 and 607 individuals in cultivated and fallow fields respectively.

3.3.2 Population dynamics

Population density for *M. natalensis* was higher in fallow field habitats than cultivated habitats ($\beta = 0.61$, SE = 0.13, t = 4.569, $p \leq 0.0001$, Table 3.2, Fig. 3.1). Further, *M. natalensis* population density was higher in both the second dry season ($\beta = 0.546$, SE = 0.256, t = 2.136, p = 0.046) and in the second wet season ($\beta = 0.68$, SE = 0.22, t = 3.099, p = 0.006, Table 3.2, Fig. 3.2). Variation in *M. natalensis* density was not substantially affected by sampling month and year (Table 3.2). A further linear regression analysis was performed on *M. natalensis* population density and rainfall since earlier studies have demonstrated this factor to have a strong influence on this species population changes (Leirs *et al*., 1997). Our results showed a positive significant relationship but with a weak coefficient of determination (R^2 =15, p=0.001) (Fig. 3.3).

Table 3.2: Generalized Linear Mixed Model parameter estimates for fixed effect factors; habitat and seasons on M. natalensis population density

Random effects	**SD**			
Years	0.555			
Months	0.005			
Fixed effects	**Estimate**	**SE**	**t-value**	**p-value**
Intercept	1.929	0.389	4.957	0.000
Fallow habitat	0.607	0.133	4.569	0.000
Dry season 2 (Short dry season)	0.546	0.256	2.136	0.046
Wet season 1 (Major planting season)	0.418	0.206	2.027	0.057
Wet season 2 (Minor planting season)	0.682	0.220	3.099	0.006

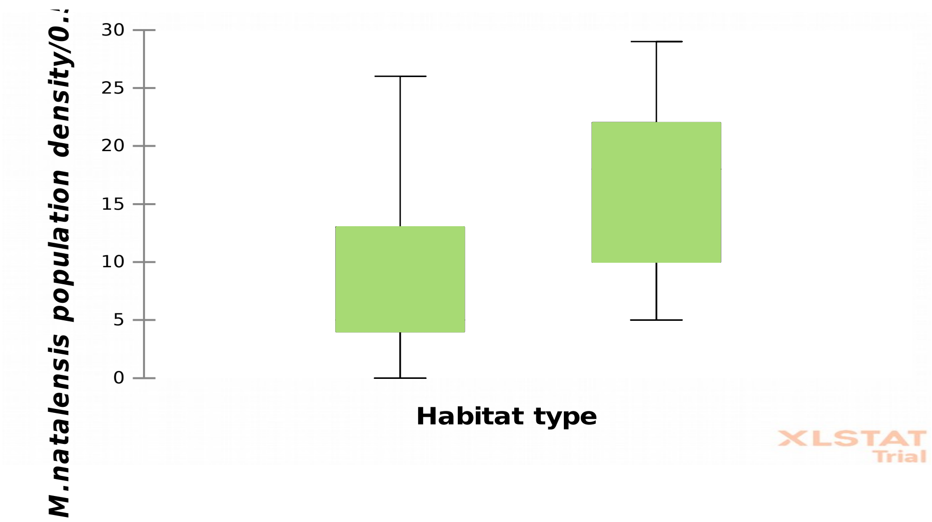


Figure 3.1: Box plots with mean, median, 25th and 75th quartile range for *M. natalensis* population density in cultivated and fallow field habitats for trapped animals in Mayuge district for a period of 2016-2018.

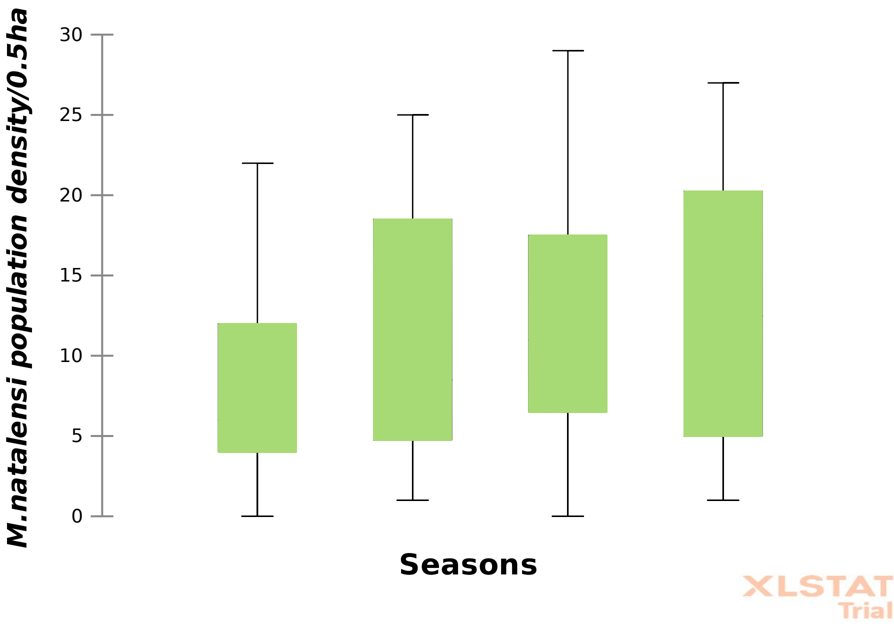


Figure 3.2: Box plots with mean, median, 25th and 75th quartile range for seasonal *M. natalensis* population density in Mayuge district for the period of 2016-2018.

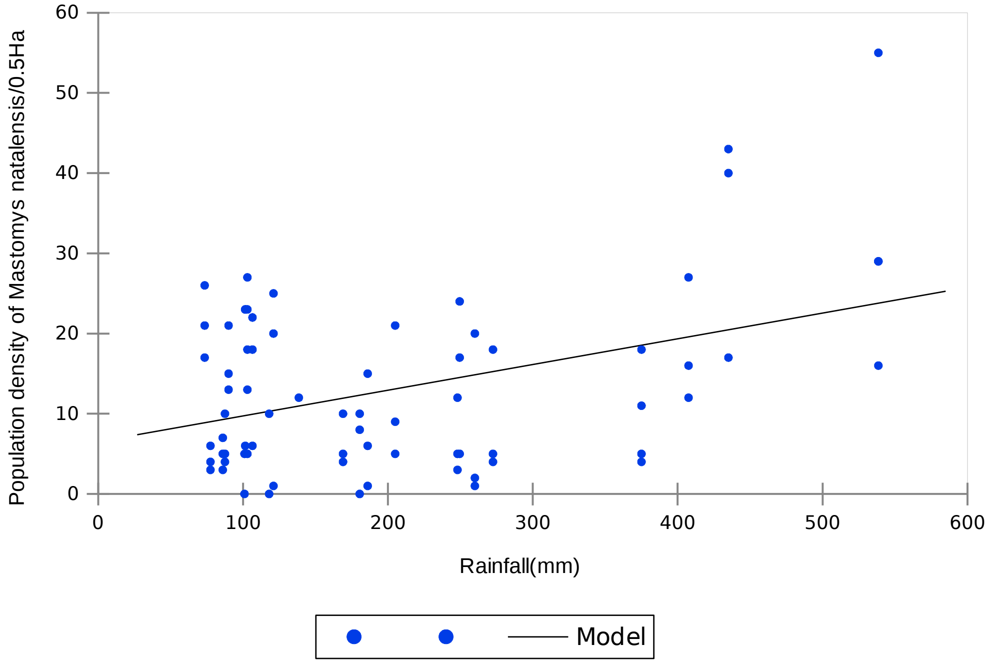


Figure 3.3: Relationship between population density for *M. natalensis* and total monthly rainfall in Mayuge district eastern Uganda for the period 2016-2018.

3.3.3 Breeding patterns

Here, the percentage of actively breeding females was higher in Dry season 2(β =.0.81, SE= 0.23, t =3.51, p = 0.002) followed by wet season 1(β = 0.52, SE= 0.25, t = 2.07, p = 0.049, Table 3.3, Fig. 3.4). Amount of rainfall and habitat (fallow and cultivated) showed very low model estimate values in relationship to the intercept and non-significant (Table 3.3). Likewise, the variation in percentage of actively breeding females was not substantially affected by sampling month and year (Table 3.3).

Table 3.3 Generalized Linear Mixed Model parameter estimates for fixed effect factors habitat, seasons and total monthly rainfall on sexually active breeding M. natalensis

Random effects	**SD**			
Years	2.724			
Months	0.076			
Fixed effects	**Estimate**	**SE**	**t-value**	**p-value**
Intercept	3.524	0.210	16.786	0.000
Fallow habitat	-0.123	0.148	-0.827	0.410
Dry season 2 (Short Dry season)	0.806	0.229	3.508	0.002

Wet season 1 (Major planting season)	0.523	0.253	2.065	0.049
Wet season 2 (Minor planting season)	0.323	0.228	1.417	0.169
Total monthly Rainfall	-0.0001	0.001	-0.086	0.932

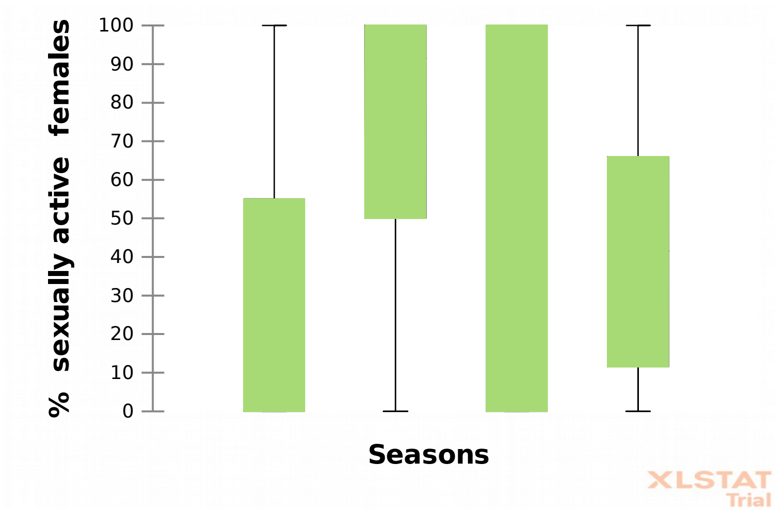


Figure 3.4: Box plots with mean, median, 25th and 75th quartile range for seasonal percentage sexually active females in Mayuge during the period of 2016-2018.

3.3.4 Recruitment

Data on newly trapped animals in the Capture Mark Recapture trappable population was computed as percentage proportion of newly trapped animals against overall captured animals. The percentage recruitment of *M. natalensis* in the trappable population was higher in Dry season 2 (β = 0.49, SE = 0.15, t = 3.29, p = 0.005, Table 3.4, Fig. 3.5). Habitat showed very low model estimate values in relationship to the intercept and non-significant (Table 3.4). Also, the variation in percentage recruitment was not substantially affected by sampling month and year.

3.3.5 Sex ratio

There was no significant difference on the effect of the test parameters, habitat (df=1, F=0.076, p=0.784) and season (df=1, F = 2.980, p=0.116) on the percentage of males to females for the trapped animals during the whole study period. The ratio of females to males was at parity.

Table 3.4: Generalized Linear Mixed Model parameter estimates for fixed effect factors; habitat and seasons on newly trappable M. natalensis animals (recruitment) in a trappable population

Random effects	**SD**			
Years	0.150			
Months	0.079			
Fixed effects	**Estimate**	**SE**	**t-value**	**p-value**
Intercept	3.679	0.148	24.865	0.000
Fallow habitat	0.027	0.106	0.258	0.796
Dry season 2 (Short Dry season)	0.486	0.148	3.285	0.005
Wet season 1 (Major planting season)	0.047	0.161	0.292	0.774
Wet season 2 (Minor planting season)	0.016	0.183	0.088	0.931

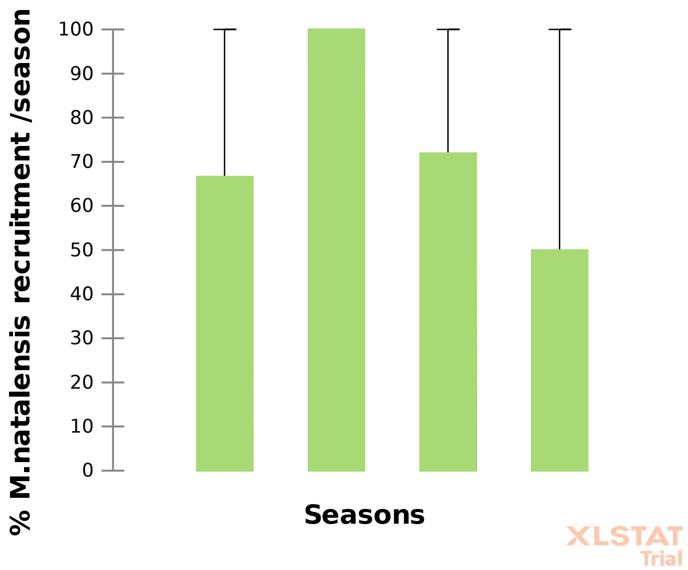


Figure 3.5: Box plots with mean, median, 25th and 75th quartile range for seasonal percentage recruitment of *M. natalensis* in a trappable population in Mayuge during the period of 2016-2018.

3.4 Discussion

3.4.1 Population dynamics

In the present study, we explored partly the population ecology of *M. natalensis* in an agricultural setting following the Capture Mark Release trapping in the fallow and cultivated field habitats where it emerged as the most dominant rodent species. Earlier studies conducted in different parts of East and Southern Africa in agricultural systems reported this particular species as the most important rodent pest species, with its population noted to exhibit irregular fluctuations depending on the geographic locality and climate (Leirs, 1995, 1996; Makundi *et al.*, 2007; Agerie and Bekele, 2013; Mulungu *et al.*, 2013). We therefore hypothesized that the population dynamics in terms of population density, breeding pattern and recruitment would significantly vary in space and season. In terms of population density, indeed spatial characteristics (habitat type) played a significant role in estimating population density with higher population density in fallow habitat compared to cultivated habitat.

We attribute our findings to the stability of fallow habitats which generally experience minimal human interaction but also tend to offer better ground cover for protection from predatory animals. This likely explanation was also suggested by several other scholars who reported higher population densities of *M. natalensi*s in fallow habitats compared to other habitats (Makundi *et al.*, 2009; Mulungu *et al*., 2013; Addisu and Bekele, 2013). Additionally, our findings are in conformity with earlier stated theories which suggest that biological species are known to differ in their distributions across space, where some habitats offer a wider range of resources for species to persist than others (Brown, 1984; Brown *et al*., 1996; Gyllenberg and Hanski, 1997; Mulungu *et al.*, 2011b). In particular, the studied species is reported to be a good colonizer of disturbed habitats/agricultural farm lands (Afework and Leirs, 1997; Magige and Senzota, 2006; Massawe *et al*., 2006) but its population density can be impacted by the levels of human activities in those habitats (Leirs *et al*., 1997; Hieronimo *et al*., 2014).

Secondly, the influence of seasons on population density of *M. natalensis* was modelled and found to be important, with highest densities in wet season 2 and lowest in Dry season 1. We thus attribute the higher densities in wet season 2 to have resulted from our observed higher percentage of actively breeding females in Dry season 2. We thus deduce that the higher breeding in wet yielded a growing population that peaked wet season 2.

Consequently, wet seasons are associated with increasing vegetation which provides both quality and quantity food for the rodents, but also offers ground cover which shields the ground dwelling rodents from predatory birds.

Our results are generally in agreement with several earlier studies on the population dynamics of *M. natalensis* whose reports demonstrate seasonal population changes in relationship to food supply and vegetation cover, factors driven by rainfall patterns (Leirs, 1995; Leirs *et al*., 1997; Linzey and Kesner, 1997; Makundi *et al*., 2007; Sheyo and Kilonzo, 2012; Massawe *et al*., 2012; Makundi *et al*., 2015; Mulungu, 2017; Chidodo, 2017; Mlyashimbi *et al*., 2018). Particularly, higher trap catches of *M. natalensis* were recovered in the wet season in northern Ethiopia and Western Usambara Mountains in Tanzania (Makundi *et al*., 2007; Chekol *et al.*, 2012) and these noted that rainfall was the main driver of these population changes which they believed to have triggered more vegetative plant growth which indirectly yielded more food and ground cover for rodents population growth. Our study further showed a positive linear relationship between amount of rainfall and *M. natalensis* population density but with a very weak coefficient of determination (R^2 =15) implying that there are other key predictors *M. natalensis* population changes in the studied area.

3.4.2 Breeding patterns of *M. natalensis*

In the present study, only sexually active breeding females were considered since previous studies have demonstrated that it’s actually the females that are key in regulating population changes (Mulungu, 2017). Our results showed that actively breeding females were present both in wet and dry seasons but with significantly higher percentages in Dry season two (Dry-2) for each year of trapping. This is a short dry period which occurs in the second part of the year after a major planting season (Wet-1). The significantly higher percentage of the actively breeding females in this season could have been due to the availability of abundant food for rodents from wet season 1 planting, and this could have triggered more females into active breeding. Earlier studies rodent breeding show synchronized seasonal reproductive patterns with the most favorable periods of the year, a strategy to maximize reproductive success (Bronson, 1985; Gittleman and Thompson 1988). Other reports suggest that several African rodent species time their reproduction with occurrence of rainfall events and plant productivity, to maximize growth and survival of newly born individuals by benefiting from availability of high-quality food and suitable environmental conditions (Neal, 1986; Leirs *et al*., 1994, 1997; Bekele and Leirs, 1997; Makundi *et al*., 2007). The results of this study concur well with earlier findings since significantly higher percentages of actively breeding *M. natalensis* occurred following the major planting season when abundant drying cereal crops and other food crops were plentiful in the gardens.

On the other hand, habitat types showed low non-significant estimates for actively breeding females, a result that indicated that habitat alone doesn’t regulate breeding patterns in *M. natalensis*. These results just confirm earlier reports which showed that breeding patterns of small rodents in general are more influenced by weather conditions (Hubert, 1977; Leirs, 1992; Makundi *et al*., 2007; Maheretu *et al.*, 2015) rather than the habitat type.

3.4.3 Sex ratio

The male to female sex ratio of the trapped animals was observed to be insignificant in this study between habitats and across seasons. However, other previous related studies on sex ratios of rodents demonstrated a male-biased higher capture probability, and attributed it to intersexual differences in home-range size, where males show large home-ranges and increased movement in search of mates which increases their chances of being trapped in a given habitat and season (Morris *et al*., 2011; Duque *et al*., 2005; Christensen, 1996). Nevertheless, our findings are in support of Mulungu *et al*. (2012) where they found equal proportions of males to females in a study conducted in irrigated rice and fallow habitats.

3.4.4 Recruitment

The percentage of newly trapped individuals in the trappable population was significantly higher in second dry season (Dry-2). Therefore, we attribute the new individuals to be the offspring's produced by the reproductive females in the population. Similar explanations for higher proportions of new individuals can be attributed to increased food availability in the gardens following first wet season, a major planting season (Wet-1). Both quality and quantity of food have been shown to be key exogenous factors for regulating rodent population abundance and breeding cycle (Mulungu *et al*., 2014, 2012; Revitali *et al*., 2009). Likewise, Leirs *et al*. (1994) reported that rodents tend to respond much quickly to changes in weather after a long dry spell which normally results into an influx of high numbers of new individuals to the trappable population.

3.5 Conclusions

It is evident from the present study that *M. natalensis* can equally occupy cultivated fields and land fallow habitats in agro ecosystem but with relatively higher population abundances in fallow, which could be attributed to the limited human activities as compared to cultivated fields. This observation thus justifies consideration of mosaic fallow fields in management plans for effective control of agriculture rodent pest species.

Secondly the study revealed that *M. natalensis* in the study area exhibit seasonal population changes associated with weather conditions, particularly rainfall patterns where increased rainfall results into increased population growth due to the increased vegetation growth. Therefore, control efforts should be timed in wet seasons to prevent population build up which could result into large numbers that can cause significant crop damage. The study also revealed that active breeding in females of *M. natalensis* is continuous throughout the year in the studied area, though with higher percentage in dry season two which follows the major planting season. These results thus indicate that food production cycles play a major role in *M. natalensis* breeding. We therefore recommend that control efforts should be continuous on a yearly basis with increased magnitude implemented early in the first rainy season (Wet-1).

Lastly the study has shown that the ratio of male to female *M. natalensis* in the studied area was at parity. We therefore recommend that control efforts should target both sexes to prevent population growth from attaining damaging levels.

Acknowledgements

We are extremely grateful to the Ecologically Based Management of Rodent Pests in Maize and Rice in East Africa to Sokoine University of agriculture project (Grant number OPP1112579) supported by Bill and Melinda Gates foundation for the financial support of this research. We are also grateful for the tireless project field work efforts rendered by Kisakye Alex, Ouma Namulochi and Ramadhani Kigunguli from Busitema University, Namasagali campus, Uganda and Pest Management Centre, Sokoine University of Agriculture, Morogoro, Tanzania respectively.

Funding

Special thanks to the Bill and Melinda Gates Foundation that funded Alex Mayamba's PhD studies, of which this paper is part.

3.6 References

Addisu, A. and Bekele, A. (2013). Habitat preferences, seasonal abundance and diets of rodents in Alage, Southern Ethiopia. *African Journal of Ecology* 52: 284 - 291.

Afework, B. (1996). Population dynamics of the Ethiopian endemic rodent, *Praomys albipes* in the Menagesha State Forest. *Journal of Zoology* 238: 1 - 12.

Bekele, A. and Leirs, H. (1997). Population ecology of rodents of maize fields and grassland in central Ethiopia. *Belgium Journal of Zoology* 127: 39 - 48.

Bonwitt, J., Sáez, A. M., Lamin, J., Ansumana, R., Dawson, M., Buanie, J. and Brown, H. (2017). At Home with Mastomys and Rattus : Human-Rodent Interactions and Potential for Primary Transmission of Lassa Virus in Domestic Spaces. *American Journal Tropical Medical Hygene* 96: 935 - 943.

Borremans, B., Hughes, N. K., Reijniers, J., Sluydts, V., Katakweba, A. A. S., Mulungu, L. S. and Leirs, H. (2014). Happily together forever: Temporal variation in spatial patterns and complete lack of territoriality in a promiscuous rodent. *Population Ecology* 56: 109 - 118.

Bronson, F.H. (1985). Mammalian reproduction: an ecological perspective. *Biology of Reproduction* 32: 1 - 26.

Brown, J.H., Stevens, G.C. and Kaufman, D.M. (1996). The geographic range: Size, shape, boundaries and internal structure. *Annual Review Ecololgy System* 27: 597 - 623.

Brown, J.H. (1984). On the relationship between abundance and distribution of species. *Belgium Journal of Zoology* 124: 255 - 279.

Chekol, T., Bekele, A. and Balakrishnan, M. (2012). Population density, biomass and habitat association of rodents and insectivores in Pawe area, northwestern Ethiopia. *Tropical Ecology* 53: 15 - 24.

Christensen, J.T. (1996). Home range and abundance of *Mastomys natalensis* (Smith, 1834) in habitats affected by cultivation. *African Journal of Ecology* 34: 298 - 311.

Dieterlen, F. (1967). A study of the population of rodents in Kivu (Congo) (in German). *Teil I Zoological Journal of Biological System* 94: 369 - 426.

Duque, U.G., Joshi, R.C., Martin, A.R., Marquez, L.V. and Sebastian, L.S. (2005). Rat pest species breeding patterns in the trap barrier system plus a trap crop (TBS + TC) at the PhilRice-CES farm: management implications. *International Rice Research Notes* 30(1): 26 - 28.

Ferrera, S.M. and Van Aarde, R.J. (1996). Changes in community characteristics of small mammals rehabilitating coastal dune forests in northern KwaZulu/Natal. *African Journal of Ecology* 34: 113 - 130.

Fiedler, L.A. (1988). Rodent pest problems in East Africa. Rodent pest management. In: Prakash, I.(ed.). Rodent pest Management.Boca Raton, Florida. USA. CRC Press. pp. 35 - 65.

Gittleman, J.L. and Thompson, S.D. (1988). Energy allocation in mammalian reproduction. *American Zoologist* 28: 863 - 875.

Gyllenberg, M. and Hanski, I. (1997). Habitat Deterioration, Habitat Destruction and Metapopulation Persistence in a Heterogenous Landscape. *Theoretical Population Biology* 52: 198 - 215.

Hieronimo, P., Kimaro, D. N., Kihupi, N. I., Gulinck, H., Mulungu, L. S., Msanya, B. M. and Deckers, J. A. (2014). Land use determinants of small mammals abundance and distribution in a plague endemic area of Lushoto district, Tanzania. *Tanzania Journal of Health Research* 16: 1 - 12.

Jacob, J. (2008). Response of small rodents to manipulation of vegetation height in agro ecosystems. *Integrative Zoology* 3: 3 - 10.

Karim, M. and Zeger, S. (1992). Generalized Linear Models with random effects; salamander mating revisited. *Biometrics* 48: 631- 644.

Kasetisart, J. (2009). Population dynamics of rodent pest species in upland farming systems of Lao PDR. *National Sciences* 43: 125 - 131.

Kingdon, J. (1974). *East Africa mammals: an atlas of evolution in Africa.* Volume II Part B (Hares and Rodents). Academic Press, London. pp. 704.

Knudson, C. (2018). *An Introduction to Mode-Fitting with the R-package glmm*. *Cran*, pp. 1-16.

Leirs, H., Verhagen, R. O. N., Sabuni, C.A., Mwanjabe, P. and Verheyen, N.W. (1997). Spatial dynamics of *Mastomys natalensis* in a field-fallow mosaic in Tanzania. *Belgium Journal of Zoology* 127: 29 - 38.

Leirs, H. (1995). Population ecology of *Mastomys natalensis* (Smith, 1834): implications for rodent control in Africa. A report from the Tanzania–Belgium Joint Rodent Research Project (1986–1989). Agricultural Edition No. 35. Belgian Administration for Development Cooperation, Brussels. 268pp..

Leirs, H., Verhagen, R. and Verheyen, W. (1994). The basis of reproductive seasonality in Mastomys rat (Rodentia: Muridea). *Journal of Tropical Ecology* 10: 55 - 66.

Leirs, H., Verhagen, R., Verheyen, W., Mwanjabe, P. and Mbise, T. (1996). Forecasting rodent outbreaks in Africa: an ecological basis for Mastomys control in Tanzania. *Journal of Applied Ecology* 33: 937 - 943.

Linzey, A.V. and Kesner, M.H. (1997). Small mammals of a woodland-savannah ecosystem in Zimbabwe. I. Density and habitat occupancy patterns. *Journal of Zoology* 243: 137 - 152.

Magige, F. and Senzota, R. (2006). Abundance and diversity of rodents at the human-wildlife interface in Western Serengeti, Tanzania. *African Journal of Ecology* 44: 371 - 378.

Makundi, R. H., Massawe, A. W., Mulungu, L. S. and Katakweba, A. (2009). Species diversity and population dynamics of rodents in a farm-fallow field mosaic system in Central Tanzania. *African Journal of Ecology* 48: 313 - 320.

Makundi, R.H., Massawe, A.W. and Mulungu, L. (2007). Reproduction and population dynamics of *Mastomys natalensis* Smith, 1834 in an agricultural landscape in the Western Usambara Mountains, Tanzania. *Integrative Zoology* 2: 233 - 238.

Makundi, R.H., Oguge, N.O. and Mwanjabe, P.S. (1999). *Rodent Pest Management in East Africa – an ecological approach. In: Ecologically-Based Rodent Management* (Eds G. R. Singleton, L. Hinds, H. Leirs and Z. Zhang), For International Agricultural Research, Canberra, Australia. pp. 460 - 476.

Martin, G.H. and Dickinson, N.M. (1985). Small mammal abundance in relation to microhabitat in dry sub-humid grassland in Kenya. *African Journal of Ecology* 23: 223 - 234.

Massawe, A.W., Leirs, H., Rwamugira, W.P. and Makundi, R.H. (2003). *Effect of land preparation methods on spatial distribution of rodents in crop fields*. In: Rats, Mice and People: Rodent Biology and Management (Eds G. R. Singleton, L. A. Hinds, C. J. Krebs and D. M. Spratt). Australian Centre for International Agricultural Research, Canberra. 120pp.

Massawe, A.W., Rwamugira, W., Leirs, H., Makundi, R. H. and 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.

Massawe, A.W., Makundi, R. H., Mulungu, L. S., Katakweba, A. and Shayo, T. N. (2012). Breeding Dynamics of Rodent Species Inhabiting Farm - Fallow Mosaic Fields in Central Tanzania. *African Zoology* 47: 128 - 137.

Mayamba, A., Byamungu, R.M., Makundi, R.H., Kimaro, D.N., Isabirye, M., Massawe, A. W. and Mulungu, L. S. (2019). Species composition and community structure of small pest rodents (Muridae) in cultivated and fallow fields in maize-growing areas in Mayuge district, Eastern Uganda. *Ecology and Evolution* 9: 7849 - 7860.

Meester, J., Lloyd, A. and Rowe-Rowe, D.T. (1979). A note on the ecological role of *Praomys natalensis*. *South African Journal of Science* 75: 183 - 184.

Meheretu, Y., Welegerima, K., Sluydts, V., Bauer, H., Gebrehiwot, K., Deckers, J.F., Makundi, R.H. and Leirs, H. (2015). Reproduction and survival of rodents in crop fields: the effects of rainfall, crop stage and stone-bund density. *Wildlife Research* 42: 158 - 164.

Mlyashimbi, E.C.M., Mariën, J., Kimaro, D.N., Tarimo, A.J.P., Isabirye, M., Makundi, R.H. and Mulungu, L.S. (2018). Relationships between seasonal changes in diet of Multimammate rat (*Mastomys natalensis*) and its breeding patterns in semi-arid areas in Tanzania. *Cogent Food and Agriculture* 4: 1 - 13.

Monadjem, A. (1998). Reproduction biology, age structure and diet of *Mastomys natalensis* (Muridae: Rodentia) in a Swaziland grassland. *Z S¨augetierkunde* 63: 347 - 356.

Moore, S.M., Monaghan, A., Borchert, J.N., Mpanga, J.T., Atiku, L.A., Boegler, K.A., Montenieri, J., MacMillan, K., Gage, K.L. and Eisen, R.J. (2015). Seasonal fluctuations of small mammal and flea communities in a Ugandan plague focus: evidence to implicate *Arvicanthis niloticus* and *Crocidura* spp. as key hosts in Yersinia pestis transmission. *Parasites and Vectors* 8: 11 - 22.

Morris, G., Conner, L.M. and Oli, M.K. (2011). Effects of mammalian predator exclusion and supplemental feeding on space use by hispid cotton rats. *Journal of Mammalogy* 92: 583 - 589.

Mulungu, L.S., Mahlaba, T.A., Massawe, A.W., Kennis, J., Crauwels, D., Eiseb, S., Monadjem, A., Makundi, R.H., Katakweba, A.S., Leirs, H. and Belmain, S.R. (2011a). Dietary differences of the multimammate mouse, *Mastomys* *natalensis* (Smith 1834). across different habitats and seasons in Tanzania and Swaziland. *Wildlife Research* 38: 640 - 646.

Mulungu, L.S., Mahlaba, T.A., Massawe, A.W., Kennis, J., Crauwels, D., Eiseb, S., Monadjem, A., Makundi, R.H., Katakweba, A.S., Leirs, H. and Belmain, S.R. (2011b). Differences in diet between two rodent species of *Mastomys natalensis* and *Gerbilliscus vicinus* in fallow land habitat of Central Tanzania. *African Zoology* 46: 387 - 392.

Mulungu, L.S., Ngowo, V., Mdangi, M., Katakweba, A., Tesha, P., Mrosso, F., Mchomvu, M. and Kilonzoa, B. S. (2013). Population dynamics and breeding patterns of Multimammatemouse, *Mastomys natalensis* (Smith, 1834), in irrigated rice fields in Eastern Tanzania. *Journal of Pest Management Science* 69: 371 - 377.

Mulungu, L.S., Mlyshimbi, E.C.M.**,** Ngowo, V., Mdangi, M., Katakweba, A.S., Tesha, P., Mrosso, F.P., Mchomvu, M., Kilonzo, B.S. and Belmain, S.R. (2014). Food preferences of the multimammate mouse, *Mastomys natalensis*, in irrigated rice habitats in Tanzania. *International Journal of Pest Management* 60: 1 - 8.

Mulungu, L.S., Sixbert, V., Ngowo, V., Mdangi, M., Katakweba, A.S., Tesha, P., Mrosso, F.P., Mchomvu, M., Kilonzo, B.S. and Belmain, S.R. (2015). Spatio-temporal patterns in the distribution of the multimammate mouse, *Mastomys natalensis*, in rice crop and fallow land habitats in Tanzania. *Mammalia* 79: 177 - 184.

Mulungu, L.S. (2017). *Control of rodent pests in maize cultivation: the case of Africa*. Burleigh Dodds Science Publishing Limited 82 High Street Sawston Cambridge CB22 3HJ UK. pp. 317 - 337.

Mwanjabe, P. and Leirs, H. (1997). An early warning system for IPM-based rodent control in small holder farming systems in Tanzania. *Belgium Journal of Zoology* 127: 49 - 58.

Neal, B.R. (1986). Reproductive characteristics of African Small mammals. Cimbebaria Ser. *Journal of Zoology* 8: 113 - 127.

Olayemi, A., Oyeyiola, A., Obadare, A., Igbokwe, J., Adesina, A. S., Onwe, F. and Fichet-Calvet, E. (2018). Widespread arenavirus occurrence and seroprevalence in small mammals, Nigeria. *Parasites and Vectors* 11: 4 - 16.

Peles, J.D. and Barrett, D. (1996). Effects of vegetative cover on the population dynamics of meadow voles. *Journal of Mammalogy* 77: 857 - 869.

Revitali, M.A.N.P., Ima, M.A.L., Eserve, P.E.L.M. and Elt, D.O.A.K. (2009). Population dynamics of two_Sympatric rodents in a variable environment: rainfall, resource availability and predation. *Journal of Ecology* 90: 1996 - 2006.

Singleton, G.R., Joshi, R.C. and Sebastian, L.S. (2008). *Ecological management of rodents: the good, the bad and the hindi naman masyadong pangit!* In ‘Philippine Rats: Ecology and Management’. (Eds G. R. Singleton, R. C. Joshi and L. S. Sebastian.) (Philippine Rice Research Institute: Nueva Ecija, Philippines). pp. 1 - 7.

Sluydts, V., Davis, S., Mercelis, S. and Leirs, H. (2009). Comparison of multimammate mouse (*Mastomys natalensis*) demography in monoculture and mosaic agricultural habitat: Implications for pest management. *Crop Protection* 28: 647 - 654.

Telford, S.R. (1989). Population biology of multimammate rat, *(Mastomys natalensis)* at Morogoro, Tanzania 1981–1985. *Bull Fla StateMus Biological Science* 34: 249 - 288.

Utrera, A., Duno, G., Ellis, B.A., Salas, R.A., Manzione, N. and Fulhorst, C.F. (2000). Small mammals in agricultural areas of western Ilanos of Venezuela: community structure, habitat associations, and relative densities. *Journal of Mammalogy* 81: 536 - 548.

White, G.C., Anderson, D.R., Burnham, K.P. and Otis, D.C. (1982). *Capture-recapture and removal methods for sampling closed populations Los Alamos National Laboratory*. New Mexico, Los Alamos. 82pp.

XLSTAT (2017). Data Analysis and Statistical Solution for Microsoft Excel. Addinsoft, Paris, France (2017). [http://www.addinsoft.com]. Site visited on 2/4/2020.

CHAPTER FOUR

PAPER III

FITNESS OF THE PESTIFEROUS SMALL RODENT (MASTOMYS NATALENSIS) IN AN AGROECOSYSTEM IN LAKE VICTORIA CRESCENTS ZONE, EASTERN UGANDA

Alex Mayamba[1, 4, 5*]; Bram Vanden Broecke[2]; Herwig Leirs[2]; Brian. E. Isabirye[3]; Robert. M. Byamungu[4]; Alice Nakiyemba[1]; Moses Isabirye[1]; David Kifumba[1]; Apia. W. Massawe[5]; Didas. N. Kimaro[6]; Mshaka. E. Mdangi[7] and Loth. S. Mulungu[5].

[1]Faculty of Natural Resources and Environment, Busitema University, P. O. Box 236, Tororo, Uganda, [2]Evolutionary Ecology Group, Universiteit Antwerpen, Universiteitsplein 1, 2610 Wilrijk, Belgium, [3]Kawanda Agribusiness Consult, Kampala Uganda.[4]Department of Wildlife and Management, Sokoine university of Agriculture, Tanzania [5]Pest Management Centre, Sokoine University of Agriculture, P. O. Box 3110, Morogoro, Tanzania, [6]Department of Engineering Sciences and Technology, Sokoine University of Agriculture, P.O. Box 3003, Morogoro, Tanzania. [7]Department of Training, Extension services and Research, Ministry of Agriculture, P.O. Box 2182, Dodoma, Tanzania.

Email: alexmayamba@gmail.com

Accepted in Mammalia

Manuscript ID: 2019.0101.R

Abstract

A 2.5-year study was conducted to understand the fitness of *M. natalensis* in an agroecosystem in relationship with environmental predictors. The study was conducted in Mayuge district, in the Lake Victoria crescents zone in Eastern Uganda. Fitness was measured in terms of survival, maturation and recapture probability and estimated using multi-event capture-recapture models. Survival rates were higher after high rainfall in the previous month and increased with increasing population density of the animals. Maturation rate on the other hand showed no significant association with any predictor variables while capture probability significantly associated with sex of the animals, with higher capture probability for males. The results demonstrate that fitness of *M. natalensis* in agroecosystem is dependent on rainfall, sex and current population density. The above results were associated with increasing vegetation which provides cover for animal nesting and abundant food for the animals during rainfall periods thus increased survival, high mobility in males in search for mates thus exposing animals to high chances of being captured and increased prey saturation at high population density resulting into high animal survival. These results have important implications for the timing of management strategies, i.e. control efforts should be enforced during the rainfall seasons to prevent high population buildup in the succeeding seasons.

Key words: capture-recapture, *Mastomys natalensis,* maturation estimates, multistate model, survival.

4.1 Introduction

The multimammate mouse (*Mastomys natalensis*) is a serious rodent pest species in agriculture particularly in cereal crops within East Africa (Makundi *et al*., 1999; Stenseth *et al*., 2003). Multimammate mouse are a significant small rodent pest species in cereal crops production in Africa. Their occurrence is estimated to cause over 80% damage to maize in some locations and seasons and about 5 – 12% damage to field rice crop (Mulungu *et al*., 2003, 2015, 2017).

Currently, most pest managers use lethal control options whenever rodent population build up is reported, but this has been shown to be less effective due to animal resurgence after a short period after treatment (Leirs *et al.*, 1997) always results into unintended affects to non-target species in the environment (Singleton *et al.*, 2007) and is expensive (Mdangi *et al*., 2013; Mulungu, 2017). Rodent populations tend to quickly recover following reduction events through reproduction or immigration from nearby populations (Leirs *et al*., 1997; Cowan *et al*., 2003), which downplays the use of rodenticides to control rodents in a given locality. Consequently, as a strategy to improve current rodent control options, forecast models are arguably one important approach with potential to predict rodent outbreaks (Leirs *et al*.,1996). Their application has been shown to be economically rewarding in controlling rodent population, since farmers would not spend money on control when it is not needed and only apply control when an outbreak is predicted thus mitigating losses (Davis *et al*., 2004).

Unfortunately, current available literature in the region offers limited and patchy information on how key ecological processes regulate rodent fitness and population size (Swanepoel *et al*., 2017). This thus limits development of regional models for rodent prediction and early warning control systems for species inhabiting agricultural fields and surrounding areas. Developments of appropriate rodent forecasting models require an understanding of the key ecological aspects of the target species such as survival and maturation rates. These have been shown to be important in regulating rodent population changes (Oli and Dobson, 2001; Lima *et al*., 2003; Sluydts *et al*., 2007). These traits are typically dependent on food and mate availability, vegetation cover and climatic conditions (Saïd *et al*., 2005; Begg *et al*., 2005; Hayes *et al*., 2007). Specifically, survival and maturation are important in regulating rodent populations over time and space, therefore a solid understanding of these is critical to improve prediction of future population changes for proactive rodent management (Leirs *et al*., 1997; Witmer, 2007).

In this study we estimated maturation, survival and recapture probability of *M. natalensis* as measures of animal species fitness in agricultural crop fields and surrounding fallow land. Knowledge on survival and maturation estimates can be employed to design more effective and appropriate predictive models to control rodent pest species at the most vulnerable stages (Witmer, 2007).

4.2 Materials and Methods

4.2.1 Study site

The study was conducted in Kigulu parish, Kigandalo sub-county, Mayuge district in Eastern Uganda (06°16′S, 37° 31′E), approximately 1020 m above sea level (Fig. 4.1). The study area experiences a bimodal rainfall pattern, characteristic of Eastern Uganda in the Lake Victoria crescents agro-ecological zone. The first rainy season normally occurs between the months of March to end of May followed by a short dry period (June-August). The second rainy season starts towards end of August to end of November, then a dry spell from December to February of the following year. The zone is characterized as Banana-coffee system, majorly engaged in growing crops including, bananas, coffee, maize, sweet potato, beans, vegetables and rice (Musiitwa and Komutunga, 2001; Haneishi *et al*., 2013). Farming in this zone is majorly by small scale farmers with mean farm plots of about 1.5 acres (0.6ha) (Haneishi *et al.*, 2013). Due to the intense demand for agricultural and pasture land, there is a lot of land use intensification and fragmentation thus natural habitats and forests occur in small patches.

4.2.2 Trapping fields/grids

Permanent trapping fields for the experiment were obtained with permission of the landowners. A purposive sampling technique was used in the selection of study fields, and targeted both crop cultivated field habitats and fallow land habitats. Each of the two (2) categories were replicated twice making a total of four trapping fields, separate from each other at a minimum distance of 500m to avoid population immigration from one grid to another (Borremans *et al.*, 2015) At each of the identified field sites, a 70 m x 70 m grid was marked with 49 permanent trapping points, for placement of 49 Sherman live traps during each trapping session. The fallow land fields were initially covered with heavy thick patches of tick berry (*Lantana camara)* but were subsequently reduced by animal grazing. Other weedy species noted were perennial and annual grasses (Gramineae) of several species, which are common in disturbed soils and uncultivated fallow lands. They included guinea grass (*Panicum maximuma*) couch grass (*Digitaria scalarum*), black jack (*Bidens pilosa*), Star grass (*Cynodon dactylon)* and wondering jew (*Commellina bengelensis*). The fallow fields were surrounded by cultivated fields which, during the wet season, were planted with maize, beans, cassava and sweet potatoes. After crop harvest, these fields were left with standing stubble and slash and ox-plough were the main land preparation methods before the next wet/planting season started. The cultivated fields were found already planted with maize intercropped with beans by the farmers in the first year of the study (2016) but in the subsequent seasons, farmers introduced cassava as a way of crop rotation to control witch weed (*Striga sp.*) in the area (Oswald and Ransom, 2001). Fragments of mixed crop gardens comprising of coffee, beans, bananas, sweet potato and cassava also surrounded these cultivated study fields.

4.2.3 Trapping procedure

The trapping procedure followed that of Aplin *et al*. (2003) using the Capture Mark Release (CMR) trapping technique. Sherman Live traps (Light Folding Aluminium, 7.6 x 8.9 x 22.9 cm, H.B. Sherman Traps, Inc., Tallahassee, FL, USA) were used to trap the rodents. Traps were baited with peanut butter mixed with maize flour and the trapping sessions conducted at 4-weekly intervals, for three consecutive days. At every trapping session, traps were inspected every morning and captured animals were checked for sexual maturity status, weighed, toe clip coded and released at the points of capture. The study lasted for 2 and half years from January 2016 to May 2018. The nomenclature by Wilson and Reeder (2005) and Happold (2013) was used as the main reference to identify the rodent species captured in the study areas.

4.2.4 Statistical analysis

Survival, maturation and capture probability were estimated using multi-event capture-recapture models (Pradel, 2005) in E-SURGE V2.1.4 (Choquet *et al*., 2009a). Survival was defined as the monthly probability for an individual to survive from one month to the next while maturation was defined as the probability for a juvenile to become an adult.

Survival and maturation were hypothesized to be affected by various biological and environmental factors including sex, field habitat (fallow and cultivated fields), previous rainfall and current rodent population density. These were categorized in order to study their effects on survival and maturation. For each month, we calculated the sum of the total rainfall in the two previous months. The mean value for each month was 406mm rainfall (range = 98 – 1145mm). Rainfall was thus categorized into three; low rainfall (less than 300mm), medium rainfall (between 300-500mm) and high (more than 500 mm).

Due to the low number of recaptures, it was not possible to calculate the density in each field for each trapping session. Therefore, the mean unique individuals trapped in all fields for each month was calculated and divided into two categories: low (average lower than 10 individuals) and high (average higher than 10 individuals) density. A goodness of fit (GOF) test was carried out with the program U-CARE prior to the survival analysis to evaluate potential confounding factors such as an excess of transience animals and trap-dependence (Choquet *et al*., 2009b; Pradel *et al*., 2003). The GOF test showed that there were no deviations indicating trap-dependence (see results), which suggests that animals trapped in the previous trap night have the same probability of being recaptured as individuals that were not trapped in the previous trap night. Additionally, the GOF showed no excess of transient individuals (see results), meaning that there was no difference in the probability of being captured for the first time compared to subsequent recaptures (Choquet *et al.*, 2009b; Rémi *et al*., 2005).

A multivariate multistate Cormack-Jolly-Seber model with three potential states: sub adult, adult and dead, was used. This allowed us to estimate the probability of three events: apparent survival (φ), maturation (ψ) and recapture (P). As mentioned before, trapping was done using Pollock's closed robust design, where the population is assumed to be closed (i.e. no entry or exit of individuals into the population) within each trap session and open between trapping session (Pollock, 1982). Monthly survival was estimated between each trapping session and fixed to 1 within a trapping session, while the capture probability was estimated within each session.

The three parameters were modelled in subsequent steps: first we modelled maturation, then recapture probability and lastly survival (Sluydts *et al.,* 2007; Mariën *et al*., 2018). Models were ranked using Akaike's information criterion (AICc) (Burnham and

Anderson, 2004), where the model with the lowest AIC value was selected as a starting point for the next modelling step. Recapture probability was fully time dependent in all models during the first two modelling steps (maturation) and we allowed survival to differ with cumulative rainfall of the past two months, since this has been shown to affect survival in *M. natalensis* (Julliard *et al.*, 1999; Sluydts *et al*., 2007). All three parameters were allowed to vary between sex (male and female) and field (fallow or cultivated). Survival and maturation probability were allowed to differ between density (high or low) and with cumulative rainfall of the last two months (high, medium or low) in the full model with a potential interaction between them. Lastly, Sluydts *et al*. (2007) found that survival in *M. natalensis* differed between subadults and adults and hence reproductive age was included in the final model as well.

4.3 Results

In the CMR data set, there were 1030 captures of *M. natalensis* with 550 unique individuals.

Goodness of fit (GOF)

The GOF showed no deviations against the assumption of transience (test 3G.SR, χ^2 = 57.653, df = 77, p = 0.951) nor against trap dependence (TEST M. ITEC, χ^2 = 50.612, df = 39, p = 0.101). This allowed further analysis of the data without any biased estimates due to transience or trap dependence.

4.3.1 Model selection

We first modelled maturation and found that the model with the lowest Akaike Information Criteria (AICc) value was the model where the maturation probability per month was constant through time (ψ_{cte}: AICc = 3399.9, deviance = 3333.6, Np = 32; Table 4.1). We therefore kept maturation probability constant in the subsequent modelling steps.

During the second modelling step, the recapture model with the lowest AICc value had an additive effect between time and sex (P_{T+S}: AICc = 3397.7, deviance = 3329.3, Np = 33; Table 4.1). Another recapture model with field as an extra additive effect (P_{T+S+F}: AICc = 3398.4, deviance = 3327.8, Np = 34; Table 4.1) was only one AICc unit removed from the best fitted recapture model. Lastly, we modelled survival where the model with the lowest AICc value had an interaction between rainfall and density and an additive effect of field (φ_{R*D+F}: AICc = 3392.3, deviance = 3315.2, Np = 37; Table 4.1).

However, the survival model with only the interaction between rainfall and density (φ_{R*D}: AICc = 3393.2, deviance = 3318.2, Np = 36) was less than one AICc unit removed from the best fitted survival model, suggesting that they both adequately fit the data. Indeed, the interaction between rainfall and density seemed important, since all models with the lowest AICc value included this interaction. We therefore chose the final best fitting model with lowest AICc and lowest number of parameters which contained the following factors: ψ_{cte}, P_{T+S}, $\varphi_{R*D.}$

Table 4.1: Modelling of maturation, recapture and survival. Highlighted (bold) models where the best models (with the lowest AICc) and were selected in each step and used as a starting point for the subsequent step. For each model, the number of parameters (Np), deviance and AICc are given. ΔAICc is the difference in AICc between the current model and the top ranked one

Model No.	Maturation (ψ)	Recapture (P)	Survival (φ)	Np	Deviance	AICc	ΔAICc
1	**Cte**	**T**	**R**	**32.0000**	**3333.5852**	**3399.8985**	**0.0000**
2	D	T	R	33.0000	3332.3422	3400.8027	0.9042
3	R	T	R	34.0000	3330.6304	3401.2429	1.3444
4	R*D+S	T	R	39	3320.0948	3401.5385	1.6400
5	S	T	R	33.0000	3333.1017	3401.5622	1.6637
6	R*D+F	T	R	39	3320.4671	3401.9108	2.0123
7	F	T	R	33.0000	3333.5173	3401.9778	2.0793
8	R*D	T	R	37.0000	3326.2896	3403.3865	3.4880
9	D+S	T	R	35.0000	3330.6337	3403.4029	3.5044
10	R*D+S+F	T	R	40.0000	3319.9980	3403.6223	3.7238
11	S+F	T	R	34.0000	3333.0451	3403.6576	3.7591
12	R+S	T	R	36.0000	3328.9926	3403.9233	4.0248
13	D+F	T	R	35.0000	3331.3692	3404.1385	4.2400
14	R+F	T	R	36.0000	3329.8127	3404.7434	4.8449
15	R+F	T	R	36.0000	3330.3801	3405.3108	5.4123
16	D+S+F	T	R	36.0000	3330.6319	3405.5626	5.6641
17	R+D+S	T	R	37.0000	3328.6842	3405.7812	5.8827
18	R+D+F	T	R	37.0000	3329.6458	3406.7427	6.8442
19	R+D+S+F	T	R	38.0000	3328.6551	3407.9230	8.0245
20	**Cte**	**T+S**	**R**	**33**	**3329.2526**	**3397.7131**	**0.0000**
21	Cte	T+S+F	R	34	3327.8097	3398.4222	0.7091
22	Cte	T	R	32	3333.5852	3399.8985	2.1854
23	Cte	T+F	R	33	3332.2922	3400.7528	3.0397
24	**Cte**	**T+S**	**R*D+F**	**37**	**3315.2497**	**3392.3466**	**0.0000**
25	**Cte**	**T+S**	**R*D**	**36**	**3318.2209**	**3393.1516**	**0.8050**
26	Cte	T+S	R*D+S+F	38	3314.3285	3393.5964	1.2498
27	Cte	T+S	R*D+A+F	38	3314.8579	3394.1258	1.7792
28	Cte	T+S	R*D+S	37	3317.3395	3394.4364	2.0898
29	Cte	T+S	R*D+A	37	3317.7803	3394.8772	2.5306
30	Cte	T+S	R*D+A+S +F	39	3313.994	3395.4377	3.0911
31	Cte	T+S	R*D+A+S	38	3316.9563	3396.2242	3.8776
32	Cte	T+S	R+F	34	3325.7841	3396.3966	4.0500
33	Cte	T+S	R	33	3329.2526	3397.7131	5.3665
34	Cte	T+S	R+A+F	35	3325.224	3397.9933	5.6467
35	Cte	T+S	R+S	34	3328.1635	3398.776	6.4294
36	Cte	T+S	R+A+S+F	36	3324.1977	3399.1284	6.7818
37	Cte	T+S	R+A	34	3328.6013	3399.2138	6.8672
38	Cte	T+S	R+A+S	35	3327.5857	3400.355	8.0084

39	Cte	T+S	F	32	3335.2957	3401.6089	9.2623
40	Cte	T+S	cte	31	3338.3889	3402.5596	10.2130
41	Cte	T+S	A+F	33	3334.6598	3403.1203	10.7737
42	Cte	T+S	S+F	33	3334.6598	3403.1203	10.7737
43	Cte	T+S	D+F	33	3334.8849	3403.3454	10.9988
44	Cte	T+S	S	32	3337.3756	3403.6889	11.3423
45	Cte	T+S	A	32	3337.6743	3403.9875	11.6409
46	Cte	T+S	D	32	3337.9831	3404.2963	11.9497
47	Cte	T+S	A+S+F	34	3333.7407	3404.3532	12.0066
48	Cte	T+S	D+S+F	34	3333.8551	3404.4676	12.1210
49	Cte	T+S	D+A+F	34	3334.3015	3404.914	12.5674
50	Cte	T+S	A+S	33	3336.7421	3405.2026	12.8560
51	Cte	T+S	D+S	33	3336.933	3405.3936	13.0470
52	Cte	T+S	D+A	33	3337.3237	3405.7842	13.4376
53	Cte	T+S	D+A+S+F	35	3333.3468	3406.116	13.7694
54	Cte	T+S	D+A+S	34	3336.3562	3406.9687	14.6221

Abbreviations: A, reproductive age (sub adult or adult); D, current density (categorical: high or low); F, field type (fallow or cultivated); R, cumulative rainfall of the previous two months (categorical: low, medium or high); S, sex (male or female); T, full time dependence where the probability could change every trapping session; cte, model with no fixed effects, only an intercept.

4.3.2 Maturation estimates

From the best fitting model (as described above) we found a monthly maturation probability of 0.13 (95% CI: 0.09 – 0.18). This value did not differ between males and females, nor did it change with density or rainfall.

4.3.3 Recapture estimates

To account for differences in trapping effort over the months, we allowed the recapture estimates to change monthly. We found that there were differences in recapture estimates through time with a minimal recapture probability of 0.01 (95% CI: [0.00, 0.04]) and maximal of 0.43 ([0.19, 0.70]; Fig. 4.1). The best fitting model included, besides this time dependence, an additive effect of sex where males had, on average, a higher recapture probability of 0.04 (min = 0.002, max = 0.07) than females (Fig. 4.1).

4.3.4 Survival estimates

Our final model revealed that survival in *M. natalensis* was affected by an interaction between cumulative rainfall in the past two months and current density. There were no real differences in survival probability between low (0.50, [0.40, 0.61]) and high density (0.43, [0.35, 0.52]) when rainfall in the past two months was low (Fig. 4.2**)**. However, when rainfall increased in the previous two months, there were clear differences in survival probability between high and low densities. When the cumulative rainfall in the previous two months was between 300-500mm, survival probability in high densities was higher (0.85, [0.50, 0.97]) than when density was low (0.61, [0.49, 0.71]). This discrepancy in survival probability between high (0.78, [0.53, 0.92]) and low (0.45, [0.33, 0.57]) density became even larger when rainfall in the last two months was higher than 500mm (Fig. 4.2).

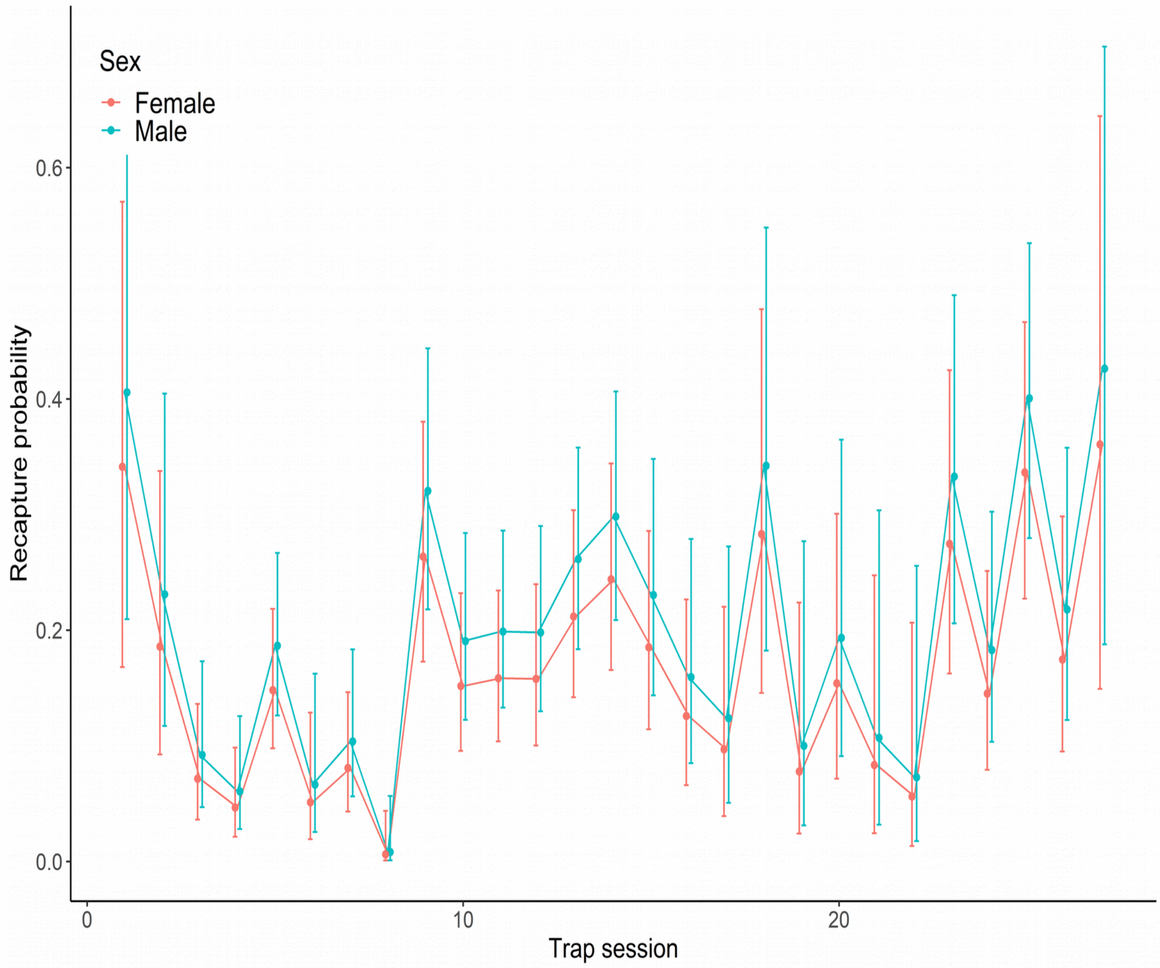


Figure 4.1: Recapture probability of males (blue lines) and females (red lines) for every trapping session. Error bars represent the 95% Confidence intervals of each estimate.

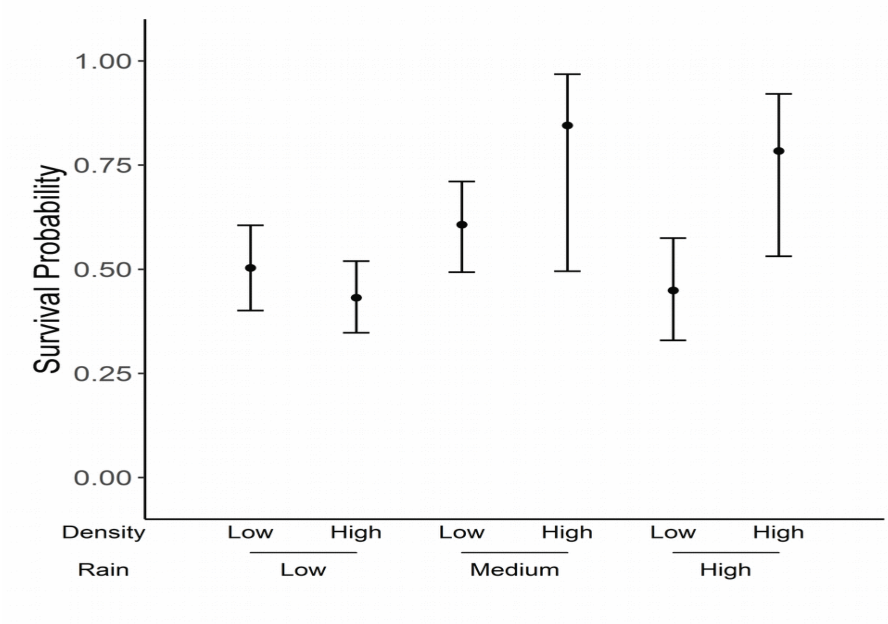


Figure 4.2: Monthly Survival probability of *Mastomys natalensis* in periods where cumulative rainfall in the last two months was lower than 300mm (Low), between 300-500mm (Medium) or higher than 500mm (high) Within these periods, there were differences in survival probability when current density was low (<10 captured individuals) or high (>10 captured individuals). The error bars represent the 95% confidence interval

4.4 Discussion

In this study survival and maturation were the key demographic processes investigated since they have been shown to play a significant role in rodent population dynamics and can be utilized to improve the timing of application of poisons for effective control of rodents (Lima *et al*., 2003). Additionally, the recent scientific developments emphasize an ecologically based rodent control approach with integration of forecasting systems (Davis *et al*., 2004; Palis *et al*., 2011), therefore understanding survival and maturation processes will improve on forecasting systems. Regionally, while considerable information on survival and maturation of *M. natalensis* and how these traits shape population abundance exists, these have majorly concentrated in Tanzania and thus regional models are not feasible (Swanepoel *et al*., 2017). For example, survival and maturation have been studied and results are variable and dependent on both density-dependent and density-independent factors (Leirs *et al*., 1994; Sluydts *et al*., 2007; Massawe *et al*., 2012;

Mulungu *et al*., 2015). These demographic characteristics play a significant role in regulating population growth and have been identified as important aspects in regards to rodent pest management in any given geographical location (Leirs *et al*., 1994; Lima *et al*., 2003; Sluydts *et al*., 2007).

4.4.1 Maturation

In this study maturation rates were not influenced by the different variables (rainfall, population density, age, sex and habitat). The results thus differ from earlier studies that have shown clear relationships with some of the mentioned response variables (Leirs *et al*., 1997; Sluydts *et al*., 2007). For example, Leirs *et al*. (1997) estimated maturation rate of female *M. natalensis* to increase with an increasing amount of preceding rainfall, which is a trigger for increased food availability for the animal's quick maturation. The insignificant relationship in our study may thus possibly be attributed to the mosaic mixed cropping system in the study area, a scenario which could possibly have offered a diversity of foods to the surviving animals for normal growth and development even during periods of absence of seasonal crops like maize, beans and other cereals. It is likely that the animals consumed other available tuber food crops including sweet potatoes and cassava, which comprise almost the same nutrients like the cereals for normal growth and development (Amagloh *et al*., 2015).

Alternatively, the low recapture numbers obtained in the study might have possibly affected attainment of significant effects of the various studied response variables on maturation rates of the animals. In another closely related study on maturation estimates of field voles in Europe, it was observed that maturation estimates studies may need to be conducted in large outdoor enclosures and monitored more closely, about 7-10 days interval to easily capture the sudden changes in growth (Eccard *et al*., 2002). Therefore, an additional outdoor enclosed experiment or a trapping at more regular intervals (7-10 days) could provide more reliable data to estimate the effect of sex, rainfall and population density of the animals on maturation rates of *M. natalensis* in Uganda.

4.4.2 Survival

On the other hand, survival in *M. natalensis* was affected by an interaction between cumulative rainfall in the past two months and current population density. Model estimates revealed higher survival rates during the medium to high rainfall (300mm and above) and was more pronounced when population density was high (above 10animals/ha). These findings are in agreement with earlier studies that reported higher survival rates of small rodents in rainfall seasons (Lima *et al*., 2001; Sluydts *et al*., 2007). Abundant rainfall is reported to result into increased availability of food resources for rodents and abundant vegetation cover, which provides protection to rodents from predatory animals thus increasing their chances of survival (Leirs, 1995; Mlyashimbi *et al*., 2018). Consequently, during the dry seasons (low rainfall) there is reduced vegetation cover which is likely to expose the animals to predation. The above condition results into reduced food resource availability thus increased competition for food among animals which is reported to affect survival rates (Lima *et al*., 2001).

Secondly, our study report discrepancy results of higher survival at higher population densities. Most previous studies have demonstrated low survival at higher animal densities (Leirs *et al*., 1997; Sluydts *et al*., 2007). The contrary results in our study could have originated from two possible phenomena; the generally low population density during the study which could only allow two population density categories; low density (less than 10 animals/ha) and high density (above 10 animal/ha). When compared with similar referenced studies above, they report up to about 300animals/Ha at high population density. Therefore, our categorization of more than 10 individuals/ha as high may have been a small number to result into significant competition for the available resources to cause a negative effect on animal survival. In fact Leirs *et al*. (1997) suggested that studies on effect of density dependent factors are more effective when conducted on highly fluctuating populations. Alternatively, the findings could be attributed to the effect of reduced predation as a result of the prey saturation effect when animals where more than 10 compared to when they were less than 10 individual animals/Ha thus increasing the survival probability at high density. The later explanation was also suggested by Julliard *et al*. (1999) as one possible reason for the positive survival effect on sub adult *M. natalensis* at high population density. The findings further confirm that density indeed affects demographic characteristics differently under different selection pressure as predicted by earlier theories of life history evolution (Schaffer, 1974; Charlesworth, 1994).

On the other hand, this study showed that sex and age of the animals had no significant relationship on survival of *M. natalensis* whereas earlier studies in the East African region showed that they significantly influence survival (Leirs, 1995; Julliad *et al*., 1999; Sluydt *et al*., 2007). This phenomenon may be backed up by Lidicker (1978) earlier study who predicted that demographic variations can occur within same species among different populations. Therefore, the population of *M. natalensis* in Uganda seems to differ from the other populations in the region since age and sex does not affect survival compared to other populations in Eastern Africa.

4.4.3 Recapture

In terms of recapture probability estimates, this study demonstrated higher recapture probabilities for males compared to females. Explanations to this finding could be due to the fact that males tend to exhibit high mobility when they are sexually mature as they roam around in search for multiple mates (Kirkland and Layne, 1989; Kennis *et al*., 2008). The increased male mobility has been shown to result into increased exposure to predation (Koivunen *et al*., 1996), pathogens (Isaac, 2005) and also reduced foraging time as animals are exposed to unfamiliar habitats (Skorping and Jensen, 2004). Secondly, another possible explanation for high recapture probability for males in this study could be linked to the different home range sizes for the different sexes in *M. natalensis*. For example, adult females have been shown to have smaller home-ranges during breeding seasons as they stay close to their burrow to feed pups or to protect them against infanticide (Ebensperger and Blumstein, 2007; Borremans *et al*., 2014; Stacey *et al*., 2017).

4.5 Conclusion

This study has showed that the fitness of *M. natalensis* as demonstrated through survival, maturation and recapture probability was variable in the agroecosystem in the Lake Victoria crescents in Uganda. Specifically, animal survival was enhanced when rainfall appeared in the last two months and when current animal population density was high. Rainfall as a factor is associated with increasing vegetation, which provides both quality and quantitative food but also offers nesting sites for the animals. These results have thus shown that fitness of *M. natalensis* is highly dependent on vegetation which is produced as a result of rainfall. Management efforts should therefore be timed and concentrated during the rainy seasons, when vegetation is abundant to prevent further population build up in the following months which could result into high crop damage. In addition, fitness measured in terms of recapture probability showed that females have less chances of being recaptured. The results have important applications on the management strategy to be applied, for example the use of traps may not be efficient in controlling female populations thus their capture rates are low. On the contrary, maturation rate of the animals was not significantly influenced by sex, rainfall and population density in this study. The unique results were attributed to possibly be due to the low recapture rates of the animals in the study which could have affected attainment of variations in maturation rates to obtain significant relationships with predictor variables. To a lesser extent the authors attribute the mixed cropping system practiced in this area, to have offered a diversity of foods to the animals thus the animals were not constrained by the effect of lack of nutritious food for normal growth.

Acknowledgments

We are extremely grateful to the Ecologically Based Management of Rodent Pests in Maize and Rice in East Africa, a project granted to Sokoine University of Agriculture (Project number OPP1112579) by the Bill and Melinda Gates foundation. We would like to thank the project research team; Ramadhan Idd Kingunguli, Alex Kisakye and Khalid Kibwana for their help with practical and fieldwork, and the farmers who offered their land where the trials were established. We also acknowledge the support from Busitema University, Namasagali campus for their support in different aspects during the implementation of field activities in the study sites.

Ethical considerations

This research was carried after thorough review by Sokoine University of Agriculture, Tanzania, Wild life department. Further research approval was obtained from the Uganda Wild life Authority for conducting research on live animals in Uganda.

Authors' Contributions

Mayamba. A, Mulungu. L. S and Massawe. A.P; conceived the ideas and designed methodology. All authors contributed to data collection. Vanden Broecke Bram, Mayamba A, Mulungu. L.S, Leirs, H. and Isabirye. B analyzed the data and led the writing of the manuscript. All authors critically reviewed the drafts and gave final approval for publication.

Data accessibility statement

We the authors of this manuscript have collectively agreed to have the data used in the results section to publicly avail that information to a public domain Dryad once this paper has been accepted for publication under the Journal of Mammalia.

Yours sincerely, **Alex Mayamba**, on behalf of the authorship team

4.6 References

Amagloh FK, Chiridza T, Lemercier ME, Broomfield A, Morel PCH. and Coad J. (2015). Sweetpotato- and Cereal-Based Infant Foods: Protein Quality Assessment and Effect on Body Composition Using Sprague Dawley Rats as a Model. *Plos One* 10: 2 -11.

Begg CM, Begg KS, Du Toit JT. and Mills MGL. (2005). Spatial organization of the honey badger *Mellivora capensis* in the southern Kalahari: home-range size and movement patterns. *Journal of Zoology* 265: 23 - 35.

Borremans B, Sluydts V, Makundi, RH. and Leirs H. (2015). Evaluation of short-, mid- and long-term effects of toe clipping on a wild rodent. *Wildlife Research* 42: 143–148.

Borremans B, Hughes NK, Reijniers J, Sluydts V, Katakweba AAS, Mulungu, L.S. and Leirs H. (2014). Happily, together forever: temporal variation in spatial patterns and complete lack of territoriality in a promiscuous rodent. *Population Ecology* 56: 109–118.

Burnham, KP. and Anderson DR. (2004). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* 2nd edition, Springer, New York. 119pp.

Choquet R, Rouan L. and Pradel, R. (2009a). Program E-Surge: A Software Application for Fitting Multievent Models. In D. L. Thomson, E. G. Cooch and M. J. Conroy (Eds.), *Modeling Demographic Processes In Marked Populations.* pp. 845 – 865.

Choquet R, Lebreton J D, Gimenez O, Reboulet AM. and Pradel R. (2009b). U-CARE: Utilities for performing goodness of fit tests and manipulating Capture Recapture data. *Ecography* 32: 1071–1074.

Cole DC. and Cole L. (2000). A long-term study of *Rattus norvegicus* in the London borough of Enfield using baiting returns as an indicator of sewer population levels. *Epidemiology and Infection* 125: 441 – 445.

Colvin BA. and Jackson WB. (1999). Urban rodent control programs for the 21st century. *Ecologically-based Management of Rodent Pests* (eds G.R. Singleton, L.A. Hinds, H. Leirs and Z. Zhang), ACIAR Monograph no. 59. Australian Centre for International Agricultural Research, Canberra. pp. 243–257.

Cowan DP, Quy RJ. and Lambert MS. (2003). Ecological perspectives on the management of commensal rodents. *Rats, Mice and People: Rodent Biology and Management* (eds G.R. Singleton, L.A. Hinds, C.J. Krebs and D. Spratt), ACIAR Monograph no. 96. Australian Centre for International Agricultural Research, Canberra. pp. 433–439.

Davis SA, Leirs H, Pech R, Zhang Z and Stenseth NC. (2004). On the economic benefit of predicting rodent outbreaks in agricultural systems. *Crop Protection* 23: 305–314.

Ebensperger LA. and Blumstein DT. (2007). Nonparental infanticide. In: Wolff JO, Sherman PW (eds) *Rodent societies: an ecological and evolutionary perspective*, 1st edn. The University of Chicago Press, Chicago and London, pp. 267–279.

Eccard JA, Klemme I, Horne TJ. and Ylönen H. (2002). Effects of competition and season on survival and maturation of young bank vole females. *Evolutionary Ecology* 16: 85–99.

Happold, DCD. (ed.). (2013). *Mammals of Africa,* volume III*:* Rodents, Hares and Rabbits. Bloomsbury Publishing, London. 784pp.

Haneishi Y, Okello S, Asea G, Tsuboi T, Maruyama A, Takagaki, M. and Kikuchi, M. (2013). Exploration of rainfed rice farming in Uganda based on a nationwide survey: Evolution, regionality, farmers and land. *African Journal of Agriculture Research* 8: 3318 - 3329.

Hayes LD, Chesh AS. and Ebensperger LA. (2007). Ecological predictors of range areas and use of burrow systems in the diurnal rodent, Octodon degus. *Ethology* 113: 155-165.

Isaac JL. (2005). Mass loss during the mating season in male common brushtail possums (*Trichosurus vulpecula*): implications for age-specific variation in mating strategy. *Journal of Zoology* 266: 181–185.

Jackson WB. (1998). *Ecology of pest rodents in the urban environment. Modern Trends in Ecology and Environment* (ed. R.S. Ambasht), Backhuys, Leiden. The Netherlands. pp. 101– 113.

Julliard R, Leirs H, Stenseth, NC, Yoccoz NG, Prévot-Julliard AC, Verhagen R. and Verheyen, W. (1999). Survival-variation within and between functional categories of the African multimammate rat. *Journal of Animal Ecology* 68: 550–561.

Kennis J, Sluydts V, Leirs H. and van Hooft WFP. (2008). Polyandry and polygyny in an African rodent pest species, *Mastomys natalensis*. *Mammalia* 72: 150-160.

Kirkland GL. and Layne N. (1989). Advances in the study of *Peromyscus (Rodentia)* Texas Tech University Press. 178pp.

Koivunen V, Korpima E. and Hakkarainen H. (1996). Differential avian predation on sex and size classes of small mammals: doomed surplus or dominant individuals? *Annual Zoology Journal* 33: 293–301.

Lambert MS, Quy RJ, Smith RH. and Cowan DP. (2008). The effect of habitat management on home-range size and survival of rural Norway rat populations. *Journal of Applied Ecology* 45: 1753 – 1761.

Leirs H. (1992). *Population ecology of Mastomys natalensis (Smith 1834) multimammate rats: possible implications for rodent control in Africa*. PhD Thesis. University of Antwerp, Belgium. 120pp.

Leirs H, Verhagen RON, Christopher AS, Patrick M. and WNV. (1997a). Spatial dynamics of Mastomys natalensis in a field-fallow mosaic in Tanzania . *Belgium Journal of Zoology* 127: 29–38.

Leirs H, Stenseth NC, Nichols JD, Hines JE, Verhagen R. and Verheyen W. (1997b). Stochastic seasonality and nonlinear density dependent factors regulate population size in an African rodent. *Nature* 389: 176–180

Leirs H, Stuyck J, Verhagen R. and Verheyen W. (1990). Seasonal variation in growth of *Mastomys natalensis* (Rodentia: Muridae) in Morogoro, Tanzania. African *Journal of Ecology* 28: 298–306.

Lidicker WZ. (1978). *Regulation of numbers in small mammals—historical reflections and synthesis*: in Populations of small mammals under natural conditions (D. P. Snyder, ed.). Special Publication Series, Pymatuning Laboratory of Ecology, University of Pittsburgh 5: 1–237.

Lima M. and Jaksic FM. (1999). Population dynamics of three Neotropical small mammals: Time series models and the role of delayed density-dependence in population irruptions. *Australian Journal of Ecology* 24: 25-34.

Lima M, Julliard R, Stenseth NC. and Jaksic FM. (2001). Demographic dynamics of a neotropical small rodent (*Phyllotis darwini*): feedback structure, predation and climatic factors. *Journal of Animal Ecology* 70: 761-775.

Makundi RH, Oguge NO. and Mwanjabe PS. (1999). *Rodent Pest Management in East Africa – an ecological approach. In: Ecologically-Based Rodent Management* (Eds G. R. Singleton, L. Hinds, H. Leirs and Z. Zhang). For International Agricultural Research, Canberra, Australia. pp. 460–476.

Mariën J, Sluydts V, Borremans B, Gryseels S, Vanden Broecke B, Sabuni CA. and Leirs H. (2018). Arenavirus infection correlates with lower survival of its natural rodent host in a long-term capture-mark-recapture study. *Parasites and Vectors* 11: 90.

Mdangi M, Mulungu LS, Massawe AW, Eiseb S J, Tutjavi V, Kirsten, F. and Belmain, S.R. (2013). Assessment of rodent damage to stored maize (*Zea mays* L.) on smallholder farms in Tanzania. *International Journal of Pest Management* 59(1): 55–62.

Massawe AW, Makundi RH, Mulungu LS, Katakweba A. and Shayo TN. (2012). Breeding dynamics of rodent species inhabiting farm-fallow mosaic fields in Central Tanzania. *African Zoology Journal* 47: 128 – 137.

Mlyashimbi ECM, Mariën J, Kimaro DN, Tarimo AJP, Isabirye M, Makundi R. H, Massawe AW, Mdangi ME, Kifumba D, Nakiyemba A, Leirs, H, Belmain SR. and Mulungu LS. (2018). Relationships between seasonal changes in diet of Multimammate rat (*Mastomys natalensis*) and its breeding patterns in semi-arid areas in Tanzania, *Cogent Food and Agriculture* 4: 1.

Mulungu LS. (2017). *Control of rodent pests in maize cultivation*: the case of Africa. *In: Achieving sustainable maize cultivation* 2: (ed. Dr Dave Watson). Francis Dodds, Burleigh Dodds Science Publishing. 82 High Street Sawston Cambridge. UK. 318 - 337pp.

Mulungu LS, Ngowo V, Mdangi EM, Katakweba AS, Tesha P, Mrosso FP, Mchomvu M, Massawe A.W, Monadjem A, Kilonzo B. and Belmain SR. (2015a). Survival and recruitment of the multimammate mouse, *Mastomys natalensis* (Smith 1834), in a rice agro-ecosystem. *Mammalia* 80: 205 – 210.

Mulungu LS, Sixbert V, Ngowo V, Mdangi M, Katakweba AS, Tesha P, Mrosso FP, Mchomvu, M, Kilonzo, BS. and Belmain, SR. (2015b). Spatio-temporal patterns in the distribution of the multimammate mouse, *Mastomys natalensis*, in rice crop and fallow land habitats in Tanzania. *Mammalia* 79: 177 - 184.

Musiitwa F. and Komutunga ET. (2001). Agricultural systems. In Joseph K. Mukiibi ed. *Agriculture in Uganda. NARO*, CTA and Fountain Publishers. pp. 220 - 230.

Oli MK. and Dobson FS. (2001). Population cycles in small mammals: the α-hypothesis. *Journal of Mammalogy* 82: 573–581.

Oswald A. and Ransom JK. (2001). Striga control and improved farm productivity using croprotation. *Crop Protection* 20: 113–120.

Pollock K.H. (1982). A Capture-Recapture Design Robust to Unequal Probability of Capture. *The Journal of Wildlife Management* 46: 752.

Pradel R. (2005). Multievent: An Extension of Multistate Capture-Recapture Models to Uncertain States. *Biometrics* 61: 442–447.

Pradel R, Wintrebert CMA, Gimenez, O, Biometrics S, Mar N, Pradel R. and Gimenez O. (2003). A Proposal for a Goodness-of-Fit Test to the Arnason-Schwarz Multisite Capture-Recapture Model. *International Biometrics Society* 59: 43–53.

Rémi C, Anne-marie R, Jean-Dominique L, Olivier G. and Roger P. (2005). *U-CARE 2 . 2 User 's Manual*. CEFE, Montpellier, France. 34pp.

Saïd S, Gaillard JM, Duncan P, Guillon N, Servanty S, Pellerin M, Lefeuvre K, Martin C. and Van Laere G. (2005). Ecological correlates of home range size in spring-summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. *Journal of Zoology* 267: 301 - 308.

Singleton GR, Brown PR, Jacob J. and Aplin KP. (2007). Unwanted and unintended effects of culling: A case for ecologically-based rodent management. *Integrative Zoology* 2: 247–259.

Skorping A. and Jensen KH. (2004). Disease dynamics: all caused by males? *Trends in Ecology and Evolution* 19: 219–220.

Sluydts V, Davis S, Mercelis S. and Leirs H. (2009). Comparison of multimammate mouse (Mastomys natalensis) demography in monoculture and mosaic agricultural habitat: Implications for pest management. *Crop Protection* 28: 647–654.

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

Stacey LH, Brown CR. and Booth W. (2017). Ecological and phenotypic effects on survival and habitat transitions of white-footed mice. *Journal of Mammalogy* 98: 1356 –1366.

Stenseth NC, Leirs H, Skonhoft A, Davis SA, Pech, RP, Andreasson HP, Singleton GR, Lima M, Machangu RS, Makundi RH, Zhang, Z, Brown PR, Shi D. and Wan X. (2003). Mice, rats and people: the bio-economics of agricultural rodent pests. *Frontiers in Ecology and Environment* 1: 367 - 375.

Swanepoel LH, Swanepoel CM, Brown PR, Eiseb SJ, Goodman SM, Keith M. and 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.

White GC. and Burnham KP. (1999). Program MARK, survival estimation from populations of marked animals. *Bird Study* 46: 120- 138.

White J, Horskins K. and Wilson J. (1998). The control of rodent damage in Australian macadamia orchards by manipulation of adjacent non-crop habitats. *Crop Protection* 17: 353 - 357.

Witmer G. (2007). The ecology of vertebrate pests and integrated pest management (IPM). *In ‘Perspectives in Ecological Theory and Integrated Pest Management*’. (Eds M. Kogan and P. Jepson.) Cambridge University Press: Cambridge, UK. 410 pp.

CHAPTER FIVE

PAPER V

FACTORS INFLUENCING THE DISTRIBUTION AND ABUNDANCE OF SMALL RODENT SPECIES IN AGRICULTURAL LANDSCAPES IN EASTERN UGANDA

Alex Mayamba[1, 2, 4 *], Robert M. Byamungu[2], Bram Vanden Broecke[3], Herwig Leirs[3], Apia W. Massawe[4], Proches Hieronimo[5], Alice Nakiyemba[1], Moses Isabirye[1], David Kifumba[1], Didas N. Kimaro[5], Mshaka E. Mdangi[6] and Loth S. Mulungu[4]

[1]Faculty of Natural Resources and Environment, Busitema University, P. O. Box 236, Tororo, Uganda,

[2]Department of Wildlife and Management, Sokoine University of Agriculture, Tanzania,

[3]Evolutionary Ecology Group, Universiteit Antwerpen, Universiteitsplein 1, 2610 Wilrijk, Belgium,

[4]Pest Management Centre, Sokoine University of Agriculture, P. O. Box 3110, Morogoro, Tanzania,

[5]Department of Engineering Sciences and Technology, Sokoine University of Agriculture, P.O. Box 3003, Morogoro, Tanzania.

[6]Ministry of Agriculture, P.O. Box 2182, Dodoma, Tanzania

***Corresponding Author**: Alex Mayamba,

Published: J. Vertebr. Biol. 2020, 69(2): 20002

Available online DOI: 10.25225/jvb.20002

Email: alexmayamba@gmail.com

Abstract

Rodents continue to surface in agro ecosystem environments where they are mostly considered as agricultural pests. Their distribution and abundance are however, known to vary across fields with certain landscape characteristics favoring higher infestation than others. For example, Normalized Difference Vegetation Index (NDVI), a vegetation characteristic has been shown to greatly influence distribution and abundance of these animals in a semi-arid environment in Tanzania. Other key factors reported include elevation, climate, soil properties and land management practices with variable importance on rodent abundance in a given landscape. This study thus aimed at establishing the various ecological factors in the landscape that influence small rodent distribution and abundance across agricultural landscapes in Uganda, information that could be used to improve development of adaptive control measures for rodent pests. Rodent trapping surveys were conducted in three agro ecosystem landscapes: Butaleja, Mayuge and Bulambuli in eastern Uganda in the period of November 2017 to June 2018 covering both dry and wet seasons. Data were collected on rodent abundance and richness, vegetation characteristics, land use/cover characteristics, soil physical properties, land use/cover characteristics on farm management practices and soil physical characteristics at quadrat level. Additionally, Geological Information System (GIS) and remote sensing were used to generate vegetation characteristics (NDVI), land use/cover from satellite images. Analysis of data was performed using the Boosted Regression Tress (BRT) modelling technique and One -Way ANOVA to establish the key predictor variables that influence rodent abundance and richness. Our results showed that land use characteristics specifically crop field status (state of the field including hygiene, crop type and growth stage) is the most important predictor variable with an overall relative importance of 31.8% prediction for rodent abundance across the studied landscape units.

Similarly, the BRT model for species richness showed field crop status scoring highest with an overall relative importance of 39.8% at predicting small rodent species richness. Second in importance for overall rodent abundance across the landscapes was NDVI with 13.8% while percentage composition of soil silt particles ranked second with 15.6% for species richness. Our findings have important implications on small rodent management, where land use characteristics especially the state of the field crops should be a critical concern as different conditions tend to sustain rodent abundances differently. The study thus recommends that control efforts should be planned to involve all farmers in farming community as rodents can thrive in a wide range of crop fields including sugarcane plantations where they can dwell and grow into high population densities and can later attack cereal crops resulting into substantial crop damage.

Key words: Boosted Regression Trees, abundance, NDVI, field crop status, landscape units

5.1 Introduction

Agriculture is the most dominant land use throughout much of Uganda (MAAIF, 1996). Sadly, this sector suffers from several production constraints such as droughts, low soil fertility, poor quality seeds, as well as pests and diseases. The latter is considered as the most important factor reducing the potential agriculture production resulting into chronic food insecurity in most rural communities in the country (Oerke, 2006; MAAIF, 2010). Among the different pests, rodents are responsible for a significant amount of pre and post-harvest losses particularly to cereal crops in Uganda and the rest of East African region (Leirs *et al*., 1997; Makundi *et al*., 2006; Mulungu *et al*., 2010; Mayamba *et al*. 2019). Their distribution and abundance have been shown to vary temporaly and spatially as regulated by different ecological factors including land use/land cover types (Franscina *et al*., 2014; Heironimo *et al*., 2014), soil properties (Meliyo *et al*., 2015, Massawe *et al*., 2008) climate (Leirs *et al*., 1997, 1995), land management practices (Heironimo *et al*., 2014; Massawe *et al*., 2006). For instance NDVI, a vegetation characteristic index which indicates the greeness of an area, has been demostrated to be the most important predictor variable with a high positive relationship on small rodent richness and abundance in a semi arid climate in Tanzania (Chidodo, 2017). Other earlier reports have demostrated that rainfall is the most important predictor variable for population abundance particularly for *Mastomy natalensis* in a bimodal climate in Tanzania (Leirs *et al*., 1997). Additionaly, soil types have also been linked to infleunce rodent abundance with sandy loam soils shown to sustain higher rodent abundances compared to clay soils (Meliyo *et al*., 2015; Mlyashimbi *et al*., 2019). Given the dynamics in the influence of various ecological factors to rodent abundance, there is need to further analyze the landscape ecological factors in the region in order to establish the key predictors in the different landscapes to improve development of suitable and appropriate control efforts including development of predictive models.

Currently, control efforts are normally reactive and aimed at mortality control (Mulungu *et al*., 2010; Krijger *et al*., 2017), via the use of different chemicals (rodenticides), which are relatively expensive for the peasant farmers, affect non target organisms in the environment and less effective as there is often animal recolonization shortly after treatment (Stenseth, 2001; Stenseth *et al.*, 2003; Singleton *et al*., 2007; Mulungu *et al*., 2010). Better and effective rodent control measurements are therefore needed which are based on ecological information (Mulungu, 2017; Swanepoel *et al*., 2017). For instance, Parry and Schellhorn (2013) suggest that there is a large variation in pest infestation probability between landscapes, suggesting that certain features of the landscape are responsible in making a certain field more or less prone to pest infestations.

Agricultural land use is another important attribute affecting rodent abundance. Indeed, the intensification of agriculture tends to favor more generalist species compared to habitat-specialist species which prefer low intensified farmland landscapes (Norma *et al*., 2003; Butet *et al*., 2006; Fraschina *et al*., 2014). Additionally, the use of machinery, introduction of new crops, changing agricultural practices and farming systems (Massawe *et al*., 2006; Robinson *et al*., 2012) and the growing use of chemicals such as fertilizers and pesticides are reported to influence the dynamics of biodiversity in agricultural landscapes (Mclaughlin and Mineau, 1995; Stoate *et al*., 2001).

Unfortunately, despite the importance of rodent-caused damage in agricultural landscape agro ecosystems, knowledge on the key factors influencing rodent distribution and abundance is still minimal in Uganda (Mayamba *et al*., 2019). So far, the available studies on this subject in the country provide information on the ecological aspects of rodents in national parks and natural forest landscapes (Southern, 1962; Delany, 1971, Isabiryea and Kasenene, 1987; Clausnitzer and Kityo, 2001). An alternative is to look at studies from other regions such as Tanzania where most of the studies that focused on the role of key ecological factors on rodent abundance have been conducted (Kimaro *et al*., 2014; Hieronimo *et al*., 2014; Swanepoel *et al*., 2017; Chidodo *et al*., 2019). However, this information is limited to the studied localities and difficult to extrapolate to other regions with different environments. For example, the application of NDVI reported as the most important predictor variable of rodent abundance in a unimodal semi-arid region in Tanzania (Chidodo, 2017) could be different in areas with a bimodal rainfall pattern. It is therefore, important to study key ecological factors that shape rodent species abundance in any given locality in order to design accurate management options and develop rodent outbreak predictive models.

This study set out to understand and document the important landscape ecological factors namely land use/cover, terrain characteristics, climate soil physical properties that influence small rodent species abundance and richness across contrasting agro ecosystem landscapes in Eastern Uganda. The information is expected to be utilized in developing more robust temporal and spatial probabilistic models for predicting potential rodent pest out breaks in the country.

5.2 Materials and Methods

5.2.1 Description of study site

The study was conducted in three districts in Eastern Uganda with contrasting agro-ecosystem; (a) Kigulu parish in Mayuge district, (06°16′S, 37° 31′E), in a mid-altitude zone (approximately 1100masl), which is characterized by small scale farming composed of mixed cropping with maize as a major seasonal food and cash crop. (b) Kapisa parish in Butalejja district (0° 57' 43.9668" N34° 5' 44.8692" E), which is a mid-to low altitude zone (approximately 1050 masl) and characterized by several swamps and low-lying areas which are supplied with water from River Manafa. These low lying- areas are utilized for growing lowland rice as a major cash crop enterprise for many of the households in the district. Other crops grown include maize, sorghum, cassava, sweet potato beans etc.

(c) Bukhalo parish in Bulambuli district: The area lies at 1° 18' 0" N and 34° 15' 0" E at the foot of Mt Egon at approximately 1160 masl and above. The area is mainly characterized by small to medium scale maize farming. During some seasons they actively grow cotton as a cash crop. A Map of the location of the study sites is shown in Fig. 5.1 and a detailed description of each of the studied sites is given in Table 5.1.

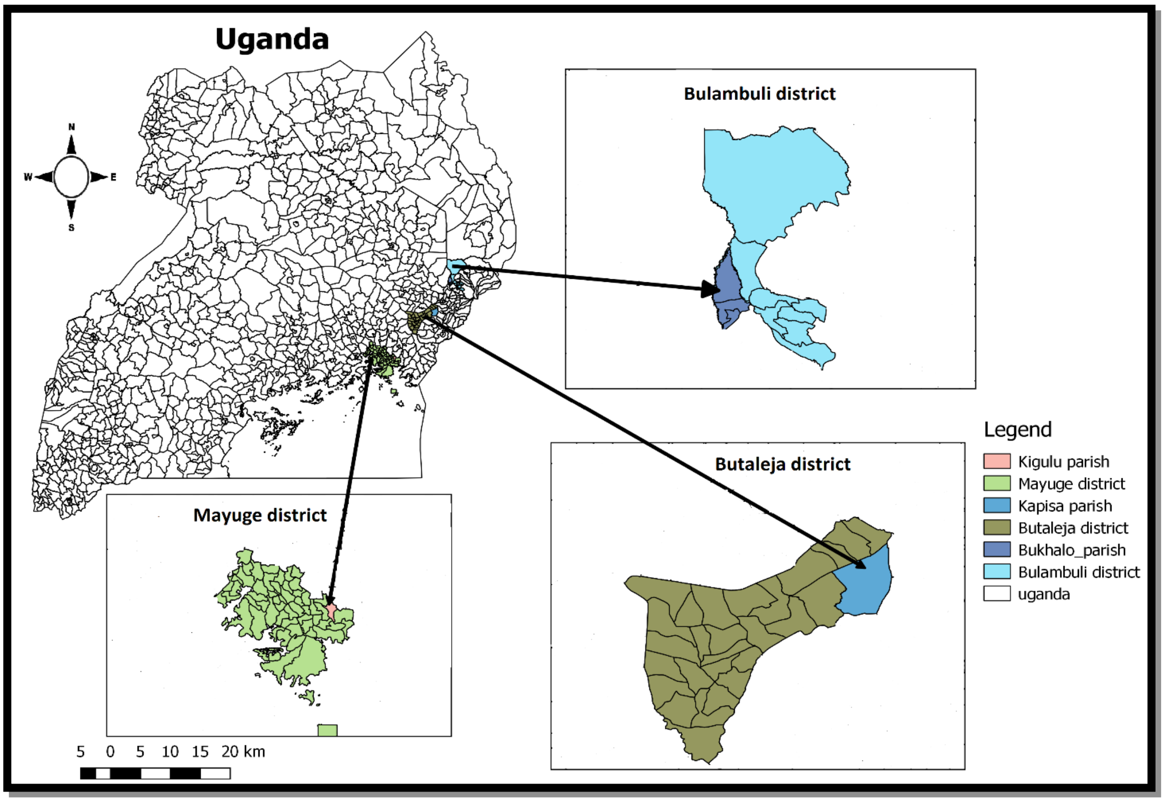


Figure 5.1: Location of study sites.

Table 5.1: Detailed description of landscape characteristics of the studied landscape units (UBOS, 2010)

Landscape units	Landscape characteristics
Kigulu parish, Kigandalo subcounty Mayuge district	➢ Mixed cropping system (maize, sweetpotato,beans,sugarcanes) ➢ Medium altitude ➢ Two distinct rainy seasons per year ➢ Crop production characterized by small fragmented plots ranging from less than an acre to about 5 acres ➢ Crop cultivation plots are intermingled with temporary fallow lands which contain shrub trees and short thickets ➢ Land clearing is by both hand hoe and oxen plough ➢ Complex of undulating and rocky hills ➢ Soil type; Black and Grey non cracking clays often calcareous with moderate drainage ➢ FAO soil class; Gleysols
Kapisa parish, Kapisa subcounty, Butaleja district,	➢ Characterized by low-lying wetland patches ➢ Mid to lowland altitude ➢ Lowland rice crop mainly grown in the wetland patches ➢ Crop cultivation plots are intermingled with temporary fallow lands which contain shrub trees and short thickets ➢ Land clearing is dominantly done by hand hoe ➢ Soil type; greyish and yellowish-brown sands and sand clays with moderate to excessive drainage ➢ FAO soil class; Gleysols or Petric plinthosols
Bukhalo parish, Bukhalo subcounty, Bulambuli district	➢ Foot hills of Mt Elgon ➢ Medium to high altitude ➢ Land clearing mainly by tractor ploughing ➢ Maize fields on about 1ha and above ➢ Crop cultivation plots are intermingled with temporary fallow lands which contain shrub trees and short thickets ➢ Sometimes practice relay cropping ➢ Soil type; dark brown clays and clay loams with moderate drainage ➢ FAO soil class; Vertisols or Luvisols

5.2.2 Acquisition of remote sensing data

Multi temporal Landsat 8 (Operational Land Imager: OLI) images were obtained to map landscape characteristics including land use/land cover types for different periods in the dry and wet seasons (Table 5.2 and Table 5.3). All the images used were already orthorectified, terrain corrected and georeferenced. The high-resolution Google earth satellite images were used for interpretation of land use and land cover (LULC) types to develop training data sets for supervised classification of vegetation characteristics.

Table 5.2: Temporal characteristics of Landsat 8 (OLI) data acquisition

District	Season	Required period	Landsat 8(OLI 30m) date
Mayuge	Dry 1	Dec, Jan and Feb	7/Feb/2018
	Wet 1	Mar, Apr and May	3/Apr/2018
	Dry 2	June and July	17/Jul/2018
	Wet 2	Sept, Oct and Nov	21/Nov/2017
Butaleja	Dry 1	Dec, Jan and Feb	15/Jan/2018
	Wet 1	Mar, Apr and May	27/Apr/2018
	Dry 2	June and July	21/Jul/2018
	Wet 2	Sept, Oct and Nov	21/Nov/2017
Bulambuli	Dry 1	Dec, Jan and Feb	15/Jan/2018
	Wet 1	Mar, Apr and May	27/Apr/2018
	Dry 2	June and July	21/Jul/2018
	Wet 2	Sept, Oct and Nov	21/Nov/2017

5.2.3 Mapping of vegetation characteristics

Remote sensing, Geographical information system (GIS) and field surveys were employed in mapping of vegetation characteristics and their associated attributes (Ralaizafisoloarivony *et al.,* 2014; Weih and Riggan, 2010). Vegetation characteristics (NDVI), land use types (land management practices, crop type, garden status and crop field status a descriptive factor including field hygiene, crop type and growth stage) were described and estimated using square quadrats (100 m * 100 m) placed randomly in each of the sub counties in the studied landscape units. Spatial location of the vegetation types were recorded using Etrex 10 Germin Global Position System (GPS) receiver with accuracy of less than 5m. Land cover classification system (LCCS) and Earth Cover Classification System (ECCS) guidelines by FAO and Open Foris Initiative (OFI) respectively, were used to identify vegetation types, from which General vegetation Classes were generated (Gregorio and Jansen, 2005).

5.2.4 Generation of general land cover and land use types

The Landsat 8 (OLI) images obtained from United States Geological Survey (USGS) at different seasonal periods, as described in Table 5.2, were used for mapping land use / land cover types as described by a set of attributes for each studied site (Table 5.1). Spatial referenced field data allowed us to define characteristic tone, texture and patterns of land use / cover classes on the display of the Landsat 8 (OLI) color composite image (Hieronimo *et al*., 2014).

Cluster pixels in Landsat 8 (OLI) satellite images were categorized into six classes using supervised classification procedure: agriculture, settlement, dry farmlands, dense vegetation, open fields and shrubs. To obtain these classes, a region of interest (ROI) was defined for each of the land cover classes in the output image. Maximum likelihood classification was performed to assign each pixel in the image to the class that has the highest probability to obtain land use/cover maps for each studied landscape site at a spatial resolution of 30m * 30m. Sample data sets created for each vegetation class was used for categorization of the spectral classes into general vegetation classes (land use/lad cover classes) in ArcMap 10.1 and Semi-Automatic Classification plugin (SCP) in the QGIS software (Fig. 5.2). These features were described at micro spatial scales to obtain sample data sets for classification of the image into land use/land cover attributes (Table 5.3) used for predicting spatial and temporal small rodent's distribution and abundance.

Table 5.3: Macro and micro land use/land cover classes

Micro Class	**Description**
Human settlement	Man-made structures e.g. buildings
Agriculture	Cultivated areas
Dense vegetation	Forested areas
Dry farmlands	Crops at dry harvest stages
Shrubs	Short thickets
Open fields	Cleared land for planting, without crop or vegetation

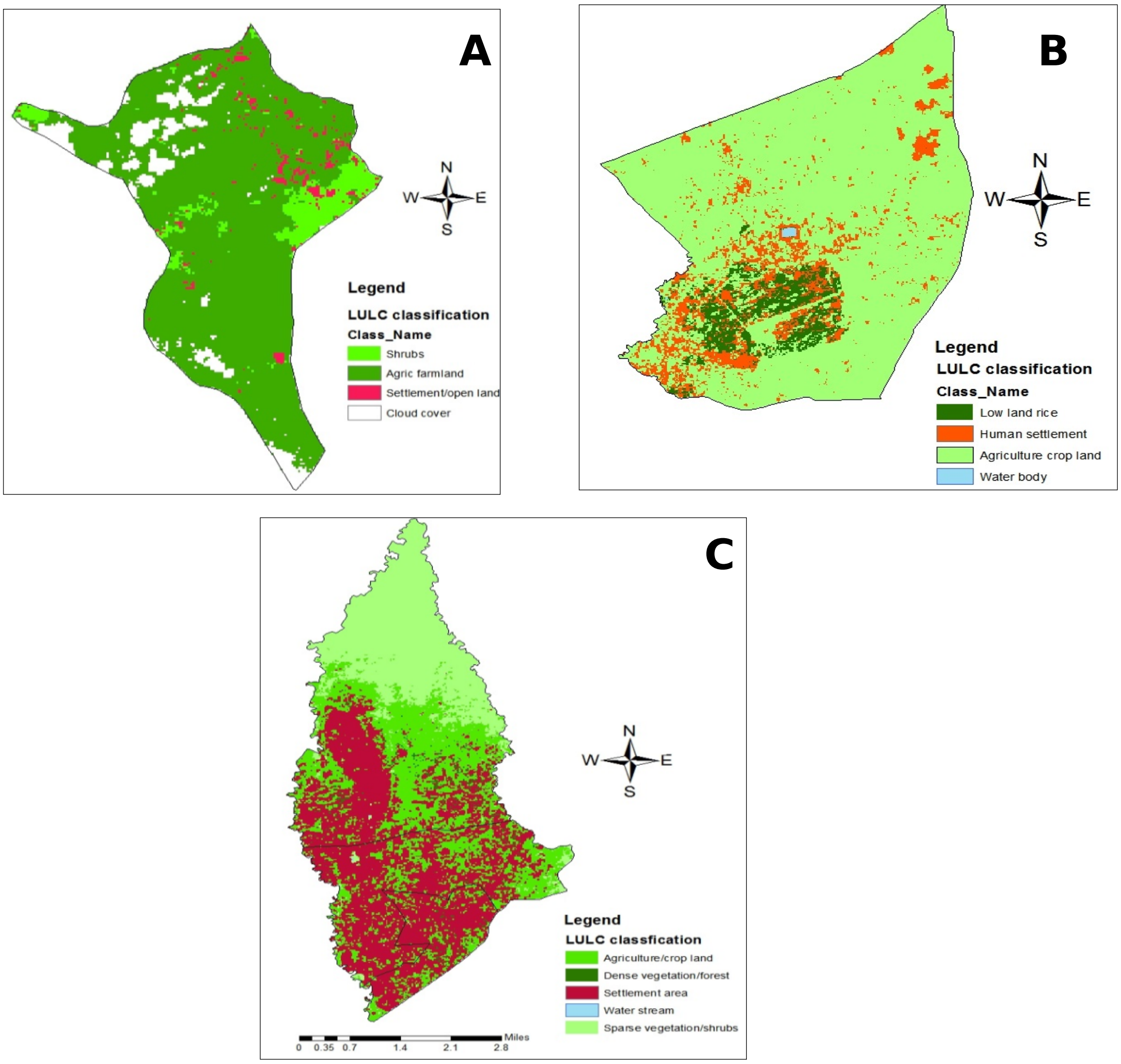


Figure 5.2: Land use/land cover (LULC) map representative of A-Kigulu parish, Mayuge district, B-Kapisa parish, Bualeja district and C-Bukhalo parish, Bulambuli district.

5.2.5 Determination of NDVI across vegetation habitats

NDVI was determined from Landsat 8 (OLI) satellite images covering the periods corresponding with the rainfall patterns as described in Table 5.2. It was calculated as the normalized difference in reflectance band between red channel (0.636-0.673µm) and Near Infrared (NIR) channel (0.851-0879 µm) electromagnetic spectrum using Equation 2 (Pettorelli *et al*., 2011).

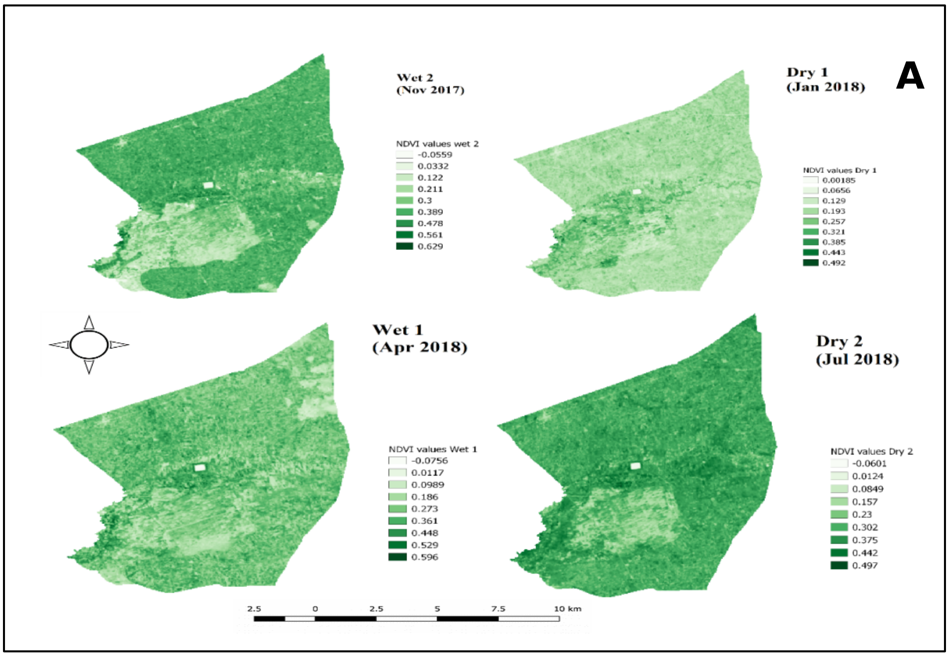
$$NDVI = \frac{NIR - R}{NIR + R}$$

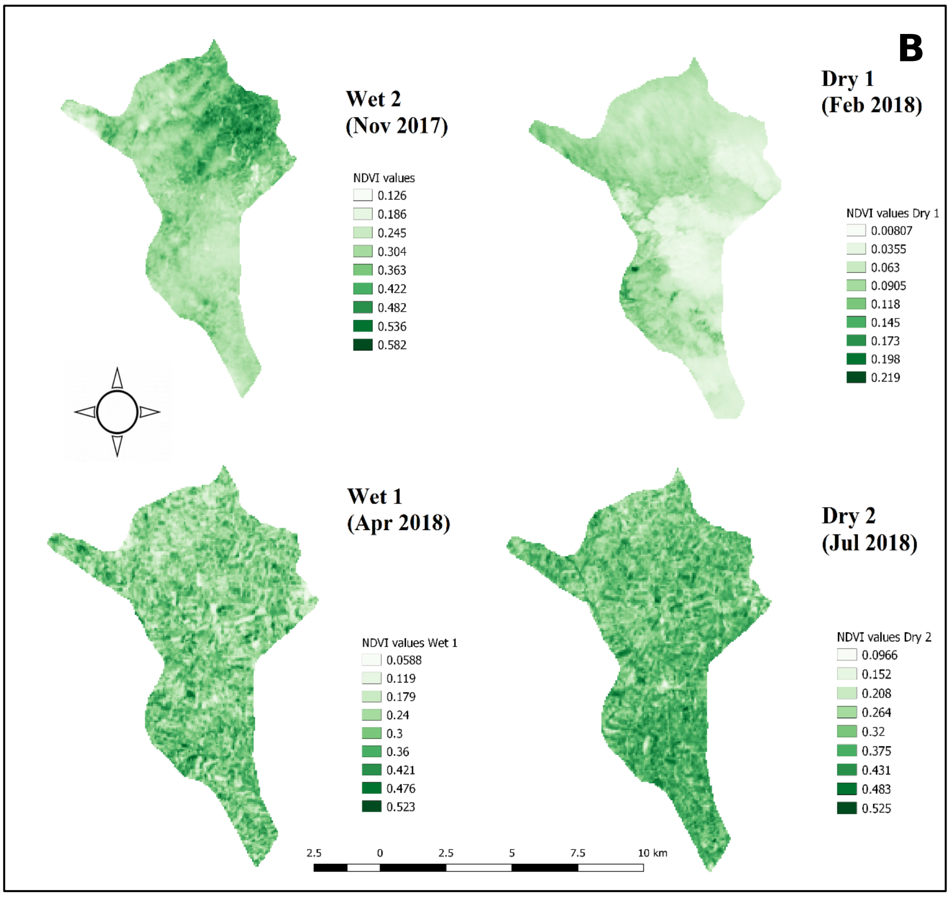
……………………………………………………………….1 Where by: NDVI = Normalized Difference Vegetation Index

R= Surface reflectance in the red portion of the electromagnetic spectrum

NIR= Reflectance in the Near Infra-Red band of the Electromagnetic spectrum

To eliminate the effect of clouds, the Maximum Value composite (MVC) algorithm in QGIS was used during NDVI data processing. In MVC procedure, the multi-temporal geo-referenced NDVI data were evaluated on a pixel basis, to retain the highest NDVI value for each pixel location. The raster calculator tool in QGIS was used to generate the NDVI maps for the different study sites across the sampling seasons (Fig. 5.3A-C).


A
Wet 2
(Nov 2017)
NDVI values wet 2
-0.0559
0.0332
0.122
0.211
0.3
0.389
0.478
0.561
0.629
Dry 1
(Jan 2018)
NDVI values Dry 1
0.00185
0.0656
0.129
0.193
0.257
0.321
0.385
0.443
0.492
Wet 1
(Apr 2018)
NDVI values Wet 1
-0.0756
0.0117
0.0989
0.186
0.273
0.361
0.448
0.529
0.596
Dry 2
(Jul 2018)
NDVI values Dry 2
-0.0601
0.0124
0.0849
0.157
0.23
0.302
0.375
0.442
0.497
2.5
0
2.5
5
7.5
10 km


B
Wet 2
(Nov 2017)
NDVI values
0.126
0.186
0.245
0.304
0.363
0.422
0.482
0.536
0.582
Dry 1
(Feb 2018)
NDVI values Dry 1
0.00807
0.0355
0.063
0.0905
0.118
0.145
0.173
0.198
0.219
Wet 1
(Apr 2018)
NDVI values Wet 1
0.0588
0.119
0.179
0.24
0.3
0.36
0.421
0.476
0.523
Dry 2
(Jul 2018)
NDVI values Dry 2
0.0966
0.152
0.208
0.264
0.32
0.375
0.431
0.483
0.525
2.5
0
2.5
5
7.5
10 km

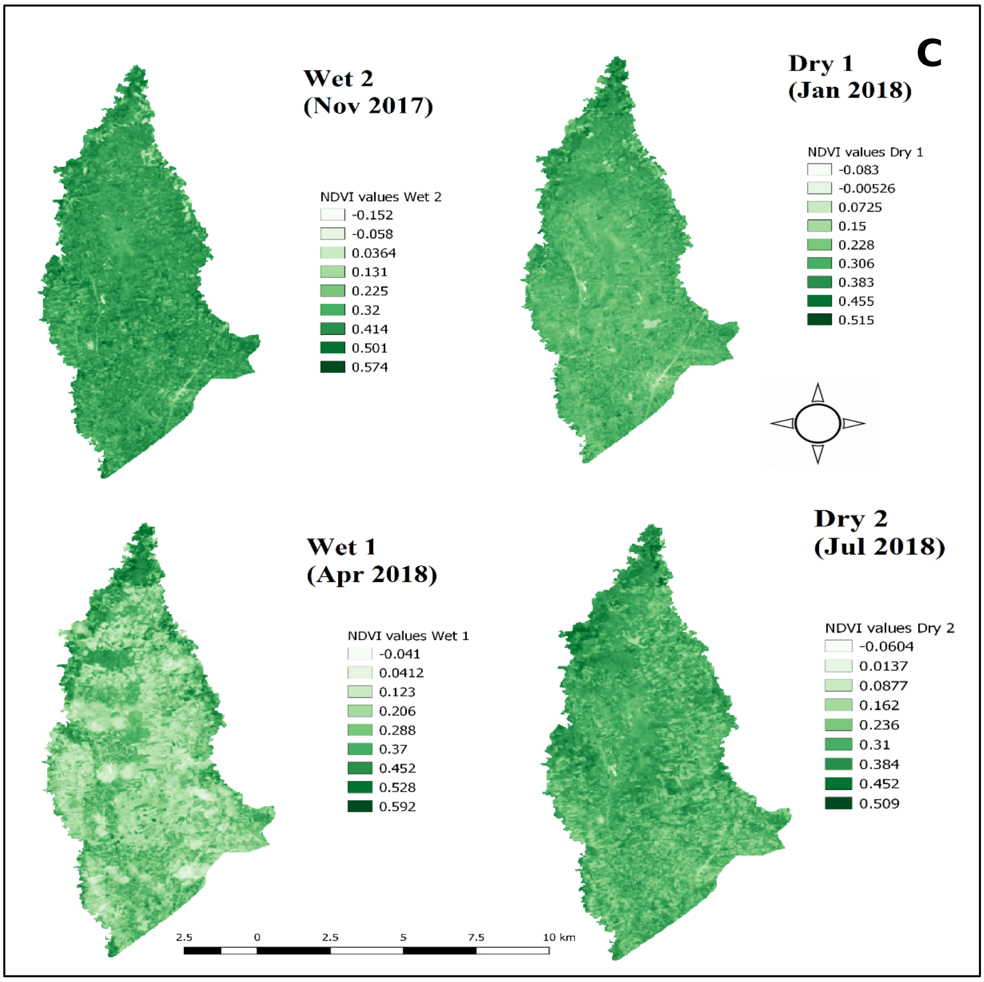


Figure 5.3: Normalized Difference vegetation Index (NDVI) maps covering the different seasons across the three study sites: A; Kapisa parish in Butaleja landscape unit, B; Kigulu parish in Mayuge landscape unit and C; Bukhalo parish in Bulambuli landscape unit.

Further extraction of NDVI values for each trapping field was done using the identifier tool where five NDVI value points were randomly selected around the georeferenced coordinates with in the trapping quadrat and an average computed as a representative NDVI value for that field. This was done for all the trapping fields.

5.2.6 Ground truthing and field characterization

Based on logistics, 20 quadrats (100 m * 100 m) in each parish in the mentioned districts (landscape units) were randomly selected using a randomization tool in QGIS, with a buffer zone around main roads and setting a minimum separation distance of 500m from each quadrat. A total of 60 quadrats were therefore geographically located for ground truthing and detailed spatial landscape vegetation characteristics were collected such as type of crop present in the field, the field hygiene (weedy or clean, stage of crop development (vegetative, mature stage, dry harvest stage and overall description of field status; combination of crop type, field hygiene and crop development and soil physical characteristics (silt sand and clay particle composition).

5.2.7 Rodent trapping

Trapping of rodents was achieved following the procedure by Aplin *et al.* (2003) using Sherman Live traps (H.B. Sherman Traps, Inc., Tallahassee, FL, USA). In each of the 60 georeferenced quadrats, 49 Sherman live traps were set in a 70 m x 70 m configuration (seven trapping lines each with seven trapping stations, 10 m apart). Traps were baited with peanut butter and maize flour and were inspected for two trap nights at each quadrat. Trapping commenced in Wet season 2 (November 2017), Dry season 1 (Jan-Feb) 2018, Wet season 1(March/April 2018) and ceased Dry season 2 (July 2018). The nomenclature by Wilson and Reeder (2005) was used as the main reference to identify the rodent species captured in the study areas and later cross referenced with Happold (2013). The community structure in this study was described as relative composition based on the trappable rodent species in the study sites.

5.2.8 Rainfall data acquisition

Data for daily precipitation for the months of data collection was obtained from the Uganda National Meteorological Authority for the three different studied landscape units (Butaleja, Mayuge and Sironko). Data were summarized into total monthly precipitation and monthly rainy days, parameters that were used late in modelling their influence on smallrodent abundance and richness across the studied landscape units.

5.2.9 Data analysis

Data on rodent species recovered from the 20 trapping grids in each landscape unit were pooled together to obtain total small rodent species composition per landscape unit.

Boosted Regression Tree modelling

Boosted Regression Tree (BRT) modelling technique was used to establish the relationships between landscape ecological factors and rodent abundance and species richness across the studied landscapes. Nineteen (19) landscape ecological factors; including mean NDVI, percent coverage of farm land, percent coverage of settlement, percent coverage of shrubs, percent coverage of dense vegetation, percent coverage of sparse vegetation, farm management practices (crop type, garden status and field crop status), soil physical characteristics (silt, sand and clay particle percentage composition), rainfall (rainy days and total monthly rainfall, rainfall seasons) and elevation were taken as predictor variable while rodent abundance and richness as the response variables. The analysis was performed separately for each landscape unit and finally pooled together to generate an overall influence of predictor variables across the studied landscape units. Boosted Regression Trees were constructed in R statistical program version 3.5.8 (R Development Core Team, 2006) using custom code (Elith *et al*., 2008) . Analyses were based on a poisson distribution. The 10-fold cross-validation (CV) was used for model development and validation, with the benefit of still using the full data set to fit the final model. Models were fitted using the gbm.step function following selection of appropriate settings for learning rate (0.01–0.0001) and bag fraction (0.5–0.75) as found by repeated trial-and-error. Tree complexity i.e. the number of nodes in a tree, was set to 5, according to recommendations by Elith *et al*. (2008) for small datasets. The measure of model performance was cv deviance and standard error (Elith *et al*., 2008, Williams *et al.*, 2010). The combination of learning rate and bag fraction settings with the lowest cv deviance and standard error was the one selected to produce the final BRT model (Williams *et al*., 2010). Also, during data exploration all predictor variables were tested for ecologically acceptable level of collinearity (i.e. individual variance inflation factor (VIF) of <5) between predictor variables (Zuur *et al*., 2010; Aertsen *et al*., 2012). Partial dependency plots were used for interpretation and to quantify the relationship between each predictor variable and small rodent abundance and richness (Elith *et al*., 2008). The land uses variables generated from Landsat images were computed as percentage coverage of each land use in the studied landscape unit Farm practices including crop type, field crop status and garden status were taken as observational records in the 100*100 quadrats.

Where the most important predictor variable was categorical, a One-Way ANOVA was performed to establish the significant effects between species richness and abundance with the predictor variables (XLSTAT, 2017 version 2019). The data was first tested for normality and where necessary log 10 transformations were conducted to meet the assumptions of ANOVA. Further, where significant effects where obtained the posthoc mean separation using the Turkey's Honest Significant Difference (HSD) test was performed.

5.3 Results

5.3.1 Rodents species richness and abundance

The study yielded 21 168 trap nights with 478 493 and 733 small rodent individuals trapped in Bulambuli, Butalejja and Mayuge landscape units respectively. These comprised of 14 rodent species with the multimammate rat (*Mastomys natalensis)* being the most abundant species with 1136 (66.7%) individual animals across the three landscape units. There were a number of species that were rare in the study area, with less than 5 individual animals trapped per species during the whole study period and these included; *Gerbilisicus kempi, Gramommys dolichurus*, *Dasmys incomtus, Oenomys hypoxanthus, Rattus rattus*, *Thallomys paedulcus* and *Steatomys parvus*. The results also showed that species richness was high in Mayuge (11 species) compared to Butaleja (9 species) and Bulambuli (8 species) landscape units (Table 5.4).

Table 5.4: Species composition of rodents in the trapping survey conducted in Mayuge, Butalejja and Bulambuli districts during the study period

Species	Number of animals in Bulambuli	Number of animals in Butaleja	Number of animals in animals in Mayuge	Total number of animals
Mastomys natalensis	346(72.4)	298(60.5)	492(67.3)	1136(66.7)
Lemniscomys zebra	28(5.9)	114(23.1)	28(3.8)	170(10)
Mus triton	45(9.4)	43(8.7)	115(15.6)	203(11.9)
Aethomys hindei	35(7.3)	13(2.6)	55(7.5)	103(6.0)
Lophuromys sikapusi	1(0.2)	2(0.4)	19(2.6)	22(1.3)
Arvicanthis niloticus	19(4)	19(3.9)	8(1.1)	46(2.7)
Thallomys paedulcus	0(0)	2(0.4)	0(0.0)	2(0.1)
Graphiurus murinus	2(0.4)	0(0.0)	11(1.5)	13(0.8)
Steatomys parvus	0(0.0)	0(0.0)	2(0.3)	2(0.1)
Gerbilliscus kempi	0(0.0)	1(0.2)	0(0.0)	1(0.1)
Dasmys incomtus	0(0.0)	0(0.0)	1(0.1)	1(0.1)
Rattus rattus	2(0.4)	0(0.0)	0(0.0)	2(0.1)
Gramommys dolichurus	0(0.0)	1(0.2)	1(0.1)	2(0.1)
Oenomys hypoxanthus	0(0.0)	0(0.0)	1(0.1)	1(0.1)
Total	478	493	733	1704
Number of species	8	9	11	14
Simpson Diversity Index	0.551	0.655	0.5788	
Chao-1	8	10	13	

5.3.2 Influence of landscape ecological factors on small rodent abundance

5.3.2.1 Vegetation characteristics

NDVI was the only considered attribute in the model and ranked second in Butaleja and Bulambuli with (24% and 19.6 % relative influence respectively, seventh in Mayuge with 5.6% relative influence and with an overall 8.5% relative influence in fourth place ranking on small rodent abundance prediction (Fig. 5.4 and 5.5).

5.3.2.2 Land use/land cover

This included both land use/cover classes and farm management practices. Out of the nineteen-predictor variable, three variables (crop field status, crop type and percent settlement coverage) were among the first eight ranked variables in predicting small rodent abundance in the different landscape units and across. Specifically, field crop status was the most important predictor variable with 34.3%, 26.7%, 65.6% and 31.8% relative importance in Butaleja, Mayuge, Bulambuli and over all respectively (Fig. 5.4 and 5.5). Results also show that the effect of field crop status in Butaleja landscape unit, showed a significant difference (df=16, F=1.75, p=0.010) on small rodent abundance, and the posthoc mean separation showed that fields with mature vegetative growing maize intercropped with beans had the highest species abundance (19±5 animals/0.5ha) and lowest abundance in mature open bushy dry maize field (Table 5.5). In Mayuge landscape unit, the effect of crop field states also showed significant differences (df = 14, F = 1.250, p = 0.026) on small rodent abundance with significantly higher abundances in mature vegetative sugarcane field (25±4 animals/0.5ha), mature vegetative maize intercropped with sweet potato (21±11) and fallow fields (19±5animal/0.5ha). Lowest small rodent abundance was recorded in mature open banana fields (Table 5.5). In Bulambuli landscape unit, also the effect of field crop status showed a significant difference (df = 11, F = 1.886, p = 0.054) on small rodent abundance with significantly higher abundances in mature vegetative clean maize intercropped with beans field (11±1 animals/0.5ha), mature bushy dry maize field (11±2 animals/0.5ha) and fallow field (11±2 animals/0.5ha), with higher abundances significantly different from the other crop fields. Lowest small rodent abundance was recorded in mature banana fields both bushy and clean (Table 5.5). The overall effect of crop field status also showed a significant difference (df = 19, F = 1.598, p = 0.054) on overall small rodent abundance. Mature vegetative sugarcane field showed significantly higher small rodent population abundance (21±5animals/0.5ha), followed by mature maize intercropped with sweet potato field (17±9 animals/0.5ha). Lowest abundances were recovered in mature banana fields (Table 5.5).

The relative importance of crop type and % settlement coverage was relatively low with both combined together contributing 14.2%, 22.4%, 3.9% and 11.7% relative influence in Butaleja, Mayuge, Bulambula landscape units and overall, respectively. The R-dependence plots showed a negative relationship with increase in % settlement coverage on small rodent abundance (Fig. 5.4A, B and 5.5C, D).

5.3.2.3 Soil physical characteristics

The percentage composition of silt, sand and clay particles in the soil were considered in the model. Soil silt particle composition was the most important predictor variable ranking third in Mayuge landscape unit with 9.3% relative influence. The overall modelling ranked percent soil silt particle second in importance with 15.6% relative influence. Silt particle composition ranges above 30% showed appositive relationship with small rodent abundance. Soil sand and clay particle composition showed to be important in Mayuge landscape unit but less important in the other landscape units (Fig. 5.4A, B and 5.5C, D).

5.3.2.4 Climatic variables

Rainfall was the only climatic variable considered for modelling rodent abundance. Total monthly rainfall and rainy days were the two parameters used for model prediction. The relative influence of total monthly rainfall was relatively low with 8.9%, 9.1%, 0.7% and 4.1% for Butaleja, Mayuge, Bulambuli landscape units and overall, respectively (Fig. 5.4A, B and 5.5C, D). Rainy days had much less influence on rodent's abundance. The dependence plots showed a positive relationship when rainfall exceeded 200mm in Mayuge landscape unit and overall.

Table 5.5: Mean (±SE) for small rodent population abundance across the studied districts and overall

Category	Butaleja	Mayuge	Bulambuli	Overall
Mature vegetative Sugarcane field	7±0b	25±4a		21±5a
Mature maize+sweet potato field	6±0b	21±11a		17±9ab
Fallow field	8±2b	19±5a	11±2a	12±2bc
Mature vegetative clean maize+beans field	19±0a	6±1c	11±1a	11±2bc
Mature sorghum field	11±4ab			11±1bc
Mature bushy dry maize field	5±0b	12±2ab	11±2a	11±1bc
Mixed cropping field		11±3ab	5±1ab	10±2bcd
Bushy vegetative maize field	13±5ab	8±5bc	8±2ab	10±1bcd
Mature vegetative clean maize+groundnuts field	11±5ab		7±4ab	10±3bcd
Mature bushy cotton field	9±1b			9±1cd
Mature bushy cassava field	8±2b			8±2cd
Mature sweet potato field	11±1ab	4±2cd	7±2ab	8±2cd
Mature millet field	10±1b	3±0d		7±5cd
Mature clean cassava field	7±1b	7±0bc	7±5ab	7±1cd
Mature coffee field		7±3c		7±3cd
Vegetative clean maize field	7±0b	9±0bc	7±2ab	7±1cd
Mature clean dry maize field	7±0b		4±1b	5±1cd
Vegetative low land rice field	5±1b	3±0c		5±1cd
Mature bushy banana field	8±0b	1±0d	4±1b	3±2d
Mature clean banana field		1±0d	2±1b	3±1d
Df	16	14	11	19
F	1.75	1.250	1.886	1.598
P-value	0.010	0.026	0.054	0.054

Mean values followed by same letters are not significantly different from each other

Other predictor variables included elevation (altitude) ranking third in importance in Butaleja and with 14.7% relative influence and a sharp change in prediction at above 1100 masl. In Bulambuli and overall the relative influence of elevation was low, 5% and 5.4% relative influence respectively.

5.3.3 Influence of landscape ecological factors on small rodent species richness

5.3.3.1 Vegetation characteristics

NDVI was the only vegetation variable considered and was 2nd in overall ranking with 13.5% relative influence and a weak positive relationship above 3 index value (Fig. 5.7H). In terms of specific landscape units, NDVI contribution to richness was variable; it ranked 3rd in Butaleja, 4th in Mayuge, 2nd in Bulambuli with 10.1%, 5.7% and 12.1% relative influence respectively (Fig. 5.6E, F and 5.7G).

5.3.3.2 Land use/land cover characteristics

Land use characteristics including farm management practices including field crop status and crop type showed a higher influence on small rodent species richness. In Butaleja the model showed ranked field crop status the most important predictor variable with 49.1% relative importance (Fig. 5.6E). Furthermore, the effect of field crop status on richness showed non- significant difference (df = 15, F = 1.089, p = 0.378) at 5% level of significance. Within Mayuge landscape unit field crop status still ranked the most important variable with 40.3% relative importance with crop type ranking second with 16.4% relative importance (Fig. 5.6F). The effect of field crop status showed a significant difference (df = 14, F = 1.938, p = 0.034) on rodent species richness. The mean separation test showed that fallow field (4±1 rodent species /0.5ha), mature sugarcane field (4±1rodent species /0.5ha) and mature clean cassava field (4±0 rodent species /0.5ha) had significantly higher rodent species richness compared to other fields. Lowest species richness was recorded in mature harvested millet field (1±0 l rodent species /0.5ha) (Table 5.6). Within Bulambuli landscape unit field crop status ranked the most important with a very high relative influence (64.9%) (Fig. 5.7G). The effect of field crop status showed a significant difference (df = 15, F = 2.953, p = 0.0003) on rodent species richness. The posthoc mean separation showed bushy vegetative maize field and bushy mature dry maize fields with higher rodent species richness both with 3±1 rodent species/0.5ha. Lowest small rodent species richness was recorded in clean mature banana field with only 1 rodent species recovered (Table 5.6).

The overall ranking of predictor variables on species richness similarly showed field crop status the most important variable with 39.8% relative importance. The effect of field crop status showed a significant difference (df = 19, F = 2.334, p = 0.002) on small rodent species richness at 5% level of significance, with a posthoc mean separation showing mature sorghum field with highest rodent species richness (4±2 rodent species/0.5ha) while clean mature banana field had the lowest number of recorded small rodent species/0.5ha (Fig. 5.7H).

5.3.3.3 Climatic influence

Climatic variables including total monthly rainfall and rainy days were the principal variables considered. Generally, there was a weak influence of rainfall on species richness with 9.9% relative influence in Butaleja landscape unit, 7.3% in Mayuge, 1.6% in Bulambuli and 4.7% for overall relative influence. The dependence plots of the fitted function showed a negative relationship with increase in total monthly rainfall above 200mm. Number of rainy days was shown to have had very minimal influence on species richness.

5.3.3.4 Soil physical characteristics

The role of soil physical characteristics seemed to have a very low influence on species richness in the studied landscape units where % silt particle composition showed a 5.4% relative influence in Mayuge, less than 2% in Butaleja and Bulambuli and 5.4% overall relative influence. Elevation was the other landscape ecological variable considered for predicting species richness and it showed relatively higher importance in Butaleja with 17.5% relative influence and ranking second, low importance in Mayuge (5.1%), Bulambuli (3%) and overall (6%). The general trend showed higher richness above 1100 masl.

Table 5.6: Mean (±SE) for small rodent species richness for across the studied sites and overall

Crop field status	Overall	Butaleja	Mayuge	Bulambuli
Mature sorghum field	4±2a	4±2		
Fallow field	3±0ab	3±0	4±1a	3±0a
Mature vegetative sugarcane field	3±1abc	2±0	4±1a	
Bushy vegetative maize field	3±0abc	4±0	2±1ab	3±1abc
Mature sweet potato field	3±0abc	2±1	2±0ab	3±0a
Bushy mature cassava field	3±0abcd	3±0		
Bushy mature banana field	2±0bcdef	3±0	3±0ab	2±1de
Bushy mature dry maize field	3±0abcde	3±1	3±0ab	3±1abc
Mature maize+sweet potato field	3±abcd	3±0	3±0ab	
Mature vegetative maize+groundnuts	3±1abc	3±1		2±0cde
Clean mature dry maize field	3±0abc	3±1	3±0ab	2±0abcd
Bushy mature cotton field	2±1bcdef	2±1		
Clean mature cassava field	2±0def	2±0	4±0a	2±1de
Clean mature maize field	2±0cdef	4±0	2±0ab	2±0bcde
Low land rice field	2±0def	2±0		
Mixed cropping field	2±0ef		2±0ab	2±0bcde
Clean mature maize+beans field	2±0ef	1±0	2±0ab	2±0bcde
Mature millet field	2±1ef	2±1	1±0b	
Mature coffee field	2±1ef		2±1ab	
Clean mature banana field	1±0f		2±0ab	1±0e
Df	19	15	14	11
F	2.334	1.089	1.938	2.947
Pr > F	0.002	0.378	0.034	0.003

Mean values followed by same letters are not significantly different from each other

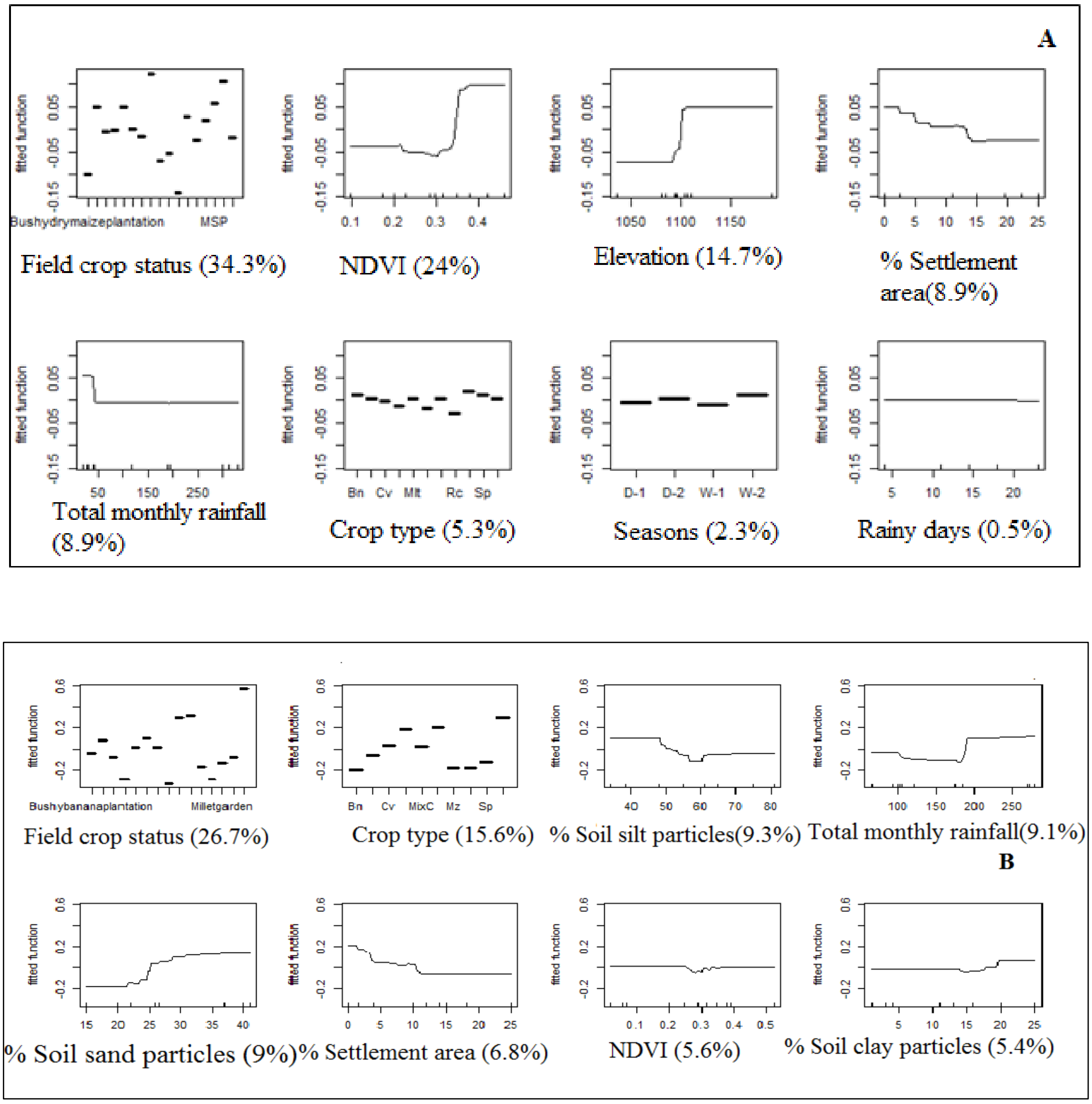


Figure 5.4: Partial dependence plots showing the relationships/effects of predictor variables with rodent population abundance. (A): Butaleja and (B): Mayuge districts. The relative importance of each variable is indicated in brackets. CV deviance=3.51, SE=0.597, number of trees=3200 and CV deviance =7.588, SE=2.134, number of trees 2950 for Butaleja and Mayuge respectively

Key: CV = cross validation, SE = Standard deviation, NDVI = Normalized Difference Vegetation Index

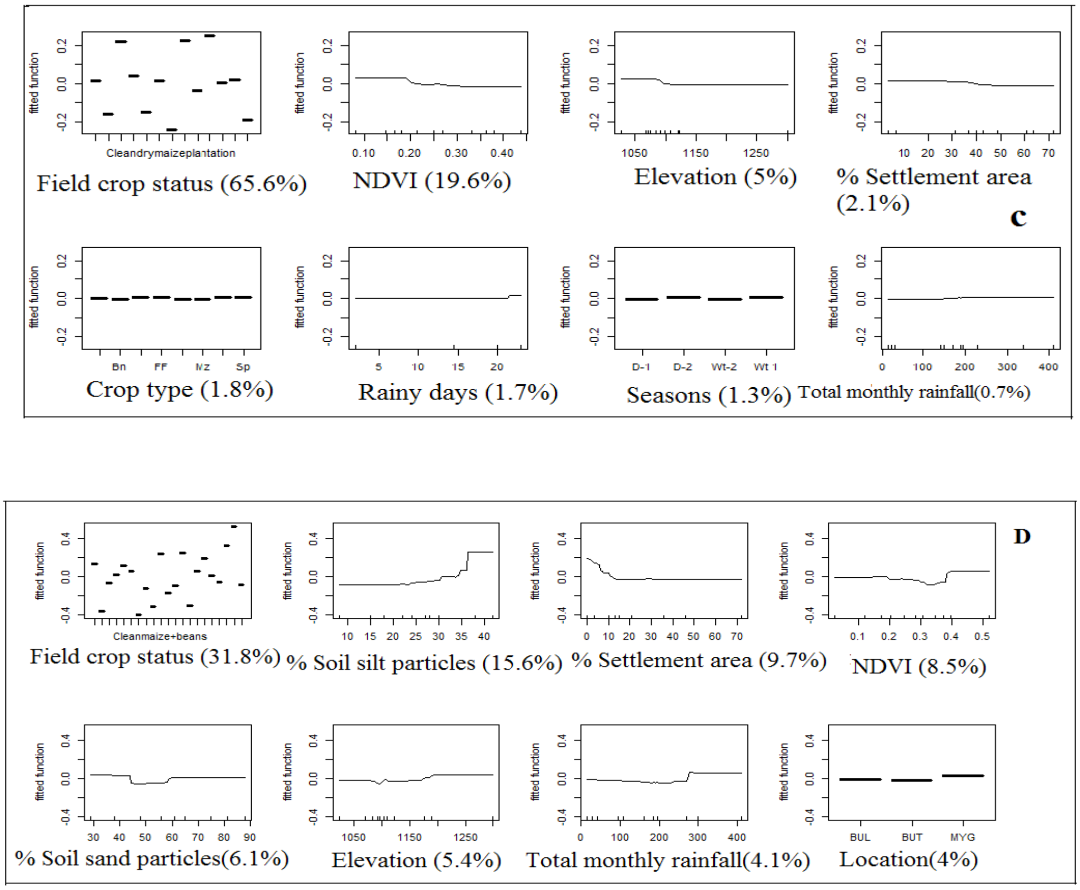


Figure 5.5: Partial dependence plots showing the relationships/effects of predictor variables with rodent population abundance. (**C**): Bulambuli district and (**D**): Overall (Pooled data for the three districts. The relative importance of each variable is indicated in brackets. CV deviance=3.486, SE=0.523, number of trees=2500 and CV deviance =5.254, SE=0.629, number of trees 1800 for Bulambuli and overall data respectively.

Key: CV = cross validation, SE = Standard error, NDVI = Normalized Difference Vegetation Index.

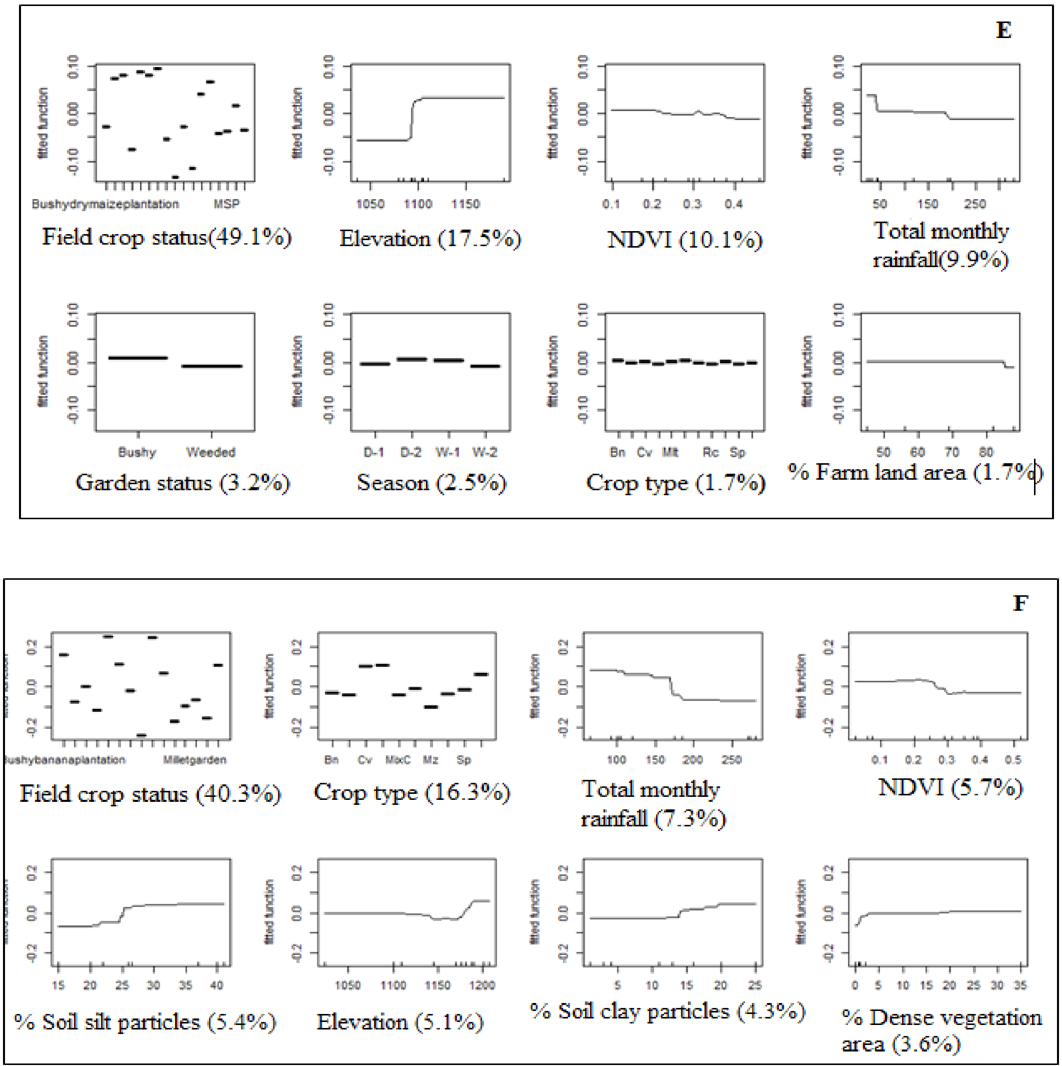


Figure 5.6: Partial dependence plots showing the relationships/effects of predictor variables with rodent species richness. **(E)**: Butaleja and **(F)**: Mayuge districts. The relative importance of each variable is indicated in brackets. CV deviance=3.411, SE=0.382, number of trees=1500 and CV deviance =0.722, SE=0.13, number of trees 4500 for Butaleja and Mayuge respectively.

Key: CV = cross validation, SE = Standard error, NDVI = Normalized Difference Vegetation Index

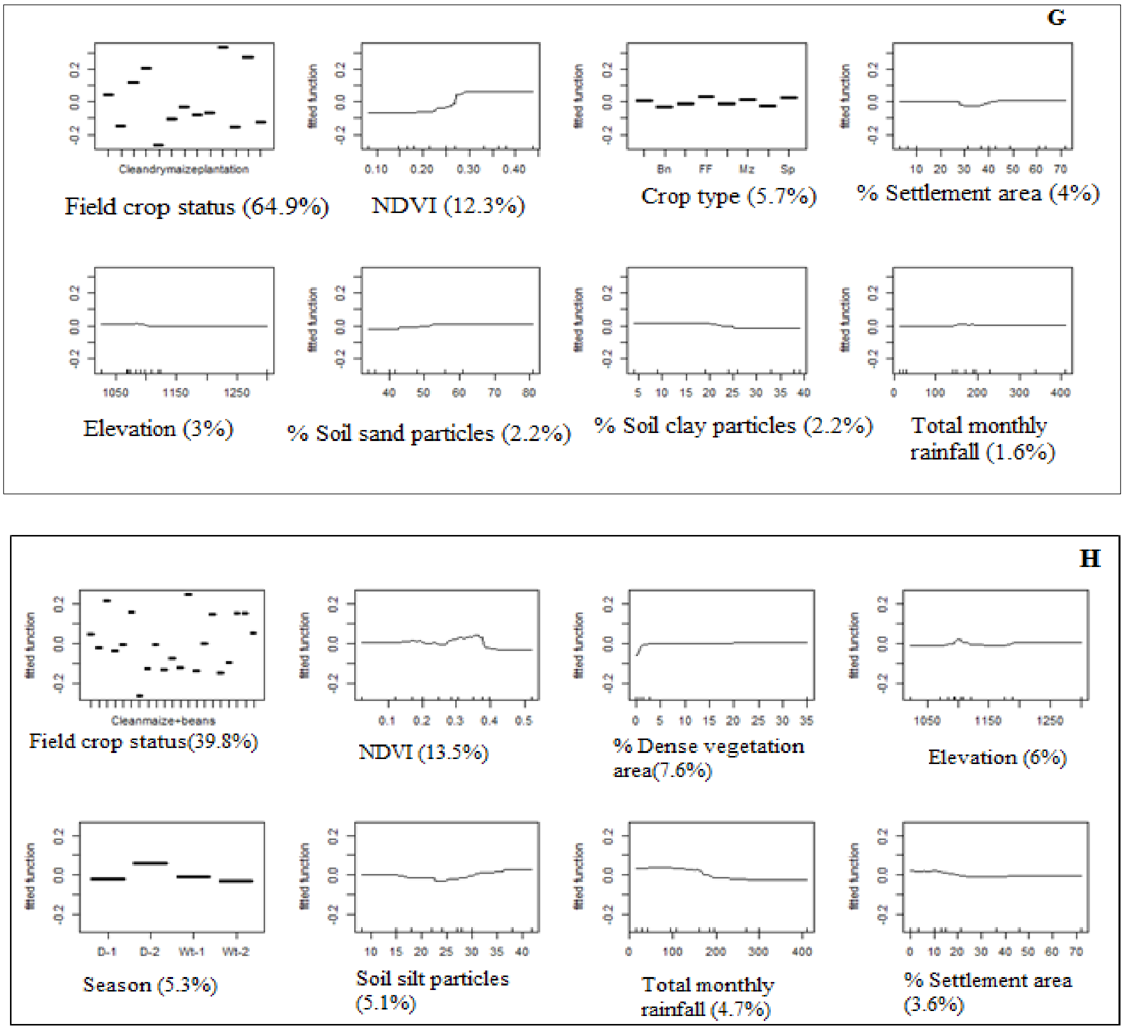


Figure 5.7: Partial dependence plots showing the relationships/effects of predictor variables with rodent species richness. (**G**): Bulambuli and (**H**): Overall (Pooled data for three districts. The relative importance of each variable is indicated in brackets. CV deviance=0.45, SE=0.068, number of trees=3500 and CV deviance =0.56, SE=0.05, number of trees 2800 for Butaleja and Mayuge respectively. Key: CV = cross validation, SE = Standard error, NDVI = Normalized Difference Vegetation Index.

5.4 Discussions

5.4.1 Rodent species richness

In the present study, 14 species of small mammals were found across the three studied landscapes in Eastern Uganda, with *M. natalensis* being the most dominant species. These results are in line with previous studies performed in most parts of sub Saharan African that have reported a similar number of rodent species inhabiting agriculture landscapes, with *M. natalensis* being the most dominant species (Makundi *et al*., 2007; Massawe *et al.*, 2012; Meheretu *et al*., 2015; Moore *et al*., 2015; Mulungu, 2017; Mayamba *et al*., 2019) This is important in light of pest damage, since *M. natalensis* is considered as the most important agricultural rodent pest species in Eastern and Southern Africa, responsible for substantial damage to crops in agricultural landscapes (Makundi *et al*., 1999; Mwanjabe *et al.*, 2002; Stenseth *et al.*, 2007; Taylor *et al.*, 2012; Swanepoel *et al.*, 2017).

Our models showed that the influence of landscape ecological factors was variable with land use characteristic variables being more important than the other in predicting rodent species richness. Specifically, crop field status, a descriptive variable which combined type of crop, growth stage and hygienic state of the field ranked the most important. Fields planted with sorghum, sugarcane, fallow and maize intercropped with beans had a relatively higher richness compared to other fields. It is possible that these fields are more heterogenous (complex) thus offering a greater variety of habitats which can support various species. Indeed, earlier reports such as that of Silva *et al*. (2005), showed that the structural complexity of landscapes, as measured by coverage and shape of residual forest patches, positively correlated with greater species richness, with their explanation that complex habitats exhibit micro habitats which offer diverse resources for several rodent species. Other studies have also demonstrated higher rodent species richness in agricultural fields where vegetation cover is well developed with less disturbance (Fischer *et al*., 2011; Fischer and Schröder, 2014). Additionally, these fields usually exhibit low human interaction/disturbance and thus are relatively stable agricultural environments, a condition which is conducive for rodents infestation, thus the higher richness (Hieronimo *et al*., 2014).

We observed a relatively low species richness across the sites and overall, a result that is supported by previous studies that small mammal assemblages inhabiting agro-ecosystems tend to be dominated by only a few species (Stefania *et al*., 2014). NDVI was another more consistent variable for predicting species richness across the different landscapes. Its influence could be associated with food availability and micro habitats as a result the available green vegetation. Similar earlier findings have shown higher small mammal richness in areas with higher NDVI index values (Chidodo, 2017).

5.4.2 Rodent abundance

Most importantly the relative abundance of rodent association in agriculture fields is more critical as numbers often result into crop damage (Fidler, 1994; Mwanjabe *et al*., 2002; Mulungu, 2017). Our models showed that land use characteristics, specifically, field crop status is the most important predictor for rodent abundance. This is probably due to the additive effect of field crop status; encompasses two key components: food (both quality and quantity) and suitable habitats in terms of ground cover for the rodents to dwell in. The latter may provide the animals with more shelter opportunities which may reduce predation risk thus increase in abundance (Kotler, 1984; Adler, 1995; Shanker, 2001; Jacob, 2003; Massawe *et al*., 2006; Guidobono *et al*., 2018; Gheler *et al*., 2012).

In terms of crop types, we found higher population abundances in fields with mature vegetative sugarcane, mature maize intercropped with sweet potato, fallow fields and mature vegetative clean maize intercropped with beans, compared to the others. This may suggest that rodents might have a preference for certain food types such as sweet potatoes and maize which could sustain higher population abundances. This finding is in agreement with previous reports that showed higher rodent abundances associated with maize and sweet potato crop fields (Mulungu *et al.*, 2011; Hieronimo *et al*., 2014). Our results also suggest that rodent abundance is also highly influenced by the crop type in the field with preference for crop fields that form closed canopy and with limited human activity like in sugarcane fields. Indeed, significantly higher abundances of rodents were recovered in sugarcane plantations compared to other crop fields causing a lot of damage to the crops in Hawaii, USA and Brazil and linked it to food preference as well as favorable refugia for the rodents from predatory animals (Tobin *et al*., 1990; Gheler *et al*., 2012).

Vegetation characteristics as represented by NDVI also showed a relatively higher influence on rodent abundance within the landscape units and across. The influence of this particular variable may be attributed to food availability and cover for the rodents. Earlier reports, however, ranked this variable very high with relative influence of over 80% relative influence on prediction of rodent abundance (Chidodo, 2017). The low relative influence reported in this study could be due to the short dry seasons characterized by the study location which sustain green vegetation almost all year round thus making the relative influence of this factor of less importance. Elsewhere, NDVI has been shown as a good indicator of primary productivity and cover and has long been employed to predict wildlife distribution and abundance but mostly for larger mammals and in conservation areas (Pettorelli *et al*., 2011).

Soil physical properties including percentage silt, sand and clay composition showed also less importance in regulating rodent abundance but with % silt particle composition ranking relatively higher in importance. We found out that abundances increased at approximately 30 – 40 % of silt particle composition in the soil. Similarly, within that range, also sand particles composition ranged between 40-90%. These proportional ranges qualify the soils to be classified as sandy loam following the United States Department of Agriculture (USDA) classification guide (Baillie, 2001; Soil survey staff, 1999,1975). Indeed, Sandy loam soils have been associated with supporting a variety of vegetative plants which offer food and cover to the rodents which increases their survival and maturation probability (Mulungu *et al*., 2016; Leirs *et al*.,1990). It has been demonstrated that sandy loamy soils have a good aeration and are friable making them easier for the animals to burrow in when creating nesting and breeding sites thus support higher abundances of rodents (Meliyo *et al*., 2015; Massawe *et al*., 2008; Odhiambo, 2005).

Our study also showed some discrepancy with rainfall ranking relatively low in importance in predicting rodent abundance. We attribute the results to the short dry seasons between the rainfall seasons thus a low difference in primary productivity to result into significant effect on rodent population. Leirs *et al*. (1997) reported that population abundance of small rodents tends to be affected where there are drastic clear seasonal variations between wet and dry seasons and where rodent populations are highly fluctuating.

5.5 Conclusion

In many areas of East and Southern Africa, rodents continue to cause significant impacts as agricultural pests (Swanepoel *et al*., 2017) and their abundances tend to fluctuate from place to place in relationship to environmental conditions which often results into varying damaging levels to crops (Mulungu, 2017). Efforts to understand the relative importance of various landscape ecological factors in agro ecosystem in regard to rodent species richness and abundance could thus aid development of predictive models and management strategies that are more appropriate and tailored to particular landscape.

This study is the first that has performed an analysis on the influence on different ecological factors in agricultural landscapes in Uganda and has revealed that land use characteristics play the most crucial role in rodent species richness and abundance across agricultural landscapes. Particularly, field crop status was the most important land use variable for predicting richness and abundance. Our results have important implications on the management of rodents inhibiting agro ecosystem and points towards habitat modification such as keeping fields clean and also points to applying rodent control in sugarcane plantation as they may serve as reservoirs of small rodents which may infest other crops in the surrounding environment. These findings therefore, make a significant contribution towards efforts in the control of rodent pests in agro ecosystems

Acknowledgements

We are extremely grateful to the Ecologically Based Management of Rodent Pests in Maize and Rice in East Africa to Sokoine University of agriculture project (Grant number OPP1112579) supported by Bill and Melinda Gates foundation for the financial support of this research. We are also grateful for the tireless project field work efforts rendered by Kisakye Alex, Ouma Namulochi and Ramadhani Kigunguli from Busitema University, Namasagali campus, Uganda and Pest Management Centre, Sokoine University of Agriculture, Morogoro, Tanzania respectively.

Ethical considerations

This research was carried after thorough review by Sokoine University of Agriculture, Tanzania, Wild life department. Further research approval was obtained from the Uganda Wild life Authority for conducting research on live animals in Uganda.

Funding

Special thanks to the Bill and Melinda Gates Foundation that funded Alex Mayamba's PhD studies, of which this paper is part.

5.6 References

Aertsen, W., Kint, V., de Vos, B., Deckers, J., van Orshoven, J. and Muys, B. (2012). Predicting forest site productivity in temperate lowland from forest floor, soil and litterfall characteristics using boosted regression trees. *Plant and Soil* 354: 157–172.

Aplin, K. P., Brown, P. R., Jacob, J., Krebs, C. J. and Singleton, G. R. (2003). Field methods for rodent studies in Asia and the Indo pacific. In *Design*. Australia: Australian Centre for International Agricultural Research. 89pp.

Baillie, I. C. (2001). Book Review: Soil Survey Staff 1999, Soil Taxonomy A basic system of soil classifcation for making and Agricultural Handbook 436 ; Natural Resources. *Soil Use and Management* 17: 57–60.

Butet, A., Paillat, G. and Delettre, Y. (2006). Seasonal changes in small mammal assemblages from field boundaries in an agricultural landscape of western France. *Agriculture, Ecosystems and Environment* 113: 364–369.

Chidodo, D.J. (2017). Evaluation of Normalized Difference Vegetation Index of common vegetation habitats for monitoring rodent population and outbreaks in Ismani, Tanzania (MSc. Thesis). Morogoro: Sokoine University of Agriculture, Morogoro Tanzania. 145pp.

Chidodo, D.J., Kimaro, D.N., Hieronimo, P., Makundi, R.H., Isabirye, M., Leirs, H. Massawe, A.W., Mdangi, M.E., Kifumba, D. and Mulungu, L.S. (2019). Application of Normalized Difference Vegetation Index (NDVI) to forecast rodent population abundance in smallholder agro-ecosystems in Semi-arid areas in Tanzania. *Mammalia. Plant and Soil* 7(3): 68 - 89.

Clausnitzer, V. and Kityo, R. (2001). Altitudinal distribution of rodents (muridae and gliridae) on mt elgon, uganda. *Tropical Zoology* 14: 95–118.

Delany, M. J. (1971). The biology of small rodents in Mayanja Forest, Uganda. *Journal of Zoology* 165(1): 85 – 129.

Elith, J., Leathwick, J. R., Hastie, T. and R. Leathwick, J. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology* 77: 802–813.

Fiedler, L.A. (1994). Rodent Pest Management in East Africa. FAO plant production and protection paper 123, FAO, Rome, Itally. 83pp.

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

Fischer, C., Thies, C. and Tscharntke, T. (2011). Small mammals in agricultural landscapes : Opposing responses to farming practices and landscape complexity. *Biological Conservation* 144: 1130–1136.

Fraschina, J., León, V.A. and Busch, M. (2014). Role of Landscape Scale in the Distribution of Rodents in an Agroecosystem of Argentina. *Journal of Agricultural Science* 6: 22 – 35.

Gheler-Costa, C., Vettorazzi, C.A., Pardini, R. and Verdade, L.M. (2012). The distribution and abundance of small mammals in agroecosystems of southeastern Brazil. *Mammalia* 76(2): 185–191.

Gregorio, A. D. and Jansen, L.J.M. (2005). Land Cover Classification System. In *October*. [http://www.fao.org/docrep/ 003/x0596e/x059 6e00.htm]. Site visited on 3/5/2019.

Guidobono, J.S., Cueto, G.R., Teta, P. and Busch, M. (2018). Effect of environmental factors on the abundance variations of two native rodents in agricultural systems of Buenos Aires, Argentina. *Austral Ecology* 44(1): 36–48.

Hieronimo, P., Kimaro, D. N., Kihupi, N. I., Gulinck, H. and Mulungu, L. S. (2014). Land use determinants of small mammal abundance and distribution in a plague endemic area of Lushoto District , Tanzania relationship between land use types and practices and small mammal abundance and distribution in the West Usambara Mountains in Tanzan. *Tanzania Journal of Health Research* 16(3): 1–12.

Isabirye-Basuta, G. and Kasenene, J.M. (1987). Small Rodent Populations in Selectively

Felled and Mature Tracts of Kibale Forest, Uganda. *Biotropica* 19(3): 260.

Jacob J. (2003). Short-term effects of farming practices on populations of common voles. *Agriculture, Ecosystems and Environment* 95: 321–325.

Krijger, I. M., Belmain, S. R., Singleton, G. R., Groot, P.W.G. and Meerburg, B.G. (2017). The need to implement the landscape of fear within rodent pest management strategies. *Pest Management Science* 73: 2397 – 2402.

Laudisoit, A., Leirs, H., Makundi, R. and Krasnov, B.R. (2009). Seasonal and habitat dependence of fleas parasitic on small mammals in Tanzania. *Integrative Zoology* 4(2): 196 – 212.

Legendre, P. (1993). Spatial Autocorrelation : Trouble or New Paradigm ? Author (s): Pierre Legendre Published by : Ecological Society of America Spatial Autocorrelation :Trouble Or New Paradigm ? *Ecology* 74(6): 1659 – 1673.

Leirs, H., Stuyck, J., Verhagen, R. and Verheyen, W. (1990). Seasonal variation in growth of Mastomys natalensis (Rodentia: Muridae) in Morogoro, Tanzania. *African Journal of Ecology* 28(4): 298–306.

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

Makundi, R.H., Massawe, A.W. and Mulungu, L. (2007). Reproduction and population dynamics of Mastomys natalensis Smith, 1834 in an agricultural landscape in the Western Usambara Mountains, Tanzania. *Integrative Zoology* 2: 233–238.

Makundi, R.H., Massawe, A. and Mulungu, L. (2006). Ecological considerations for management of rodent pests in Tanzania. In: Makundi, R.H. (Ed) *Management of Selected Crop Pests in Tanzania*, Tanzania Publising House. pp. 224 – 239.

Makundi, R.H., Oguge, N.O. and Mwanjabe, P.S. (1999). Rodent pest management in East Africa - an ecological approach. *Ecologically-Based Rodent Management* pp. 460 – 476.

Massawe, A.W., Rwamugira, W., Leirs, H., Makundi, R. H. and Mulungu, L. S. (2007). 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(3): 293–301.

Massawe, Apia W., Makundi, R. H., Mulungu, L. S., Katakweba, A. and Shayo, T. N. (2012). Breeding Dynamics of Rodent Species Inhabiting Farm - Fallow Mosaic Fields in Central Tanzania. *African Zoology* 47: 128 –137.

Mayamba, A., Byamungu, M.R., Makundi, R.H., Kimaro, D.N, Isabirye, M., Massawe, A.W., Kifumba, D., Herwig, L. and Mulungu, L. (2019). Species composition and community structure of small pest rodents (Muridae) in cultivated and fallow fields in maize-growing areas in Mayuge district, Eastern Uganda. *Ecology and Evolution* 9: 7849 - 7860.

Mclaughlin, A. and Mineau, P. (1995). The impact of agricultural practices on biodiversity. *Agriculture. Ecosystems and Environment* 55(95): 201–212.

Meheretu, Y., Welegerima, K., Sluydts, V., Bauer, H., Gebrehiwot, K., Deckers, J. and Leirs, H. (2015). Reproduction and survival of rodents in crop fields: The effects of rainfall, crop stage and stone-bund density. *Wildlife Research* 42(2): 158–164.

Mill, N., Peña, D., Butet, A., Delettre, Y., Paillat, G., Morant, P. and Burel, F. (2003). Response of the small mammal community to changes in western French agricultural landscapes. *Landscape Ecology* 18: 265–278.

Mlyashimbi, E.C.M., Vanden Broecke, B., Mariën, J., Kimaro, D.N., Tarimo, A.J.P. Machang'u, R.S., Isabirye, M., Makundi, R.H., Massawe, A.W., Hieronimo, P. Kifumba, D., Leirs, H., Mdangi, M.E., Belmain, S.R. and Mulungu L.S. (2019). Influences of soil types on the population dynamics and survival of Multimammate rat (*Mastomys natalensis*, Smith 1832) in semi-arid areas in Tanzania. *Crop Protection.* 178pp.

Moore, S. M., Monaghan, A., Borchert, J. N., Mpanga, J. T., Atiku, L. A., Boegler, K. A. and Eisen, R. J. (2015). Seasonal fluctuations of small mammal and flea communities in a Ugandan plague focus: Evidence to implicate Arvicanthis niloticus and Crocidura spp. as key hosts in Yersinia pestis transmission. *Parasites and Vectors* 8(1): 17 - 28.

Mulungu, L.S., Ngowo, V.D., Makundi, R.H., Massaww, A.W. and Herwig, L. (2010). Winning a fight against rodents in Africa.pdf. *Journal of Biological Sciences*

10: 333–340.

Mulungu, L.S., Mahlaba, T.A., Massawe, A. W., Kennis, J., Crauwels, D., Eiseb, S. and Belmain, S. R. (2011). Dietary differences of the multimammate mouse, Mastomys natalensis (Smith, 1834), across different habitats and seasons in Tanzania and Swaziland. *Wildlife Research* 38(7): 640 – 646.

Mulungu, L.S., Ngowo, V., Mdangi, M.E., Katakweba, A.S., Tesha, P., Mrosso, F.P., Belmain, S.R. (2016). Survival and recruitment of the multimammate mouse, *Mastomys natalensis* (Smith 1834), in a rice agro-ecosystem. *Mammalia* 80(2): 205–210.

Mulungu, L.S. (2017). *Control of rodent pests in maize cultivation: the case of Africa*. Burleigh Dodds Science Publishing Limited 82 High Street Sawston Cambridge CB22 3HJ UK. pp. 317 - 337.

Mwanjabe, P.S., Sirima, F.B. and Lusingu, J. (2002). Crop losses due to outbreaks of Mastomys natalensis (Smith, 1834) Muridae, Rodentia, in the Lindi region of Tanzania. *International Biodeterioration and Biodegradation* 49: 133–137.

Oerke, E.C. (2006). Crop losses to pests. *Journal of Agricultural Science* 144(1): 31–43.

Parry, H.R. and Schellhorn, N.A. (2013). The use of models to explore IPM strategies and design pest suppressive landscapes for sustainable agricultural practice. *20th International Congress on Modelling and Simulation*, (December), 1–6.

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M. and Kausrud, K. (2011). The Normalized Difference Vegetation Index (NDVI):

Unforeseen successes in animal ecology. *Climate Research* 46(1): 15–27.

Ralaizafisoloarivony, N.A., Kimaro, D.N., Kihupi, N.I., Mulungu, L.S., Leirs, H., Msanya, B. M. and Gulinck, H. (2014). Vegetation habitats and small mammals in a plague endemic area in Western Usambara Mountains, Tanzania. *Tanzania Journal of Health Research* 16(3): 1–12.

Robinson, R.A., Sutherland, W.J. and Sutherlandt, W.J. (2012). of Applied Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Society* 39(1): 157–176.

Silva, M., Hartling, L. and Opps, S.B. (2005). Small mammals in agricultural landscapes of Prince Edward Island (Canada): Effects of habitat characteristics at three different spatial scales. *Journal of Biological Conservation* 126: 556 – 568.

Singleton, G.R., Brown, P.R., Jacob, J. and Aplin, K.P. (2007). Unwanted and unintended effects of culling : A case for ecologically-based rodent management. *Intergrative Zoology* 2: 247–259.

Soil survey staff. (1975). *Soil Taxonomy:A Basic System of Soil Classification for Making and Interpreting Soil Surveys* (First Edit). Washigton: Soil Conservation Service, U.S. Department of Agriculture. 320pp.

Soil survey staff. (1999). *Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil Surveys* (Second Ed.). Washington DC: United

States Department of Agriculture. 89pp.

Southern, H. (1962). Notes on breeding of small mammals in Uganda and Kenya. *Bureau of Animal Population, Oxford University* pp. 503–515.

Stefania, G., Maurizia, S. and Laura, B. (2014). Decreased small mammals species diversity and increased population abundance along a gradient of agricultural intensification. *Hystrix, the Italian Journal of Mammalogy* 25: 39–44.

Stenseth, N. C., Leirs, H., Skonhoft, A., Davis, S. A., Pech, R. P., Andreassen, H. P. and Wan, X. (2003). Mice, Rats, and People: The Bio-Economics of Agricultural Rodent Pests. *Frontiers in Ecology and the Environment* 1: 367 - 375.

Stenseth, N.C., Leirs, H., Mercelis, S. and Mwanjabe, P. (2001). Comparing strategies for controlling an African pest rodent: An empirically based theoretical study. *Journal of Applied Ecology* 38(5): 1020–1031.

Stoate, C., Boatman, N.D., Borralho, R.J., Carvalho, C.R., De Snoo, G.R. and Eden, P. (2001). Ecological impacts of arable intensification in Europe. *Journal of Environmental Management* 63(4):337–365.

Swanepoel, L. H., Swanepoel, C. M., Brown, P. R., Eiseb, S. J., Goodman, S. M., Keith, M. and 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(3): 1–20.

Taylor, P.J., Downs, S., Monadjem, A., Eiseb, S.J., Mulungu, L.S., Massawe, A.W. and Belmain, S.R. (2012). Experimental treatment-control studies of ecologically based rodent management in Africa: Balancing conservation and pest management. *Wildlife Research* 39(1): 51 – 61.

Tobin, M.E., Sugihara, R.T. and Ota, A.K. (1990). Rodent Damage To Hawaiian Sugarcane. *14th Vertebr. Pest Conf. (L.R. Davis and R.E. Marsh, Eds.)*, (March), 120–123.

Weih, R.C. and Riggan, N.D. (2010). Object-based classification vs. pixel-based classification: Comparitive importance of multi-resolution imagery. *The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences* 38: 1–6.

Wiens, J.A., Stenseth, N.C., Horne, B. V. and Ims, R. A. (1993). Ecological Mechanisms and Landscape Ecology. *Oikos* 66(3): 369.

Williams, G.J., Aeby, G.S., Cowie, R.O.M. and Davy, S.K. (2010). Predictive modeling of coral disease distribution within a reef system. *PLoS ONE* 5(2): 1–10.

Zuur, A.F., Ieno, E.N. and Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1: 3–14.

CHAPTER SIX

6.0 GENERAL DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

6.1 General Discussion

This study reports eleven rodent species and one insectivorous in agro ecosystem environment, with the multimammate rat (*M. natalensis*) being the most abundant in both fallow and cultivated habitats. The observed significant differences in faunal composition in different habitats can be attributed to their inherent differences in environmental interactions such as micro climate, vegetation cover and possible local disturbances (Kotler, 1984; Heironimo *et al*., 2014). Additionally, *M. natalensis* ranked highest in abundance in cultivated fields compared to fallow habitats. This observation can be attributed to the characteristic nature of this species to easily colonize disturbed habitats compared to other species as it was observed earlier by Massawe *et al*. (2006) and Brown *et al*. (2017). The dominance of *M. natalensis* over the other species in agro ecosystems has been widely reported in the East and Southern Africa (Monadjem and Perrin, 2003; Makundi *et al*., 2009; Massawe *et al*., 2011, Mulungu *et al*., 2016; Swanepoel *et al*., 2017) and can be attributed to its ecological preference for disturbed habitats.

Secondly, fallow habitat type was relatively higher in species richness than cultivated habitat a phenomenon that could be attributed to the suitability with more endowment for dwelling of both specialist and generalist species. Similar findings of higher rodent species richness in natural habitats were reported elsewhere (Kotler, 1984; Magige and Senzota, 2006; Addisu and Bekele, 2013; Mulungu *et al*., 2015) who attributed it to habitat heterogeneity as well as suitable vegetation cover for shelter, suitable soil moisture content and moderate temperatures and continuous food supply in the natural habitats.

The study also investigated the population dynamics and breeding patterns of the key rodent pest species involved in agro ecosystems with the aim of establishing the most critical stages of rodent population build up and active breeding to enable timely application of control efforts. Following a two-year CMR study period, it was observed that the highest population density of *M. natalensis*, the most dominant species was recorded in second half of the year in second wet season (September - November). On the other hand, actively breeding females were present in the population throughout the year with relatively higher percentages in the second dry season (June-July). It is concluded that the higher breeding of females in second dry season resulted into higher population densities in the second wet season. The higher abundances in the second wet season period could further be attributed to two possibilities; increased vegetation which offers abundant quality food, but also more importantly vegetation provides increased ground cover for the residence of animals thus lowering risks of predation, a phenomenon that was also reported earlier by Kotler (1984).

The presence of actively breeding females in the population throughout the year in all seasons can be attributed to the availability of food and cover due to the mixed farming system in the study area and the relatively short dry periods, which creates suitable conditions for rodent maturation and breeding. The relatively higher percentages of actively breeding animals in the second dry season could be due the increased food availability from the drying seasonal crops/seed residues including maize and beans from the first wet season, which was the main planting season. These findings are in agreement with the explanations of earlier reports that have shown that breeding of *M. natalensis* synchronizes with periods of food availability (Mulungu *et al*., 2013; Mulungu *et al*., 2016). The study further investigated the key demographic traits (survival and maturation) in relationship to selected predictor variables; sex, population density and habitat with the aim of increasing the understanding of survival and maturation mechanisms for *M. natalensis* for better management plans. Survival of *M. natalensis* was modelled and showed higher survival estimates when rainfall was high (300mm-500mm) in the past two months and when current population density was high (above 10 animals). Rainfall tends to trigger vegetation growth which provides increased food for animals to survive but also provides ground cover which harbors the animals from predation. Similar findings were reported earlier in the neighboring Tanzania where higher survival synchronized with rainfall seasons (Sludyt *et al.*, 2007; Juliad *et al.*, 1999). The discrepancy results of higher survival at higher population density could be explained by the generally low population density which could not result into significant competition. In fact Leirs *et al.* (1997) suggested that studies on effect of density dependent factors are more effective when conducted on highly fluctuating populations.

Maturation of *M. natalensis* was also modelled and showed no significant effect with all the predictor variables; rainfall, population density, sex and habitat. Previous studies, for example, Leirs *et al*. (1997) showed maturation of female *M. natalensis* to have increased with an increasing amount of preceding rainfall and were related to an increase in food availability. The discrepancy with the current study could be associated with the mixed cropping system practiced and the relatively short dry periods, a condition which might have created favourable conditions of continuous food supply for normal growth and development even during dry season periods.

The study also attempted to model key environmental factors including land use patterns, NDVI, rainfall and farm management practices in contrasting agro ecosystems with the aim to provide key predictor variables responsible for rodent abundance and richness. The current findings revealed that farm management practices (crop field status; a description of the state of the field including hygiene, crop type and growth stage) were the most important predictor variables for both abundance and richness. Further analysis revealed mature sugarcane plantation fields, fallow fields and vegetative maize intercropped with beans had higher rodent abundances. The results could be attributed to possibly the suitable shelter in terms of ground cover and less local human activities in mature sugarcane plantation and food availability for fields with maize intercropped with beans. Similarly, earlier studies have shown higher rodent abundances in fields with dense ground cover (Kotler, 1984) and also where there are minimal human interaction disturbances (Heironimo *et al*., 2014).

Furthermore, NDVI and soil texture (proportional silt particles) were also key important predictor variables for both rodent abundance and richness. Indeed, NDVI as a vegetation index has been used widely to study the distribution and dynamics of vegetation and animal populations (Pettorelli *et al*., 2005). Specifically, Chidodo (2017) showed a strong relationship between NDVI and small mammal abundance. Similarly, the current study has also showed that NDVI plays an important role in regulating rodent abundance and richness as it is linked to greenness and food availability for the animal's enrichment.

Soil silt particle proportion also showed an overall importance in predicting species abundance. It is not surprising as earlier studies have linked soil texture class to have an influence on rodent species distribution (Meliyo *et al*., 2015; Massawe *et al*., 2008). More specifically sandy loams have been shown to support a variety of vegetative plants which offer food and cover to rodents for better survival and increased maturation (Mlyashimbi *et al*., 2019; Mulungu *et al*., 2016; Leirs *et al*.,1990) but also have good aeration and are easy to make burrows through by rodents (Massawe *et al*., 2008; Odhiambo, 2005). The R-dependence plots showed silt proportion levels to have shown a sharp positive relationship peaking at 40% which is an optimal range, with sand particles at 40-90%, which under USDA classification follows under sandy loam (Baillie, 2001). The sandy laom soils are thus likely to support a higher number of species due to the conducive environment in terms of supporting vigorous vegetation growth as well as ease of burrowing for the subterrenean species.

The results further indicated that rainfall, a key factor that has been widely shown to be an important predictor of rodent abundance (Leirs *et al.,* 1997), ranked low in relative importance for both abundance and richness. This could be attributed to the observed short dry spells and the mixed cropping patterns which allows anearly constant supply of water and vegetative plant materials, which provides good conditions for the maturation of the rodents and thus may enhance continuous breeding throughout the year thus rendering rainfall less important in predicting rodent abundance. Mulungu *et al*. (2013) earlier noted that. In connection with Mulungu *et al*. (2013) who observed continous breeding of one Mastomys natalensis in irrigated rice fields.

6.2 General Conclusions

The study has provided knowledge on rodent fauna in agro ecosystem environment in Uganda. A diversity of rodent species including *Mus triton*, *Lemniscomys zebra*, *Aethomys hindei, Lophuromys sikapusi, Arvicanthis niloticus, Mastomys natalensis* among others were found inhibiting cultivated and fallow mosaic habitats with *M. natalensis* being predominant a further justification for its being a key agriculture pest in the region. It is therefore urgent that an integrated rodent pest management program is implemented to benefit the cereal crops industry but mostly targeting the dominant species (*M. natalensis*).

The study also noted significant seasonal breeding patterns and population fluctuations of the predominant species *M. natalensis*, with the second dry season (June-July) recording the highest percentage of actively breeding females and then a peak in population density in second wet season (Sept-Nov). Lowest percentage of breeding animals and population density was observed in first dry season (Dec to Feb of the following year). Therefore, rodent management strategies should be planned and initiated early in the year (first wet season) to prevent population build up to damaging levels in the subsequent seasons.

Additionally, amount of rainfall in the previous month significantly shaped survival of *M. natalensis* with higher survival when rainfall was high (300-500mm) while maturation seems to be random. Recapture probability appeared to be higher in male animals compared to females which could have been attributed to the possibility of increased mobility in males as they search for multiple mates.

On the aspect of key ecological factors on predicting rodent abundance and richness, farm management practices particularly the combined effect of the field hygiene, crop and the growth stage, termed as field crop status ranked highest in predicting small rodent abundance and richness. Similarly, vegetation characteristics, the Normalized Difference Vegetation Index was another key predictor factor for rodent abundance thus future predictive models should consider these for accurate predictions of potential outbreaks.

This study has offered a general overview of the rodent fauna in an agro ecosystem environment in Uganda in a more detailed CMR trapping experiment and provides opportunities for further studies. For instance, the population dynamics and breeding patterns of *M. natalensis* is clearly illustrated but other key species including *A. niloticus* and *M. triton* were not well captured in the study sites and need further studying. Similarly the study concentrated in rainfed agriculture farmlands but CMR trapping in irrigated areas could offer further information to guide development of wholistic rodent management plan in Uganda.

6.3 General Recommendations

The gauge of the argument on the ecological aspects of rodents associated with cropping systems is extensive and complex even at the Uganda country level, and the following suggestions are proposed from this study's findings;

i. Rodent pest management in Uganda will have to employ a range of control methods/tools because of the widespread nature of the problem, both spatially and temporally. The methods/tools should be those that target specifically the predominant species (*M. natalensis*) reported in agro ecosystems. Control efforts will have to cover both cultivated fields and fallow fields for a sustainable attainment of rodent pest problems in agricultural environments.

ii. Management options should be timed early in the year, specifically in the first rainy season (Mar-May) to counteract potential population build up in subsequent seasons which may result into crop damage.

iii. Rodent control efforts may also have to adopt an area-wide pest management strategy to involve all farmers in a community since this study has demonstrated that farm management practices including field status in terms of hygiene, crop type and stage of development are key in regulating rodent abundance. For example, sugarcane plantations should be included in rodent control as they were found inhibiting high populations of rodents. However, the potential effectiveness of such a strategy will require further evaluation for the economic applicability.

iv. Also, since Uganda's climatic conditions and farming systems offer suitable conditions for normal rodent maturation and breeding throughout the year with higher survival during periods of high rainfall, it implies that control strategies that involve modification of environment should target survival mechanisms of the rodents.

v. The study also recommends further case studies in Uganda to allow better assessment of local dimensions of the rodent pests. Among the knowledge gaps that future studies can focus on may include among others i) detailed CMR studies in rice cropping grids and in other regions of the country with different agro ecological conditions, ii) detailed studies on rodent populations and damage estimates to both maize and rice crops to further justify resource allocation by government bodies to manage this pest in the country.

6.4 References

Addisu, A. and Bekele, A. (2013). Habitat preferences, seasonal abundance and diets of rodents in Alage, Southern Ethiopia. *African Journal Ecology* 52: 284–291.

Baillie, I.C. (2001). Book Review: Soil Survey Staff 1999, Soil Taxonomy A basic system of soil classi ® cation for making and Agricultural Handbook 436; Natural Resources. *Soil Use and Management* 17: 57 – 60.

Brown, P.R., Douangboupha, B., Htwe, N.M., Jacob, J., Mulungu, L**.,** My Phung, N.T., Singleton, G.R., Stuart, A. M. and Sudarmaji, S. (2017). *Control of rodent pests in rice cultivation*. *In: Achieving sustainable rice cultivation*, volume 2, cultivation, pest and disease management, Part 3: Rice pests and diseases. Francis Dodds, Burleigh Dodds Science Publishing. pp. 343 – 376.

Chidodo, D.J. (2017). *Evaluation of Normalized Difference Vegetation Index of common vegetation habitats for monitoring rodent population and outbreaks in Ismani, Tanzania* (MSc. Thesis). Morogoro: Sokoine University of Agriculture, Morogoro Tanzania. 178pp.

Eccard, J.A., Klemme, I., Horne, T.J. and Ylönen, H. (2002). Effects of competition and season on survival and maturation of young bank vole females. *Evolutionary Ecology* 16: 85–99.

Hieronimo, P., Kimaro, D.N., Kihupi, N.I., Gulinck, H., Mulungu, L.S., Msanya, B.M. and Deckers, J.A. (2014). Land use determinants of small mammals abundance and distribution in a plague endemic area of Lushoto district, Tanzania. *Tanzania Journal of Health Research* 16(3): 1–12.

Julliard, R., Leirs, H., Stenseth, N. C., Yoccoz, N. G., Prévot-Julliard, A. C., Verhagen, R. and Verheyen, W. (1999). Survival-variation within and between functional categories of the African multimammate rat. Journal of Animal Ecology 68: 550 - 561.

Kotler, B.P. (1984). Predation risk and the structure of desert rodent communities. *Journal of Ecology* 165: 689 – 701.

Leirs, H., Stenseth, N.C. and Nichols, J.D. (1997). Seasonality and non-linear density-dependence in the dynamics of African Mastomys rats. *Nature* 389: 176 – 80.

Leirs, H., Stuyck, J., Verhagen, R. and Verheyen, W. (1990). Seasonal variation in growth of Mastomys natalensis (Rodentia: Muridae) in Morogoro, Tanzania. *African Journal Ecology* 28: 298 - 306.

Magige, F. and Senzota, R. (2006). Abundance and diversity of rodents at the human-wildlife interface in Western Serengeti, Tanzania. *African Journal Ecology* 44: 371–375.

Makundi, R.H., Massawe, A.W., Mulungu, L.S. and Katakweba, A. (2009). Species diversity and population dynamics of rodents in a farm-fallow field mosaic system in Central Tanzania. *African Journal of Ecology* 48: 313 - 320.

Massawe, A.W., Mulungu, L.S. and Makundi, R.H. (2011). Spatial and Temporal Population Dynamics of Rodents in Three Geographically Different Regions in Africa: Implication for Ecologically-Based Rodent Management. *African Zoology* 46: 393 - 405.

Massawe, A.W., Rwamugira, W., Leir, H., Makundi, R.H. and 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.

Massawe, A.W., Rwamugira, W., Leirs, H., Makundi, R.H., Mulungu, L., Ngowo, V., and Machangu, R. (2008). Soil type limits population abundance of rodents in crop fields: case study of the multimammate rat Mastomys natalensis Smith, 1834 in Tanzania. *Integrative Zoology* 3(1): 27 – 30.

Meliyo, J., Brabers, L., Massawe, B., Msanya, B., Kimaro, D., Mulungu, L. and Leirs, H. (2015). The Effect of Soil Physical Properties and Soil Microclimate on Rodent Burrows' Abundance and their Characteristics in Western Usambara Mountains, Tanzania. *Journal of Agriculture and Ecology Research International* 2(2): 105–119.

Mlyashimbi, E.C.M., Vanden Broecke, B., Mariën, J., Kimaro, D.N., Tarimo, A.J.P., Machang'u, R.S. and Mulungu, L.S. (2019). Soil type influences population dynamics and survival of the Multimammate rat (*Mastomys natalensis*) in semi-arid areas in Tanzania. *Crop Protection* 124: 104 - 829.

Monadjem, A. and Perrin, M. (2003). Population fluctuations and community structure of small mammals in a Swaziland grassland over a three-year period. *African Zoology* 38(1): 127-137.

Mulungu, L.S., Lopa, H. and Mdangi, E.M. (2016). Comparative Study of Population Dynamics and Breeding Patterns of *Mastomys natalensis* in System Rice Intensification (SRI) and Conventional Rice Production in Irrigated Rice Ecosystems in Tanzania. *Journal of Rice Research* 4: 1-5.

Mulungu, L.S., Ngowo, V., Mdangi, M., Katakweba, A.S., Tesha, P., Mrosso, F.P., Mchomvu, M., Sheyo, P.M. and Kilonzo, B.S. (2013). Population dynamics and breeding patterns of Multimammate mouse, *Mastomys natalensis* (Smith 1834) in irrigated rice field in Eastern Tanzania. *Pest Management Science* 69(3): 371 - 377.

Mulungu, L.S., Sixbert, V., Ngowo, V., Mdangi, M., Katakweba, A.S., Tesha, P., Mrosso, F.P., Mchomvu, M., Kilonzo, B.S. and Belmain, S.R. (2015) Spatio-temporal patterns in the distribution of the multimammate mouse, *Mastomys natalensis*, in rice crop and fallow land habitats in Tanzania. *Mammalia* 79(2): 177-184.

Odhiambo, R.O. (2005). *Community structure and diet preference of rodent pests of maize (Zea mays* L.*) in Central and Southwestern Tanzania* (PhD Thesis). Sokoine University of Agriculture, Morogoro, Tanzania. 189pp.

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J.M., Tucker, C. J. and Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution* 20(9): 503 - 510.

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

Swanepoel, L. H., Swanepoel, C. M., Brown, P. R., Eiseb, S. J., Goodman, S. M., Keith, M. and 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.

APPENDICES

Appendix 1: Publishable Paper

Received: 30 October 2018 | Revised: 15 May 2019 | Accepted: 23 May 2019
DOI: 10.1002/ece3.5371

ORIGINAL RESEARCH

Ecology and Evolution Open Access WILEY

Species composition and community structure of small pest rodents (Muridae) in cultivated and fallow fields in maize-growing areas in Mayuge district, Eastern Uganda

Alex Mayamba[1,2] | Robert M. Byamungu[2] | Rhodes H. Makundi[3] | Didas N. Kimaro[4] | Moses Isabirye[1] | Apia W. Massawe[3] | David Kifumba[1] | Alice Nakiyemba[1] | Herwig Leirs[5] | Mshaka E. Mdangi[6] | Brian E. Isabirye[7] | Loth S. Mulungu[3]

[1]Faculty of Natural Resources and Environment, Busitema University, Tororo, Uganda
[2]Department of Wildlife Management, Sokoine University of Agriculture, Morogoro, Tanzania
[3]Pest Management Centre, Sokoine University of Agriculture, Morogoro, Tanzania
[4]Department of Engineering Sciences and Technology, Sokoine University of Agriculture, Morogoro, Tanzania
[5]Evolutionary Ecology Group, Universiteit Antwerpen, Antwerpen, Belgium
[6]Ministry of Agriculture Training Institute (MATI) Ilonga, Kilosa, Tanzania
[7]International Center of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya

Correspondence
Alex Mayamba, Department of Wildlife Management, Sokoine University of Agriculture, Morogoro, Tanzania.
Email: alexmayamba@gmail.com

Funding information
This work was supported by the Bill and Melinda Gates Foundation through Sokoine University of Agriculture (Project number OPP1112579) that funded Alex Mayamba's PhD studies, of which this paper was part.

Abstract

1. Pest rodents remain key biotic constraints to cereal crops production in the East African region where they occur, especially in seasons of outbreaks. Despite that, Uganda has scant information on rodents as crop pests to guide effective management strategies.
2. A capture–mark–recapture (CMR) technique was employed to study the ecology of small rodents, specifically to establish the species composition and community structure in a maize-based agro ecosystem. Trapping of small rodents was conducted in permanent fallow land and cultivated fields, with each category replicated twice making four study grids. At each field, a 60 × 60 m grid was measured and marked with permanent trapping points spaced at 10 × 10 m, making a total of 49 trapping points/grids. Trapping was conducted monthly at 4-week interval for three consecutive days for two and half years using Sherman live traps.
3. Eleven identified small rodent species and one insectivorous small mammal were recorded with *Mastomys natalensis* being the most dominant species (over 60.7%). Other species were *Mus triton* (16.1%), *Aethomys hendei* (6.7%), *Lemniscomys zebra* (5.2%), *Lophuromys sikapusi* (4.8%), *Arvicanthis niloticus* (0.9%), *Gerbilliscus kempi* (0.1%), *Graphiurus murinus* (0.1%), *Steatomys parvus* (0.1%), *Dasymys incomtus* (0.1%), and *Grammomys dolichurus* (0.1%). Spatially, species richness differed significantly ($p = 0.0001$) between the studied field habitats with significantly higher richness in fallow land compared with cultivated fields.
4. Temporally, total species richness and abundance showed a significant interaction effect over the months, years, and fields of trapping with significantly ($p = 0.001$) higher abundances during months of wet seasons and in the first and third year of trapping. In terms of community structure, higher species diversity associated more with fallow field habitats but also with certain rare species found only in cultivated fields.

Ecology and Evolution. 2019;9:7849–7860. www.ecolevol.org | 7849

over the study period. The density of animals per/0.5 ha was estimated for each three-day trapping session using the M(h) estimator of the program CAPTURE for a closed population, which allows for individual variations in trapping probability (White, Anderson, Burnham, & Otis, 1982) and is the most commonly used test in other studies thus allows better comparison with those studies.

2.4 | Data processing and analysis

Data from the four grids were pooled and formed two data sets: cultivated field and fallow land field to obtain total small rodent diversity per habitat. Species richness and abundance were calculated using the pooled data for cultivated fields and fallow land fields. All variables were tested for normality using Shapiro–Wilk test, and the strongly skewed variables were transformed prior to analyses whether necessary, to meet the assumption of normality and homogeneity of variances (Wilcoxon, 1945). Paleontological Statistics software (PAST; Hammer et al., 2002) was used to calculate diversity measures: species richness, Simpson Diversity Index, evenness, and dominance. Species accumulation curves and rank abundance curves were obtained for the two field categories using R software Vegan package (R software version 3.3.2; R Core Team, 2013). The monthly differences in small rodent richness and abundance between cultivated and fallow habitats were tested with analysis of variance (ANOVA) in XLSTAT (XLSTAT, 2017). Where the ANOVA test indicated significant differences, post hoc Tukey (HSD) test was used. Richness was used as a measure of the number of species in the two field habitats. Species diversity estimations were made by the Simpson's Diversity Index to consider both the richness and evenness. The index was calculated using the formula:

$$D=1-\frac{\sum n(n-1)}{N(N-1)}D=1-\frac{\sum n(n-1)}{N(N-1)}D=1-\frac{\sum n(n-1)}{N(N-1)}$$

where D, Simpson diversity (D'); n = number of individuals of each species, and N = total number of individuals of all species.

A *t* test was used to compare the Simpson's Diversity Indices between trapping grids.

Species turnover was computed to determine the rate of species change in time and space; temporal turnover (β_T) in species richness between years was calculated for each site as the total number of species found within that site (over the two and half years) minus the mean number of species per year for that site (α). Spatial turnover (β_S) was calculated as the total number of species found within a habitat type (over the two and half years) minus the mean number of species per site for that habitat type (over the two and half years).

The Bray–Curtis similarity index (Hammer et al., 2002) was used to compare similarities among zones and to construct a species composition similarity dendrogram for the three zones. The nonmetric multidimensional scaling ordination was used to plot species association with habitat type.

TABLE 1 Inventory of small rodent species and an insectivorous mammal recovered during the study period in the cultivated and fallow field habitats in Mayuge district, Eastern Uganda, year 2016–2018

Species	Total number of individuals (% contribution) in Cultivated field	Total number of individuals (% contribution) in Fallow field	Over all number (% contribution)
Small rodent species			
1. *Mastomys natalensis*	727 (68.5)	740 (54.6)	1,467 (60.7)
2. *Mus triton*	210 (19.8)	180 (13.3)	390 (16.1)
3. *Aethomys hendei*	35 (3.3)	128 (9.4)	163 (6.7)
4. *Lemniscomys zebra*	15 (1.4)	102 (7.5)	117 (4.8)
5. *Lophuromys sikapusi*	6 (0.6)	67 (4.8)	73 (3.3)
6. *Arvicanthis niloticus*	1	25	26
7. *Graphiurus murinus*	0	15	15
8. *Gerbilliscus kempi*	1	0	1
9. *Gramommys dolichurus*	0	1	1
10. *Steatomys parvus*	0	1	1
11. *Dasmys incomtus*	1	0	1
Insectivorous species			
1. *Crocidura* spp.	65 (6.1)	80 (5.9)	145 (6.0)
Total captured	1,061 (100)	1,352 (100)	2,413 (100)
Total trap nights	8,820	8,232	17,052
Species richness	9	10	12
Simpson's Diversity Index	0.467	0.617	

3 | RESULTS

3.1 | Small mammal species composition

Out of the 17,052 trap nights made, 1,061 and 1,355 small mammal individuals were trapped in cultivated and fallow land fields, respectively. These comprised of 11 small rodent species and one insectivorous small mammal species making a total of 12 small mammals (Table 1). Multimammate rat (*Mastomys natalensis*) was the most abundant rodent species with 727 (68.5%) individuals in cultivated fields and 740 (54.6%) individuals in fallow land fields, while the least was *Gerbilisicus kempi*, *Gramommys dolichurus*, *Dasmys incomtus*, and *Steatomys parvus*. The former four rodent species were very scarce as only one individual each was captured for the whole study period (Table 1). The results also showed that fallow fields were species richer (10 small rodent species) compared with cultivated fields (nine small rodent species; Table 1). The species accumulation curve plotted (Figure 2a) showed a good sampling effort as it tended to level off after the 20th trapping session, with minimal encounters of new species after, but also indicates that a few more species can be trapped with more years of trapping. Additionally, separate curves for the habitats were plotted and fallow fields displayed a slightly higher accumulation curve compared with cultivated fields (Figure 2b), implying a higher probability of encountering more species in fallow field habitat with sampling. The overall maximum species estimated by Chao 2, Jackknife 1, and Bootstrap richness estimators in the study area for the two and half years of the study was 13 species. Simpson species diversity index showed relatively higher diversity for fallow field (0.617) compared with cultivated field (0.467) but was not significantly different ($p > 0.05$). Species evenness was higher in fallow field (42.04%) compared with cultivated field (34.17%).

In terms of temporal variations in species richness and abundance, there was a significant ($F_{28,29} = 2.819$, $p = 0.004$) interaction effect between months and years of the study for richness within fallow land habitat. Significantly, more species were observed in the first year of trapping (2016) in June, July, and August and then November (Figure 3). Lowest species recovery was noted to have occurred in the second year of trapping (2017), specifically in the month of May (Figure 3). Within cultivated field habitat, there was

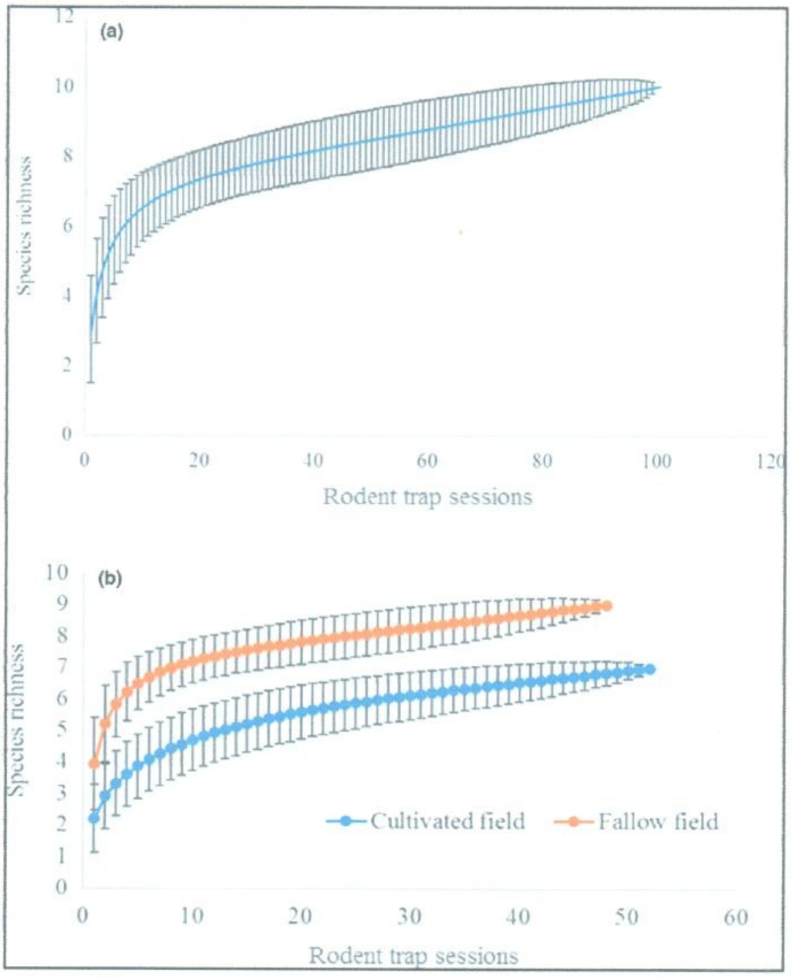


FIGURE 2 Species accumulation for all samples (a) and (b) for the separate studied fields (Fallow and cultivated fields with ± Standard deviation

FIGURE 3 Mean (±*SE*) monthly species richness over the two and half year's study period in fallow and cultivated fields in Mayuge district, Eastern Uganda

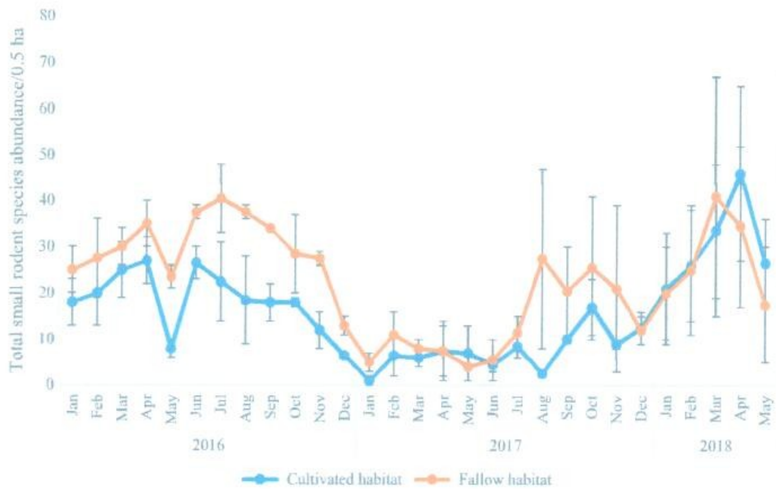


FIGURE 4 Mean (±*SE*) monthly small rodent abundance over the two and half year's study period in fallow and cultivated field habitats in Mayuge district, Eastern Uganda

also significant interaction effect between months and years of the study for species richness ($F_{28,29}$ = 1.857, p = 0.054). Significantly, fewer species recovery was observed in the second year of trapping, in January, May, and June which differed from the rest. Generally, there was almost consistence in the number of species recovered monthly over the study period (Figure 3).

The interaction effect between years and months on total small rodent species abundance also showed a significant effect for fallow land ($F_{28,29}$ = 2.334, p = 0.001). Significantly, higher abundances were obtained in the months of June (38 ± 2/0.5 ha), July (41 ± 8/0.5 ha), August (38 ± 2/0.5 ha) for 2016, and March (41 ± 26/0.5 ha) in 2018. In cultivated field habitats, the interaction effect of year and month of trapping on small rodent abundance was also significant ($F_{28,29}$ = 2.612, p = 0.007). Significantly, higher abundance was recorded in the last year of trapping (2018) in the month of April (46 ± 19/0.5 ha; Figure 4). Generally, there a was synchrony in temporal changes in rodent abundance over the years in the studied field habitats, with higher abundance in the first year of trapping, then a decline in year two and a steady rise in the third year of trapping.

In terms of species turnover, spatially there was a significant difference ($F_{1,6}$ = 9, p = 0.024) for the studied field habitats. Fallow field habitats showed significantly higher species turnover (6 ± 1) species compared with cultivated field habitat (4 ± 1). Temporal species turn over (β_T) also showed a significant difference ($F_{5,44}$ = 18.819, p = 0.0001) over the three years of the study. The first year of trapping showed a higher species turn over followed by a decline in the second year of trapping and then a rise in the third year of trapping in both habitats (Figure 5).

3.2 | Small rodent community structure across field trapping habitats

The trapping habitats were generally similar in composition with respect to rodent species. The Bray–Curtis similarity index generated three clusters—one for the cultivated fields, then separate clusters for fallow fields, with an overall cophenation correlation or cluster accuracy of 97.97% (Figure 6). A nonmetric multidimensional scaling analysis was conducted, and ordination plots were generated with a correlation method. Rodent communities were very distinct between habitats. Some species associated only with certain communities such as *G. kempi* sp. and *D. incomtus*, these only associated with cultivated habitats. The ordination plots also revealed that several of the recorded rodent species in the study associated more

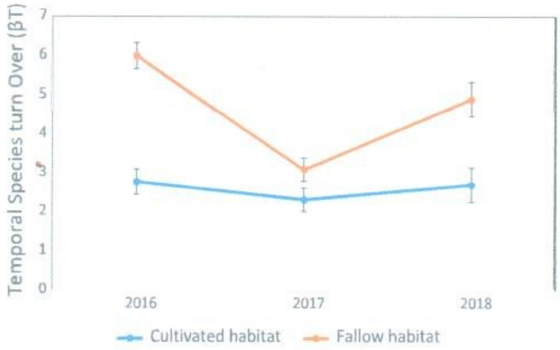


FIGURE 5 Mean (±*SE*) temporal species turn over (β_T) for the different years of study in Mayuge district, Eastern Uganda

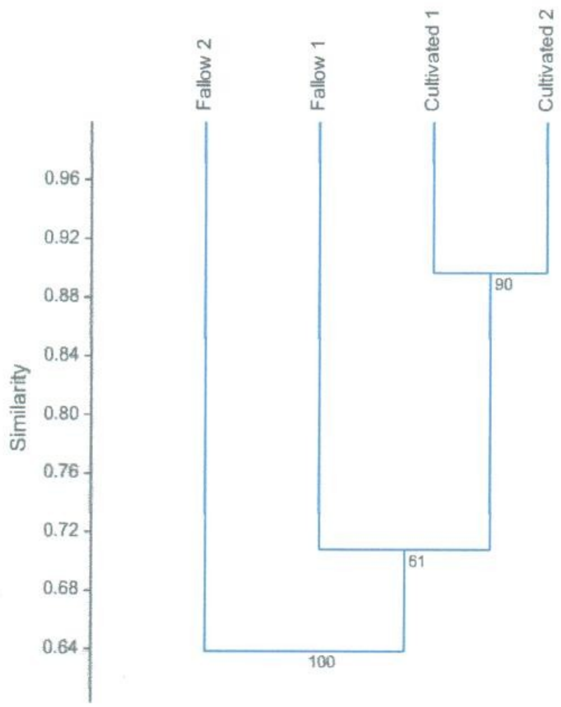


FIGURE 6 Bray–Curtis similarities in rodent composition among the trapping habitats and species communities in the study

with fallow habitats. There was one rodent species, *M. natalensis* which exhibited unique characters as it plotted almost at zero implying it's a generalist species. It associated equally in both fallow land and cultivated field habitats (Figure 7).

4 | DISCUSSION

4.1 | Small rodent species composition

This study presents the first comprehensive inventory of small rodent species in agricultural environmental setting in Uganda. Eleven small rodent species and one insectivorous mammal were recorded from both fallow land and cultivated fields. Earlier studies in the country report up to maximum of 34 small mammal species (Amatre et al., 2009; Basuta & Kasene, 1987; Clausnitzer & Kityo, 2001; Delany, 1975; Eisen et al., 2013). These report much higher species richness compared with the current study, and this was because they targeted all small mammals and their study environments (habitats) were different. For example, Eisen et al. (2013) concentrated around homesteads and within huts, where certain species almost permanently dwell such as the roof rat (*Rattus rattus*), but also migratory rodent species could be trapped in localities closer to homesteads as they search for food and escape from adverse weather conditions (Amatre et al., 2009). Particularly, some rodent species have been reported to be habitat specific, for example, *Proamys* spp. are closed forest dwellers (Basuta & Kasene, 1987) and thus could not be trapped in this study. Elsewhere in the region where studies have been conducted with similar study designs involving fallow land and maize field habitats with a capture–mark–recapture procedure, a range of between 4 and 11 species of small rodents has been reported (August, 1984; Fleming, 1975; Mares & Ernest, 1995; Makundi, Massawe, Mulungu, & Katakweba, 2010; Massawe, Rwamugira, Leir, Makundi, & Mulungu, 2006; Mulungu et al., 2013). Secondly, while the study reports eleven small rodent species, four of them which included *G. dolichurus, D. incomtus, G. kempi, and S. parvus* were very rarely encountered with less than three individuals in the whole study period. The low numbers of the later could suggest possibly unsuitable habitats for these species' settlement, breeding, and survival (Delany, 1975; Missone, 1969). The study showed differences in species composition between fallow land and maize field habitats with higher diversity index value (0.617) for fallow land compared with cultivated fields (0.467). In Tanzania, Makundi et al. (2010) observed a similar result with a higher diversity index value in fallow land habitat compared with maize habitat. This phenomenon could be explained by land use patterns, where human activities alter habitat characteristics, which may result in a positive or negative impact on rodent communities (Hoffmann & Zeller, 2005). In this study, the authors attribute human activities including land preparation, weeding, and harvesting which are key in cultivated fields to have likely resulted into lower species richness in cultivated field habitat.

The study also showed dominance of *M. natalensis*, with over 60% contribution of the total trap catches in both habitats. This particular species is reported by several authors in the East African region as an important member of the rodent community, occurring in various habitats both disturbed and undisturbed (Hubbard, 1972; Leirs, 1995; Makundi et al., 1999, 2010; Massawe, Rwamugira, Leirs, Makundi, & Mulungu, 2005; Mulungu, 2003). The higher abundance of *M. natalensis* in cultivated fields compared with fallow land further affirm the theory that this species highly adapts to new environments and is a good colonizer of disturbed areas including cultivated agricultural fields (Leirs, 1992; Massawe et al., 2005; Makundi, Massawe, Mulungu, & Katakweba, 2010; Odhiambo, Oguge, & Leirs, 2005).

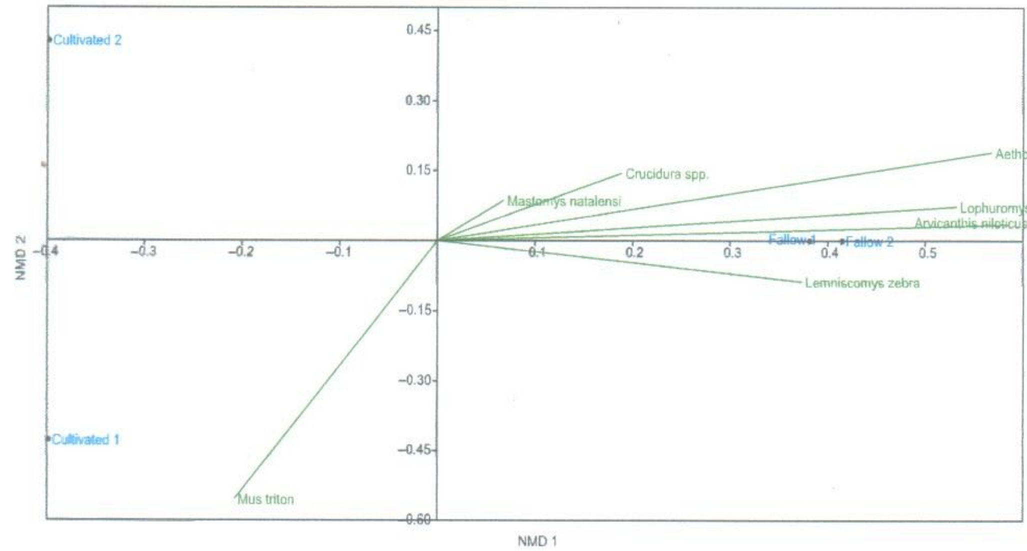


FIGURE 7 Ordination plots for nonmetric dimensional scaling (NMDS) in rodent community composition among trapping habitats

Mus spp. were second in abundance, which occurred equally in fallow land, and cultivated fields but more numbers in cultivated fields. This species is reported to be widely distributed across sub-Saharan Africa where it occurs in a variety of savannah and grassland habitats (Monadjem, Taylor, Denys, & Cotterill, 2015). *Mus triton* records in this study are in total agreement with earlier taxonomic records reported in the Kenya and Tanzania (Happold, 2013; Monadjem et al., 2015; Veyrunes et al., 2004, 2005) that it occurs across the East African countries. The relatively higher numbers of *M. triton* in cultivated fields suggest that they are also good colonizers of disturbed habitats. Earlier findings by Fuller and Perrin (2001) report related results as they recovered higher numbers in a disturbed habitat that was exposed to fire. Demeke, Afework, and Gurja (2007) in Ethiopia described that *Mus* spp. were more abundant in agricultural farmland than bush habitats. *Aethomys hendei*, commonly known as bush rat, is a generalist herbivorous species and often found in woodlands although it can be found inhabiting fields that have been under cultivation (Kingdon, 1974). In the current study, more trap catches for *A. hendeii* were recovered in fallow land as opposed to cultivation field. This is typically a bush rat, which dwells in bush thickets thus the higher abundances in fallow fields signifies habitat suitability for undisturbed habitats preferably forests (Happold, 2013; Kingdon, 1974). In the current study, *Lophuromys sikapusi* was captured at relatively low numbers. An earlier study which was conducted in a national forest in the country reported relatively higher numbers compared with this study (Basuta & Kasenene, 1987). The difference can be attributed to the habitat type as this species prefers cool mist environments (Happold, 2013; Kingdon, 1974). Its preference for cooler environments was further evidenced by more trap captures in fallow than cultivated fields, which fallow exhibited microclimatic conditions (cooler undercover temperatures) that could have been enhanced by thickets of tick berry plants that were initially dominant in fallow fields. Similarly, in Tanzania, higher numbers of *Lophuromys* spp. were trapped in forest habitats particularly when vegetation was dense and humid (Makundi, Massawe, Borremans, Laudisoit, & Katakweba, 2015).

Other species captured included *A. niloticus* commonly known as African grass rat, *G. murinus* (arboreal species), *G. kempi*, and *D. incomtus* (African Marsh rat) were recorded in relatively low numbers in the study and were mostly encountered in first year of trapping. These species were mostly captured in fallow land, a habitat which is closely related to natural forests, with relatively high weedy grasses, shrubs, trees, and form relatively dense vegetation ground cover. Such a habitat is believed to have offered favorable conditions for settlement of the above species. The results are closely related to earlier findings that reported higher numbers of *A. niloticus* during the rainy season when resources from grasses are rich with dense vegetation cover to provide shelter from predators (Massawe et al., 2005; Senzota, 1982). *G. murinus* was captured in fallow land only and encountered in the first year of trapping with no captures in the preceding years. Observations made during the study showed that vegetation cover reduced drastically in the subsequent years' in the fallow fields due to disturbances in these fields by livestock grazing. Additionally, *G. murinus* low numbers could also be attributed to its arboreal nature as it nests on trees and routinely visits the ground thus chances of being trapped with the live Sherman traps are minimal.

4.2 | Spatial patterns in species richness and diversity

Spatial variations in total small rodent species richness and diversity were observed, with fallow land displaying higher species richness and diversity. Similarly, spatial species turn over (β_S) was significantly higher in fallow land habitat. The results are not surprising, as it has already been reported that habitat characteristics/patterns play a significant role in the ecology of rodents (Delany, 1975). This study further showed that while cultivated fields are less species rich, they are still very prone to infestation by rodents of different species. Specifically, *M. natalensis*, one of the notorious rodent pest species, exhibited higher rank abundance in cultivated field as opposed to fallow. This phenomenon confirms the importance of this species as an agricultural pest that calls for more attention as already reported (Makundi, Massawe, & Mulungu, 2005; Mulungu, 2003). Furthermore, Isabirye-Basuta and Kasenene (1987) reported that the abundance and distribution of the small mammals depend mainly upon the nature and density of vegetation, which in turn influence food and shelter availability. The higher species abundances and richness in fallow fields in this study were linked to the characteristic nature of fallow land habitat which offered more vegetation for food as well as offering shelter for breeding and protection of the small rodents from possible predation as compared to cultivated fields.

Generally, habitat complexity may provide more niches that could be exploited by several species of rodents (Rosenzweig & Winakur, 1969). Niche partitioning (temporally, spatially, and trophically; Pianka, 1973) is an important factor in species co-existence in both stable and disturbed habitats. Human activities have also been reported to significantly influence the species richness and diversity at a small scale (Massawe et al., 2005). Additionally, Getachew and Afework (2015) recovered more individuals of small rodents in bushland habitat as compared to the other habitats. This was attributed to habitat's plant composition, which included *Pterolobium stellatum, Capparis tomentosa, and Urtica simensis*, which are thorny, and prevented movement of humans and livestock, thus offering a safe environment for small mammal breeding and survival. Additionally, wild animals respond to human disturbance in the same way they respond to predation, by avoiding highly disturbed areas or underutilizing them (Beale & Monaghan, 2004; Gill, Sutherland, & Watkinson, 1996), but the strength of this response is different for different species (Gill, Norris, & Sutherland, 2001). In this study, species richness and abundance were high in fallow land habitat, which could possibly be due to the low levels of human activities/ disturbance as compared to cultivated field.

4.3 | Temporal patterns in total species richness and abundance

In the current study, temporal variations were an important factor that influenced the species richness and relative abundance of the species across the fields. The monthly year to year changes in small rodent species richness and abundance were also obvious, with higher richness and abundance in the first year of trapping compared with the proceeding years of trapping. There were significant variations in monthly rodent species richness and abundances over the two and half years of the study period with generally higher richness and abundance in the months of June, July, and August in 2016 and March and April in 2018 trapping. These results are similar with earlier studies by Makundi et al., (2010) and Mulungu (2003), when they recovered more species and higher trap catches in the first year of the study. The monthly changes in small rodent abundance reported here only affirm earlier theories that suggest that rodent populations are highly dynamic and are driven by several environmental factors, but more particularly by rainfall, which influences vegetation and human activities (Leirs, 1992). It was noted that vegetation cover and human activities changed with months, and this is believed to have played a role in regulating rodent populations in both habitats. For example, due to constant human activities in cultivated fields, the rodent populations fluctuated more highly as opposed to fallow land where it was observed to have had minimal human interaction. Similar observations are reported by Addisu and Bekele (2013) who report that crop harvesting and grazing were perhaps the considerable factors for the reduction in rodent's abundance in maize fields during the dry season in their study in Ethiopia. Specifically, increased animal grazing has been widely shown to affect rodent species composition and abundance (Cao et al., 2016; La Morgia, Balbo, Memoli, & Isaia, 2015; Yihune & Bekele, 2012). Additionally, habitat fragmentation and anthropogenic activity can make areas inviable for certain fauna and can therefore alter their distribution (Markovchick-Nicholls et al., 2008).

Nevertheless, several publications report temporal rodent abundances in terms of months and years various explanations are given. For example, Mulungu et al. (2013) reported lower rodent abundances but with more female individuals breeding during the rainy season. Similarly, Massawe, Makundi, Mulungu, Katakweba, and Shayo 2012report breeding patterns of some rodent species in Central Tanzania to be seasonal and correlated well with rainfall patterns. Other studies on ecology of rodents in East Africa have associated population dynamics with the indirect influence of rainfall on reproduction patterns and habitat characteristics, including vegetation structure and cover (Delany, 1972; Leirs, 1992; Leirs, Verheyen, Michiels, Verhagen, & Stuyck, 1989; Makundi et al., 2005; Makundi, Massawe, & Mulungu, 2006; Taylor & Green, 1976; Telford, 1989). Precipitation has been reported to result into increased primary vegetation production, which in turn leads to increased rodent abundance (Gage & Kosoy, 2005). The temporal differences observed in the current study are likely attributed to several factors already reported on in earlier studies but were not quantitatively analyzed in this study, which include among others, vegetation ground cover, quality food supply, and human activities which are all governed by rainfall. Already, existing theories show that human activity can have negative impacts on many wildlife species, leading to changes in distribution (moving away from human activity), abundance, and activity patterns (Griffiths & Van Schaik, 1993). This type of scenario indeed was observed in fallow fields where species richness and abundance were high in the first year of the study but declined with time due to increased pressure as a result of human activities on this reserved piece of land. Human activities such as animal grazing have thus been observed to have an impact on rodent species distribution and abundance and can be used as a means of modifying environment as a rodent management technique in a localized setting (La Morgia et al., 2015).

Consequently, although there were no clear trends in the population dynamics from one year to another, a less similar pattern of increased rodent abundance in the second part of year from May to November was noted throughout the two and half years of the study.

4.4 | Synthesis and applications

Long-term studies that provide description of rodent species composition and community structure in agriculture settings contribute to state of the pest management reports, environmental risk assessments, and offer options for harmonizing the benefits of rodents in the ecosystem and protection from pest damage. Currently, most descriptions focus on rodents as forest dwellers as indicators of habitat quality and, as vectors of human and livestock diseases (Clausnitzer, Church, & Hutterer, 2003; Eisen et al., 2013). On the contrary, this study focused on understanding rodents as pests in a crop farming system to establish the common species and how they are distributed between cultivated fields and fallow land in such an agricultural setting.

Therefore, an understanding of rodent species composition for a given locality is particularly valuable; for conservation and management purposes. Gorvnment agencies responsible wild life conservation and pest control can utilize the information for approprite decision making for conservation and application of appropriate control measures on pestivorous species respectively. Our approach identifies the most abundant species in cropped fields and relates with other studies in the region on potential impacts these species can have on crops in an agricultural system.

ACKNOWLEDGMENTS

We are extremely grateful to the Ecologically Based Management of Rodent Pests in Maize and Rice in East Africa to Sokoine University of agriculture project (Grant number OPP1112579) supported by Bill and Melinda Gates foundation for the financial support of this research. We are also grateful for the tireless efforts from Kisakye Alex, Ouma Namulochi, and Ramadhani Kigunguli from Busitema University, Namasagali campus, Uganda and Pest Management Centre, Sokoine University of Agriculture, Morogoro, Tanzania, respectively.

CONFLICT OF INTEREST

None declared.

AUTHORS' CONTRIBUTION

Mayamba. A, Mulungu. L. S, Makundi. R.H, and Massawe. A conceived the ideas and designed methodology. All authors contributed to data collation. Mayamba A, Mulungu. L.S, and Isabirye. B analyzed the data and led the writing of the manuscript. All authors critically reviewed the drafts and gave final approval for publication.

DATA AVAILABILITY

We the authors of this manuscript have collectively agreed to have the data used in the results section to publicly avail that information to a public domain Dryad once this paper has been accepted for publication under the journal of Ecology and Evolution. https://doi.org/10.5061/dryad.qv9471s.

ORCID

Alex Mayamba https://orcid.org/0000-0001-5180-1869

REFERENCES

Addisu, A., & Bekele, A. (2013). Habitat preferences, seasonal abundance and diets of rodents in Alage, Southern Ethiopia. *African Journal of Ecology*, *52*, 284–291.

Amatre, G., Babi, N., Russell, E., Ogen-Odoi, A., Atiku, L. A., Akol, A., ... Eisen, R. J. (2009). Flea diversity and infestation prevalence on rodents in a Plague-Endemic Region of Uganda. *Journal of Tropical Medicine and Hygiene*, *81*(4), 718–724.

Aplin, K. P., Brown, P. R., Jacob, J., Krebs, C. J., & Singleton, G. R. (2003). *Field methods for rodent studies in Asia and the Indo-Pacific*. Canberra, ACT: CSIRO.

August, P. V. (1984). Population ecology of small mammals in the llanos of Venezuela. In R. E. Martin & B. R. Chapman (Eds.), *Contributions in mammalogy in honor of Robert L. Packard* (pp. 71–104). Cambrigde: Special Publications, The Museum, Texas Tech University, 22:1–234.

Basuta, G., & Kasene, J. M. (1987). Small rodent populations in selectively felled and mature tracks of Kibale forest, Uganda. *Biotropica*, *19*(3), 260–266.

Beale, C. M., & Monaghan, P. (2004). Human disturbance: People as predation-free predators? *Journal of Applied Ecology*, *41*, 335–343.

Borchert, J. N., Enscore, R. E., Eisen, R. J., Atiku, L. A., Owor, N., Acayo, S., ... Gage, K. L. (2010). Evaluation of rodent bait containing imidacloprid for the control of fleas on commensal rodents in a plague-endemic region of northwest Uganda. *Journal of Medical Entomology*, *47*, 842–850.

Cao, C., Shuai, L.-Y., Xin, X.-P., Lui, Z.-T., Song, Y.-L., & Zeng, Z.-G. (2016). Effects of cattle grazing on small mammal communities in the Hulunber meadow steppe. *PeerJ*, *4*, e2349. https://doi.org/10.7717/peerj.2349

Clausnitzer, V., Church, S., & Hutterer, R. (2003). Habitat occurrence and feeding ecology of *Crocidura montis* and *Lophuromys flavopunctatus* on Mt. Elgon, Uganda. *African Journal of Ecology*, *41*, 1–8.

Clausnitzer, V., & Kityo, R. (2001). Altitudinal distribution of rodents (Muridae and Gliridae) on Mt Elgon, Uganda. *Tropical Zoology*, *14*(1), 95–118. https://doi.org/10.1080/03946975.2001.10531145

Delany, M. J. (1972). The ecology of small rodents in tropical Africa. *Mammal Review*, *2*, 1–42.

Delany, M. J. (1975). *The rodents of Uganda*. Kettering Northamptonshire, UK: The George Press.

Demeke, D., Afework, B., & Gurja, B. (2007). Feeding ecology of pest rodents from Arbaminch forest and farmlands, Ethiopia. *SINET: Ethiopian Journal of Science*, *30*, 127–134.

Eisen, R. J., Enscore, R. E., Atiku, L. A., Zielinski-Gutierrez, E., Mpanga, J. T., Kajik, E., ... Gage, K. L. (2013). Evidence that rodent control strategies ought to be improved to enhance food security and reduce the risk of rodent-borne illnesses within subsistence farming villages in the plague-endemic West Nile region, Uganda. *International Journal of Pest Management*, *59*(4), 259–270.

Eisen, R. J., Griffith, K. S., Borchert, J. N., MacMillan, K., Apangu, T., Owor, N., ... Mead, P. S. (2010). Assessing human risk of exposure to plague bacteria in northwestern Uganda based on remotely sensed predictors. *American Journal of Tropical Medicine and Hygiene*, *82*, 904–911.

Fiedler, L. A. (1988). Rodent problems in Africa. In I. Prakash (Ed.), *Rodent pest management* (pp. 35–65). Boca Raton, FL: CRC.

Fleming, T. H. (1975). The role of small mammals in tropical ecosystems. In F. B. Golley, K. Petrusewicz, & L. Ryszkowski (Eds.), *small mammals: their productivity and population dynamics* (pp. 269–298). Cambridge, UK: Cambridge University Press.

Fuller, J. A., & Perrin, M. R. (2001). Habitat assessment of small mammals in the Umvoti Vlei Conservancy, KwaZulu-Natal, South Africa. *South African Journal of Wildlife Research*, *31*, 1–12.

Gage, K. L., & Kosoy, M. Y. (2005). Natural history of plague: Perspectives from more than a century of research. *Annual Review of Entomology*, *50*, 505–528.

Geddes, A. W. M. (1992). *The relative importance of pre-harvest crop pests in Indonesia* (p. 70). Chatham, UK: Bulletin of the Natural Resources Institute.

Getachew, B., & Afework, B. (2015). Diversity and habitat association of small mammals in Aridtsy forest, Awi Zone, Ethiopia. *Zoological Research*, *36*(2), 88–94.

Gill, J. A., Norris, K., & Sutherland, W. J. (2001). Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation*, *97*, 265–268.

Gill, J. A., Sutherland, W. J., & Watkinson, A. R. (1996). A method to quantify the effects of human disturbance on animal populations. *Journal of Applied Ecology*, *33*, 786–792.

Griffiths, M., & Van Schaik, C. P. (1993). The impact of human traffic on the abundance and activity periods of sumatran rain forest wildlife. *Conservation Biology*, *7*(3), 623–626.

Happold, D. C. D. (Ed.) (2013). *Mammals of Africa. Volume III: Rodents, hares and rabbits* (784 pp). London, UK: Bloomsbury Publishing.

Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2002). Past: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, *41*, 9.

Hoare, J. M., & Hare, K. M. (2006). The impact of brodifacoum on non-target wildlife: Gaps in knowledge. *New Zealand Journal of Ecology*, *30*, 157–167.

Hoffmann, A., & Zeller, U. (2005). Influence of variations in land use intensity on species diversity and abundance of small mammals in the Nama Karoo, Namibia. *Belgian Journal of Zoology*, *135*(Suppl.), 91–96.

Hubbard, C. A. (1972). Observations on the life histories and behaviour of some small rodents from Tanzania. *Zoologica Africana*, *7*, 419–449.

Kingdon, J. (1974). *East Africa mammals: an atlas of evolution in Africa. Volume II Part B (Hares and Rodents)*. London, UK: Academic Press.

La Morgia, V., Balbo, C., Memoli, S., & Isaia, M.. (2015). Rodents in grassland habitats: does livestock grazing matter? A comparison of two Alpine sites with different grazing histories. *Zoosystema*, *37*(4), 571–580. https://doi.org/10.5252/z2015n4.

Leirs, H. (1992). *Population ecology of* Mastomys natalensis *(Smith, 1834) multimammate rats: Possible implications for rodent control in Africa*. PhD Thesis. Antwerp, Belgium: University of Antwerp, Belgium.

Leirs, H. (1995). *Population ecology of* Mastomys natalensis *(Smith, 1834). Possible implication for rodent control in Africa*. Agricultural Edition No. 35, Brussels, Belgium: Belgium Administration for Development Cooperation.

Leirs, H. (2003). Management of rodents in crops: The Pied Piper and his orchestra. In G. R. Singleton, L. A. Hinds, C. J. Krebs, & D. M. Spratt (Eds.), *Rats, mice and people: Rodent biology and management* (pp. 183–190). Canberra, ACT: ACIAR.

Leirs, H., Singleton, G. R., & Hinds, L. A. (1999). Ecologically-based rodent management in developing countries: Where to now? Ecologically-based management of rodent pests. In G. H. Singleton, L. Hinds, H. Leirs, & Z. B. Zhang (Eds.), *Ecological-Based Management Rodent Pest* (pp. 477–484). Canberra, ACT: ACIAR.

Leirs, H., Verhagen, R., Verheyen, W., Mwanjabe, P., & Mbise, T. (1996). Forecasting rodent outbreaks in Africa: An ecological basis for Mastomys control in Tanzania. *Journal of Applied Ecology*, *33*, 937–943.

Leirs, H., Verheyen, W., Michiels, M., Verhagen, R., & Stuyck, J. (1989). The relationship between rainfall and breeding season of Mastomys natalensis (Smith 1834) in Morogoro, Tanzania. *Annales De La Société Royale Zoologique De Belgique*, *119*, 59–64.

Makundi, R. H., Massawe, A. W., Borremans, B., Laudisoit, A., & Katakweba, A. (2015). We are connected: Flea-host association networks in the plague outbreak focus in the Rift Valley, northern Tanzania. *Wildlife Research*, *42*(2), 196. https://doi.org/10.1071/wr14254

Makundi, R. H., Massawe, A. W., & Mulungu, L. S. (2005). Rodent population fluctuations in three ecologically distinct locations in north-east, central and south-west Tanzania. *Belgian Journal of Zoology*, *135*(Supplement), 159–165.

Makundi, R. H., Massawe, A. W., & Mulungu, L. S. (2006). Breeding seasonality and population dynamics of three rodent species in the Magamba Forest Reserve in the Western Usambara Mountains, north-east Tanzania. *African Journal of Ecology*, *44*, 1–6.

Makundi, R. H., Massawe, A. W., Mulungu, L. S., & Katakweba, A. (2010). Diversity and population dynamics of rodents in farm-fallow mosaic fields in central Tanzania. *African Journal of Ecology*, *48*, 313–320. https://doi.org/10.1111/j.1365-2028.2009.01109.x

Makundi, R. H., Oguge, N. O., & Mwanjabe, P. S. (1999). Rodent Pest Management in East Africa – an ecological approach. In G. R. Singleton, L. Hinds, H. Leirs, & Z. Zhang (Eds.), *Ecologically-based rodent management* (pp. 460–476). Canberra, ACT: International Agricultural Research.

Mares, M. A., & Ernest, K. A. (1995). Population and community ecology of small mammals in a gallery forest of central Brazil. *Journal of Mammalogy*, *76*, 750–768.

Markovchick-Nicholls, L., Helen, M. R., Deutschman, D. H., Widyanata, A., Martin, B., Noreke, L., & Hunt, T. A. (2008). Relationships between human disturbance and wildlife land use in urban habitat fragments. *Conservation Biology*, *22*(1), 99–109.

Massawe, A. W., Makundi, R. H., Mulungu, L. S., Katakweba, A., & Shayo, T. N. (2012). Breeding dynamics of rodent species inhabiting farm—fallow mosaic fields in central Tanzania. *African Zoology*, *47*(1), 128–137. https://doi.org/10.3377/004.047.0117

Massawe, A. W., Rwamugira, W., Leir, 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.

Massawe, A. W., Rwamugira, W., Leirs, H., Makundi, R. H., & Mulungu, L. S. (2005). Influence of land preparation methods and vegetation cover on population abun- dance of *Mastomys natalensis* in Morogoro, Tanzania. *Belgian Journal of Zoology*, *135*(Supplement), 187–190.

Mdangi, M., Mulungu, L. S., Massawe, A. W., Eiseb, S. J., Tutjavi, V., Kirsten, F., ... Belmain, S. R. (2013). Assessment of rodent damage to stored maize (Zea mays L.) on smallholder farms in Tanzania. *International Journal of Pest Management*, *59*(1), 55–62.

Misonne, X. (1969). African and Indo-Australian Muridae: evolutionary trends. Annales Musie Royal de l' Afrique Centrale series 8. *Zoologie*, *172*, 1–219.

Monadjem, A., Taylor, P. J., Denys, C., & Cotterill, F. P. (2015). *Rodents of sub-saharan Africa: A biogeographic and taxonomic synthesis*. Berlin, Germany: De Gruyter.

Moore, S. M., Monaghan, A., Borchert, J. N., Mpanga, J. T., Atiku, L. A., Boegler, K. A., ... Eisen, R. J. (2015). Seasonal fluctuations of small mammal and flea communities in a Ugandan plague focus: Evidence to implicate *Arvicanthis niloticus* and *Crocidura* spp. as key hosts in Yersinia pestis transmission. *Parasites and Vectors, 8*, 11.

Mulungu, L. S. (2003). Assessment of maize (Zea mays L) damage and yield loss due to rodents in the field. PhD Degree awarded at Sokoine University of Agriculture, Morogoro, Tanzania, 178 pg.

Mulungu, L. S., Makundi, R. H., Leirs, H., Massawe, A. W., Vibe-Petersen, S., & Stenseth, N. C. (2003). The rodent-density-damage function in maize fields at an early growth stage. In G. R. Singleton, L. A. Hinds, C. J. Krebs, & D. M. Spratt (Eds.), *Rats, mice and people: Rodent biology and management* (pp. 301–303). Canberra, ACT: Australian Centre for International Agricultural Research.

Mulungu, L. S., Ngowo, V. B., Mdangi, M., Katakweba, A. S., Tesha, P., & Furaha and Kilonzoa B. S., (2013). Population dynamics and breeding patterns of Multi-mammate mouse, *Mastomys natalensis* (Smith 1834) in irrigated rice field in Eastern Tanzania. *Pest Management Science, 69*(3), 371–377.

Mwanjabe, P. S. (1990). Outbreak of *Mastomys natalensis* in Tanzania. *African Small Mammal Newsletter, 11*, 1.

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

Nabbumba, R., & Bahiigwa, G. (2003). *Agricultural productivity constraints in Uganda; implications for investment*. Research Series No:31.

Odhiambo, C., Oguge, O. N., & Leirs, H. (2005). Movements and spatial patterns of Mastomys erythroleucus in maize cropping systems in the Kenyan Rift Valley. *Belgium Journal of Zoology, 135*(Suppl.), 83–89.

Parsons, M. H., Banks, P. B., Deutsch, M. A., Robert, F. C., & Munshi-South, J. (2017). Trends in urban rat ecology: A framework to define the prevailing knowledge gaps and on incentives for academia, pest management professionals (PMPs) and public health agencies to participate. *Journal of Urban Ecology, 3*(1), 1–8.

Pianka, E. R. (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics, 4*, 53–74.

R Core Team. (2013). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rosenzweig, M. L., & Winakur, J. (1969). Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology, 50*, 558–572.

Senzota, R. B. M. (1982). The habitat and food habits of the grass rats (*Arvicanthis niloticus*) in the Serengeti National Park, Tanzania. *African Journal of Ecology, 20*, 241–252.

Shellemiah, K., & Rubaihayo, P. (2013). *Progress in On-Farm Production and Productivity in the East African Community: 50 Years after Independence*. Kilimo Trust Technical paper N0.8, International Symposium on Agriculture; EAC partner states at 50 years, 5–7 November 2013.

Simberloff, D. (2014). Biological invasions: Much progress plus several controversies. *Contributions to Science, 9*, 7–16.

Singleton, G. R. (2003). Impacts of rodents on rice production in Asia. No 45, IRRI Discussion Paper Series. International Rice Research Institute (IRRI), Los Banos, 30 pp.

Singleton, G. R., Hinds, L. A., Leirs, H., & Zhang, Z. (1999). *Ecologically-based rodent management*. Canberra, ACT: ACIAR.

Singleton, G. R., Jacob, S. J., & Krebs, C. J. (2005). Integrated management to reduce rodent damage to lowland rice crops in Indonesia. *Agriculture, Ecosystems and Environment, 107*(1), 75–82. https://doi.org/10.1016/j.agee.2004.09.010

Stenseth, N. C., Leirs, H., Skonhoft, A., Davis, S. A., Pech, R. P., Andreassen, H. P., ... Wan, X. (2003). Mice, rats, and people: The bio-economics of agricultural rodent pests. *Frontiers in Ecology and the Environment, 1*(7), 367–375. https://doi.org/10.1890/1540-9295(2003)001[0367:m-raptb]2.0.co;2

Taylor, K. D., & Green, M. G. (1976). The influence of rainfall on diet and reproduction in four African rodent species. *Journal of Zoology, 180*, 367–389.

Telford, S. R. J. R. (1989). Population biology of the multimammate rat, (*Mastomys natalensis*) at Morogoro, Tanzania 1981–1985. *Bulletin of the Florida State Museum. Biological Sciences, 34*(6), 249–287.

Veyrunes, F., Britton-Davidian, J., Robinson, T. J., Calvet, E., Denys, C., & Chevret, P. (2005). Molecular phylogeny of the African pygmy mice, subgenus Nannomys (Rodentia, Murinae, Mus): Implications for chromosomal evolution. *Molecular Phylogenetics and Evolution, 36*, 358–369.

Veyrunes, F., Catalan, J., Sicard, B., Robinson, T. J., Duplantier, J. M., Granjon, L., ... Britton-Davidian, J. (2004). Autosome and sex chromosome diversity among the African pygmy mice, subgenus Nannomys (Murinae; Mus). *Chromosome Research, 12*, 369–382.

Waddington, S. R., Li, X., Dixon, J., Hyman, G., & de Vicente, M. C. (2010). Getting the focus right: Production constraints for six major food crops in Asian and African farming systems. *Food and Security, 2*(1), 27–48.

White, G. C., Anderson, D. R., Burnham, K. P., & Otis, D. C. (1982). *Capture-recapture and removal methods for sampling closed populations Los Alamos National Laboratory*. New Mexico, NM: Los Alamos.

Wilcoxon, F. (1945). Individual comparisons by ranking methods. *Biometrics, 1*, 80–83.

Wilson, D. E., & Reeder, D. M. (2005). *Mammal species of the World: A taxonomic and geographic reference* (pp. 2142). Baltimore, MD: JHU Press.

XLSTAT. (2017). *Data analysis and statistical solution for Microsoft Excel*. Paris, France: Addinsoft. http://www.addinsoft.com

Yihune, M., & Bekele, A. (2012). Diversity, distribution and abundance of rodent community in the Afro-alpine habitats of the Simien mountains national park, Ethiopia. *International Journal of Zoological Research, 8*(4), 137–149.

How to cite this article: Mayamba A, Byamungu RM, Makundi RH, et al. Species composition and community structure of small pest rodents (Muridae) in cultivated and fallow fields in maize-growing areas in Mayuge district, Eastern Uganda. *Ecol Evol*. 2019;9:7849–7860. https://doi.org/10.1002/ece3.5371