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RESEARCH PAPER

Socio-environmental changes and rodent populations in lowland agroecosystems of the lower delta of the River Senegal, West Africa: results of observations over a decade, 2008-2019

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Abstract[1]. In the context of food self-sufficiency, the River Senegal Valley has been undergoing profound environmental changes for several decades. Rice production has increased due to the development of vast irrigated perimeters, which has been accompanied by recurrent proliferations of rodent populations that are crop pests and reservoirs of zoonoses. The aim of our study was to determine the factors underlying these phases of increased rodent abundance over a ten-year (2008 to 2019) sampling period during the hot dry season (February-May). A total of 1,867 rodents of four species were captured, among which *Arvicanthis niloticus* and *Mastomys huberti* dominated. Our results showed that, during this season, rodent abundance (i) increases significantly with rainfall from the previous year, (ii) is higher in cultivated than in uncultivated plots, (iii) increases with plant cover, (iv) increases, for *M. huberti*, with the presence of open water. We showed that in an area that was first sparsely cultivated and then impacted by hydro-agricultural rehabilitation of irrigation and drainage infrastructure, the abundance of *A. niloticus* changed following this program, reaching the level of a nearby area that has been intensively cultivated for decades. Moreover, we showed that the proportion of adults among the captured individuals was lower in rice plots than in vegetable gardening

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[1] *A French version of the manuscript is available as Appendix S1 (see at the link in Supplementary online material after the list of literature).*

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fields and uncultivated plots. The breeding pattern of adult individuals was also affected by land use. Results suggest that uncultivated areas and vegetable gardening fields constitute refuge and breeding ground hotspots and would thus form a starting point for the invasion of rice fields. Following these results, we advocate for regular monitoring of rodent breeding and abundance patterns, with a special focus on these refuge areas, particularly during the hot dry season. We recommend implementing effective and sustainable science-based control strategies at national and community levels to keep rodent populations within tolerable limits.

Key words: rodent outbreak, breeding pattern, irrigation and water resource management project, Millennium Challenge Account-Senegal

Introduction

In order to achieve food security, major hydro-agricultural development projects are being conducted in northern Senegal. The increase in irrigated area aiming at rice and vegetable cultivation, and associated changes in land use, have had a profound environmental impact in the River Senegal Valley (see OMVS website: http://www.omvs.org). Among other consequences, such changes are expected to increase rodent abundance (Poulet 1980, 1985, Duplantier 1997, 1998, Granjon & Duplantier 2009). Rodents are among the main crop pests and also host diseases of zoonotic origin (Singleton 2003, Stenseth et al. 2003, Granjon & Duplantier 2009, Han et al. 2015, Mendoza et al. 2019). In many countries of sub-Saharan Africa, high population densities or even outbreaks of rodents have been reported (Delattre et al. 1998, Leirs et al. 2010) causing from 15% to more than 80% damage to a variety of crops (Taylor 1968, Makundi et al. 1991, Mwanjabe et al. 2002). West Africa has regularly been affected by such rodent infestations, as in Nigeria where rodents were reported to cause between 14% and 30% of field yield loss of cereals (Rabiu & Rose 2004, Rabiu 2017). In Senegal, outbreaks of several rodent species have been documented (Bernard 1976, Poulet 1980, 1982, 1985, Hubert 1982, Bori & Dalecky 2021). These phases of high density caused severe damage to crops, leading farmers to abandon their fields after yield losses of up to 100% (Poulet 1982).

The climate can be a factor influencing these episodes of proliferation. The Sahelian climate is characterized by a short and unique rainy season in northern Senegal (July to September-October), the intensity of which shows high interannual variability particularly since the 1990s (Diop et al. 2016, Bodian et al. 2020), followed by a cool dry season (November to February) and a hot dry season (March to June). Outdoors, the reproductive cycle of Sahelian rodents is linked to the annual rate of the rains, which determines the quantity of available resources (Granjon & Duplantier 2009 and references therein). Agricultural intensification in the River Senegal Valley, when combined with years of high rainfall, is likely to increase the risk of rodent outbreaks with major consequences for crop losses. Given that rodents from Senegal are the hosts of pathogens (e.g. Duplantier 1990, Duplantier & Sène 2000, Diagne et al. 2017; reviewed in Granjon & Duplantier 2009), this may also increase the potential for the emergence of zoonotic diseases. As an example, an outbreak of rodents was observed in 2020 in Senegal and Mauritania on both banks of the River Senegal, following a particularly humid rainy season. Between 14% and 37% of the area sown with rice were affected depending on the region, out of a total of 111,643 ha. This resulted in estimated total losses of ca. 84,000 tons of paddy rice, i.e. 6% to 35% of the total expected production according to region, which represents a total loss of production of more than 31.4 million USD, directly affecting nearly 40,000 households, or about 270,000 people (11% to 14% of the population of these regions; Bori & Dalecky 2021, FAO 2021).

In this context, this study presents data on rodent communities from two neighbouring areas over a decade of longitudinal monitoring (2008 to 2019) according to the environmental changes linked to a hydro-agricultural rehabilitation program that ended in 2015 in the lower delta of the River Senegal. More specifically, it aims at (i) a species-level identification of rodent communities in lowland agroecosystems, (ii) an evaluation of the impact of factors such as land use, rainfall, plant cover, presence of open water, hydro-agricultural scheme developments on rodent abundance dynamics, age structure and adult breeding pattern within the framework of a recent irrigation and water resource management project.

Material and Methods

Description of the study area

The delta of the River Senegal is a mosaic of dry and wet environments, most of which are highly anthropized. It is a vast alluvial area with (i) lowlands (known locally as "Walo") dominated by decantation basins made up of acidified halomorphic clay soils and of hydromorphic gleys to pseudogleys, on a substrate formed of fluvio-deltaic alluvium, and (ii) upland remains of ancient

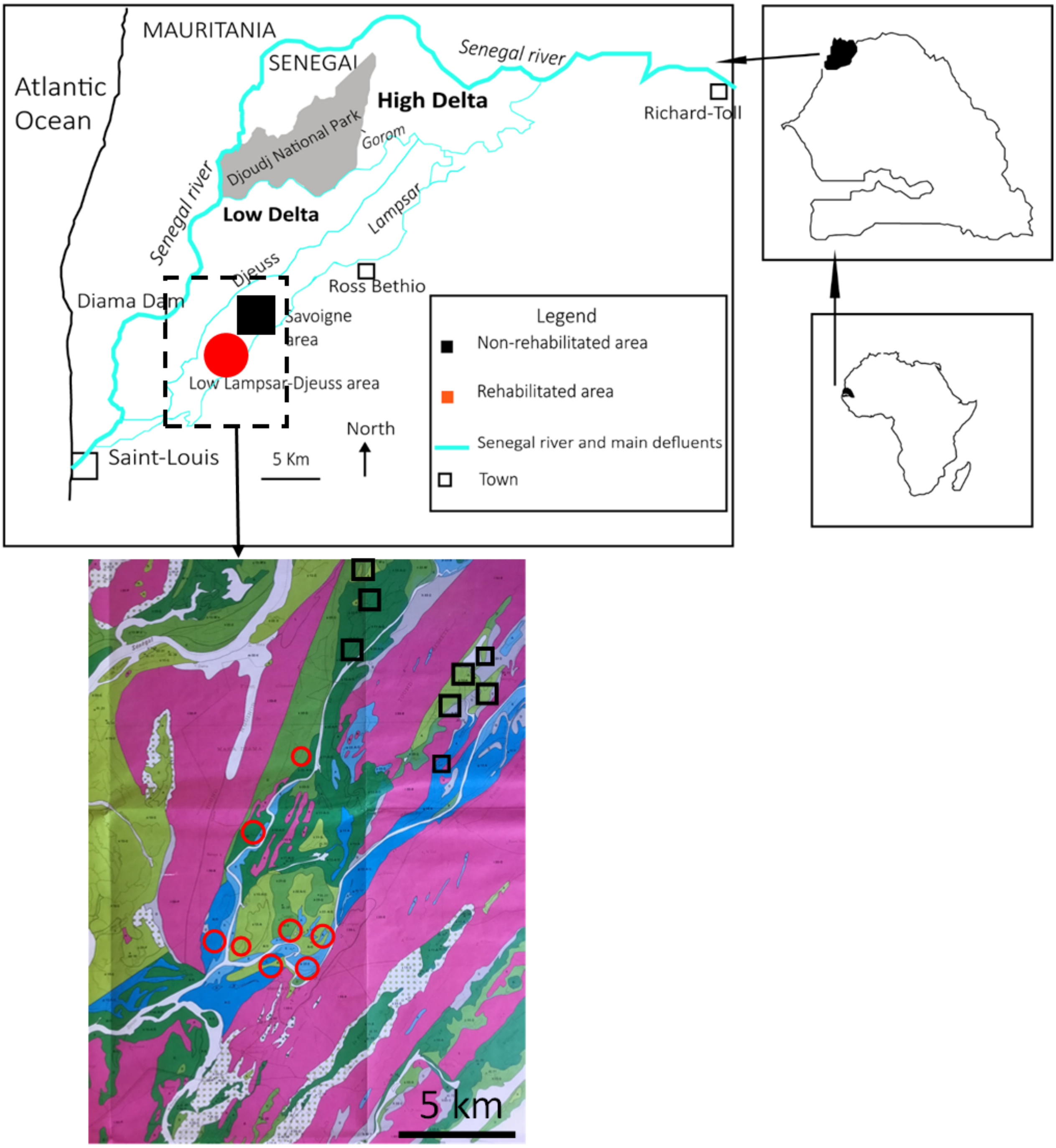

Fig. 1. Map showing the different sampled localities: the lower Lampsar-Djeuss area (red circles) has been rehabilitated by MCA-Senegal program in 2015 and is treated as an experimental site to study the impact of this irrigation and water resource management project; the Savoigne area (black squares), being characterised by a well-established irrigation infrastructure dating before 2008, has not been affected by the MCA-Senegal program and is treated as a positive control site. The upper part of the figure is adapted from Garambois et al. (2019). The lower part of the figure shows the different sampled localities on a soil map (SEDAGRI 1969), and illustrates the habitat mosaic composed of (i) lowlands ("Walo") dominated by decantation basins on a substrate formed of fluvio-deltaic alluvium, made up of acidified halomorphic clay soils (in light to dark green) and hydromorphic pseudogleys to gleys (in light to dark blue); and (ii) upland remains of ancient fixed dunes ("Diery") made up of sandy isohumic, brown-red sub-arid soils (in pink). Differences in the size of symbols of sampling localities illustrate variation in the intensity of sampling.

fixed dune systems (known locally as "Diery") comprising sandy isohumic, brown-red sub-arid soils (SEDAGRI 1969, Poulet 1982). This study was conducted in lowland agroecosystems of two neighbouring areas of the lower delta of the River Senegal, northern Senegal, that shared climatic, soil and geomorphological characteristics (Fig. 1). The most distant sampling sites were separated by less than 19 km. The first study area is located in and north of the Savoigne irrigated basin (ca. 16.200° N, 16.300° W) and has been cultivated intensively for decades, including agro-industrial crops, even before the implementation of updated irrigation infrastructure that took place thanks to the installation of the Diama and Manantali Dams in 1986 and 1987. The Savoigne area represents an historical site for rodent research that was studied in the 1970-1980s (Poulet 1980, 1982, 1985) and monitored again since 2007 within the framework of ObsMiCE (West African Observatory on small Mammals as indicators of Environmental Changes) activities. The second study area was located ca. 15 km to the southwest, along the lower part of the Rivers Lampsar and Djeuss where agricultural fields has previously been cultivated at a lower intensity level than in the Savoigne Basin. Monitoring of the lower Lampsar-Djeuss area (ca. 16.100° N, 16.383° W) was initiated in 2007. In the Savoigne area, the following crop succession has been observed for decades: rice crops during and following the rainy crop season (June-November/December), vegetable gardening in the cold off-season (November-February), then rice crops again during the hot off-season (March-June). In comparison, until 2015 in the lower Lampsar-Djeuss area, a small proportion of potentially irrigable land has been cultivated and much less intensively than in the Savoigne area, with periods of several years of fallow and cattle grazing. An irrigation and water resource management project, resulting in an 80% increase in the average area of land under cultivation (MCC 2019), was implemented as part of the Millennium Challenge Corporation compact with the government of Senegal leading to the Millennium Challenge Account-Senegal (hereafter MCA-Senegal; Mulyana et al. 2013) aligned with public policies for food self-sufficiency in rice. This scheme was justified as only approximately 30% of the 31,000 ha of potentially irrigable land in the delta have been cultivated at any time during the year, due to insufficient water delivery and poor drainage (Mulyana et al. 2013). During the one-decade monitoring of the present study (2008-2019), the lower Lampsar-Djeuss area was affected by the MCA-Senegal hydro-agricultural rehabilitation program that took place from 2012 to early 2015, whereas the Savoigne area was not affected by this project. In terms of rodent monitoring, the lower Lampsar-Djeuss and the Savoigne areas will hereafter be considered as experimental site and positive control site, respectively, of this recent irrigation and water resource management program.

Rodent sampling

Rodent trapping campaigns were carried out during the hot dry season from 2008 to 2019 (except 2013) over the following periods: 28 March-29 April 2008; 4-15 March 2009; 25 February-16 March 2010; 23 February-11 March 2011; 3-11 May 2012; 21-29 March 2014; 6-14 March 2015; 24 March-8 April 2016; 23 March-7 April 2017; 13-24 April 2018; 20-30 March 2019. Rodents were trapped both in fields that were cultivated at the date of sampling or that have been cultivated during the preceding growing season (hereafter referred to as "cultivated fields", either rice fields or vegetable gardening fields) and uncultivated plots (fallow land and swamps) using single capture wire-mesh live traps (8.5 × 8.5 × 26.5 cm). Traps were typically set in lines of 20 traps 10 m apart. Traps were set in the late afternoon of the first day, baited once a day with peanut butter, and were inspected the morning and late afternoon during three consecutive nights. Between years, the number of trap lines varied from 19 to 47 (median = 27), and sampling effort varied from 1,140 to 2,496 trap.nights (median = 1,516) and from 760 to 1,538 trap.days (median = 1,000) (Table 1). Due to logistical constraints, trap line set up could not be systematically placed at exactly the same locations from year to year over the 10-year period. Thus this study was not designed to be a cohort study, and should be viewed as transversal monitoring over time. We considered the dataset collected each year with these samples of trap lines to be a representative snapshot sample of the two study areas. We estimated the abundance of individual rodent species in each trap line as the number of rodents captured per sampling effort, thus representing trap success indices. *Arvicanthis niloticus* was trapped both night and day while *Mastomys huberti* was trapped only at night. Given that traps were inspected twice a day, we thus accounted for both the number of trap.days and trap.nights as trapping effort to calculate the trap success of *A. niloticus* and only the number of trap.nights for *M. huberti*, as follows.

$$\text{Trap success index of } \textit{A. niloticus} = \frac{\text{Number of captures}}{\text{(Number of traps) (Number of nights) + (Number of traps) (Number of days)}}$$

$$\text{Trap success index of } \textit{M. huberti} = \frac{\text{Number of captures}}{\text{(Number of traps) (Number of nights)}}$$

We considered that the basic assumption of a proportional relationship of trap success index to abundance is most likely justified as longitudinal data collected within irrigated plots from the Savoigne area show a significant relationship between density, as estimated from capture-mark-recapture protocol, and trap success index (Spearman rank-order correlation $r_S = 0.607$, $n = 21$, $P = 0.004$; *A. niloticus* data collected in 1975-1976, Table LXII in Poulet 1982). We thus proposed the hypothesis that trap success indices provide fairly good estimates of within-species fluctuations in relative abundance among years. Besides obvious between-species variation in the probability of capture of individuals, we acknowledge that future studies should aim to correct for the imperfect and potentially heterogeneous detection probability between years, seasons and habitats (Yoccoz et al. 2001, MacKenzie et al. 2006).

All rodents were sacrificed by cervical dislocation in a field laboratory, weighed, measured, dissected with preliminary identification to species level. Tissues were preserved in the "CBGP – Small Mammal Collection" (https://doi.org/10.15454/WWNUPO). Standard external morphometric data (head + body, tail, hind-foot and ear lengths) were collected and reproductive status was noted. Two age classes (adult *vs.* immature, i.e. juvenile and sub-adult) were established for each specimen based on weight measurements following Granjon & Duplantier (2009): *A. niloticus* and *M. huberti* individuals were considered adult when they weighed more than 70 g and 33 g, respectively. However, we note that this inference should be taken with caution as body weight measured during the dry season may be a less accurate age criterion than other standard body measurements such as total length (i.e. head + body) if there were to be an interruption to growth (see Leirs et al. 1990). Reproductive status was determined as active *vs.* inactive based on a combination of the following criteria: length and position (abdominal or scrotal) of testicles and the development of seminal vesicles for males; vulva (open or not), lactation and the presence/absence of developed embryos in the uterus for females (Brouat et al. 2007).

Rodent identification

Initial identification was performed in the field based on morphology and a comprehensive knowledge of the rodent fauna of the region (Granjon & Duplantier 2009). Within the *Mastomys* genus, two sibling species that are difficult to identify on morphological criteria have been collected along the River Senegal Valley: *M. huberti* and *Mastomys erythroleucus*. Molecular diagnosis was used in this genus to provide unambiguous specific identification based on mtDNA that proved to be sufficient for distinguishing these two species (Lecompte et al. 2002, 2005). Though these *Mastomys* species may hybridize in artificial laboratory conditions (with reduced back-crossing possibilities), to the best of our knowledge, hybrid individuals have never been detected in natural populations (Duplantier et al. 1990, Diagne 2012). Total DNA was extracted from various biological materials (typically pieces of liver or hind foot) preserved in 95% ethanol. DNeasy blood and tissue Kit (Qiagen) was used following the protocol of Diagne et al. (2016) for DNA extraction. PCR-amplified and Sanger sequencing methods were applied for the cytochrome *b* (cyt*b*) gene (1,140 bp) using H15915 and L14723 primers (Lecompte et al. 2002). The PCR reactional volume for one unit was 25 µl which contained (i) + (ii) with (i) a mix preparation composed of 16.3 µl of milliQ water, 1 µl of each primer H15915 (5′-TCT CCA TTT CTG GTT TAC AAG AC-3′) and L14723 (3′-T TGC TAC TAA AAA GTA CAG TAA CCA-5′), 2.5 µl of 1X Dream Taq buffer (included 2 mM of MgCl2), 2 µl of dNTP and 0.2 µl of Dream Taq and (ii) 2 µl of DNA extract. The cycling conditions in Mastercycler gradient (Eppendorf) were: denaturation at 40 °C for 5 min, followed by 40 cycles at 94 °C for 30 s, 52 °C for 1 min and 72 °C for 1 min 30 s, with a final extension at 72 °C for 10 min. PCR products were checked on 1.5% agarose gel via 100 V electrophoretic migration during 30 min and sent for sequencing at Eurofins MWG (France). Sequences obtained were cleaned

Table 1. Summary of the trapping data by year in lowland agroecosystems of the lower delta of the River Senegal, 2008-2019.

Year	Number of trap lines	Number of trap.nights	Number of trap.days	Total number of captured rodents (min.-max./trap line)	Number of *A. niloticus* captures	Number of *M. huberti* captures	Number of *Taterillus* sp. captures	Number of *X. erythropus* captures
2008	20	1,229	824	80 (0-20)	62	10	8	0
2009	19	1,140	760	135 (0-29)	66	57	12	0
2010	25	1,497	997	400 (0-82)	329	63	8	0
2011	28	1,516	1,000	245 (0-36)	145	84	16	0
2012	22	1,205	800	12 (0-4)	6	4	2	0
2014	27	1,470	928	207 (0-20)	108	83	14	2
2015	27	1,532	1,020	37 (0-10)	27	6	4	0
2016	30	1,728	1,119	138 (0-22)	96	30	12	0
2017	37	2,183	1,429	353 (0-64)	204	114	35	0
2018	42	2,496	1,538	107 (0-14)	55	39	13	0
2019	47	1,960	1,075	153 (0-22)	112	36	3	2
Total	324	17,956	11,490	1,867 (0-82)	1,210	526	127	4

and aligned using Bioedit version 7.1.9. Identification was accomplished using maximum likelihood phylogenetic trees generated with MEGA7 version 7.0.26, with the study sequences as well as reference sequences from Genbank and the CBGP molecular laboratory databases. With our samples molecular identification clearly discriminated between *Mastomys* species (see Results). Two sibling species of *Arvicanthis* are present in Senegal, but in northern Senegal *A. niloticus* is the only species in this genus (Granjon & Duplantier 2009, Dobigny et al. 2013, Bryja et al. 2019). There are two sibling species of chromosomally well-differentiated *Taterillus* known to coexist in northern Senegal: *Taterillus pygargus* and *Taterillus gracilis* (Granjon & Duplantier 2009). Poulet (1982) already showed in the 1970s that the *Taterillus* specimens from northern Senegal were mainly *T. pygargus* (96% of the individuals, *vs.* 4% of *T. gracilis*). However, these sibling species were not reliably identified using molecular sequencing techniques (Ndour 2011). As an alternative, the karyotypes of nine specimens of *Taterillus* sp. captured in lowland areas of the River Senegal Valley in 2011 were obtained by Ndour (2011) from bone marrow cells (Lee & Elder 1980) using the air-drying method (Evans et al. 1964). Metaphasic suspensions were deposited on slides and stained using 4% Giemsa, and metaphases were observed for each individual using a microscope, which allowed Ndour (2011) to determine diagnostic diploid (2n) numbers.

Environmental data

Daily rainfall data for each year were obtained for a 0.25° grid covering the two study areas, centred on 16.125° N, 16.375° W from the UCSB CHIRPS v2.0 daily-improved database (Climate Hazards Group InfraRed Precipitation with Station data; https://iridl.ldeo.columbia.edu/SOURCES/.UCSB/.CHIRPS/.v2p0/.daily-improved/.global/.0p25/; Funk et al. 2015). In statistical analyses, the total annual precipitation of the previous year was used as a predictor of rodent abundance estimates. We additionally collected local environmental variables around each individual trap over a radius of five meters and then computed an estimate for each trap-line. These variables corresponded to overall plant cover and open water. Adapted from Daubenmire (1959), six classes were established for plant cover corresponding to ranges of vegetation percentages around the traps (0-5%, 5-25%, 25-50%, 50-75%, 75-95%, 95-100%). As a trap-line estimate of the percentage of plant cover, we computed the average of the midpoints of the plant cover classes for the different traps. As a trap-line estimate, open water corresponded to percentage of traps with the presence of open water within a radius of five meters around the traps.

Ethical statement

Rodent trapping was performed with prior explicit agreement from local, traditional and administrative authorities. None of the rodent species captured in the present study had protected status (IUCN, CITES, and articles D 36-D 37 of decree no. 86-844 of 14 July 1986 of the Republic of Senegal). Animals were treated in a humane manner, following the guidelines from the American Society of Mammalogists (Sikes & the Animal Care and Use Committee of the American Society of Mammalogists 2016). Small mammals were euthanatized by cervical dislocation once trapped in accordance with Annex IV of the Directive 2010/63/EU of 22 September 2010 on the protection of animals used for scientific purposes, under the supervision of the last author as a qualified scientist with designer level in animal experimentation (training accreditation number I-34UnivMontp-F1-12) and in the use of non-housed wildlife for scientific purposes (training accreditation number I-75-MNHN-F1-15), and following the guidelines of Mills et al. (1995). Given that rodents captured in these agro-ecosystems were crop pests and potential hosts of pathogens, they could not be released from the point of view of local farmers. With the aim of maximizing the gain in terms of scientific information, euthanatized rodent individuals were dissected to precisely assess their reproductive status, as well as for long-term preservation of tissues in reference collections and for research purposes beyond the scope of this paper (e.g. sampling of the digestive tract for the screening of gastro-intestinal helminths). This study was carried out within the framework of the general convention on cooperation in scientific and technical research between the governments of Senegal and France of 17 January 1974, of the memorandum of understanding on cooperation between the government of Senegal and ORSTOM of 7 February 1991, of the agreement between the government of Senegal and IRD of 4 January 2019, and of the agreement on scientific and technical cooperation concluded between IRD and University Gaston Berger (UGB) on 23 November 1999, extended in 2005, 2010, 2015 and 2020.

Data analyses

Species diversity

Smoothed sample-based rarefaction curves, rescaled to individuals, were computed for each land-use category (uncultivated, rice fields, vegetable gardening) with the program EstimateS 9.1.0 (Colwell 2013) to assess whether sampling was sufficient to capture the most common species, and to compare land-use categories in terms of species richness (Gotelli & Colwell 2001). Species diversity estimates were expressed as Hill numbers of orders 0, 1, 2 to quantify diversity in units of equivalent numbers of equally abundant species (Hill 1973, Jost 2006, 2007, Gotelli & Chao 2013). For each land-use category, we computed three estimates of rodent species diversity: species richness ($^{\circ}D$), exponential Shannon entropy (^{1}D), and Simpson index (^{2}D) for rarefied subsamples of ca. one hundred individuals where samples (i.e. trapping lines) were randomized without replacement. The statistical comparison of these estimates between land-use categories was done using two approaches: we checked for lack of overlap between 95% confidence intervals (mean ± 1.96 SE) a conservative criterion of statistical difference, and between 84% confidence intervals (mean ± 1.41 SE) a criterion that may provide a more appropriate rule of thumb for inferring a difference at $\alpha = 0.05$ for such estimates (Gotelli & Colwell 2001; but see Colwell et al. 2012).

Co-occurrence patterns

The association of rodent species at the local scale was assessed using the patterns of species co-occurrence as follows. Data were organized as matrices of capture events: each row referred to the number of trapped individuals of a given species, while each column corresponding to a trapping line in a given year. Trap lines not including any captures were not taken into account. We compared observed and expected patterns under the null hypothesis of random assembly (Gotelli 2000) using the standardized C-score (SCS) (Stone & Roberts 1990) as a quantitative index of co-occurrence, with significant negative and positive SCS indicating aggregation and segregation, respectively. To assess statistical significance, the observed SCS were compared to values obtained from 10,000 iterations using the most frequently recommended null model with random matrices constrained for row and column totals to match the original matrix ("fixed-fixed" algorithm; Gotelli 2000). We estimated pairwise co-occurrence scores using the program Pairs 1.1 (Ulrich 2008) and applied the 95% confidence limit criterion (Gotelli & Ulrich 2010) to determine whether a particular pair of species was statistically aggregated, segregated or randomly associated.

Table 2. Number (and %) of trapped individuals of the different rodent species in three types of habitats in lowland agroecosystems of the lower delta of the River Senegal, 2008-2019.

Species	Vegetable gardening fields	Uncultivated plots	Rice fields	Total
A. niloticus	235 (67.2%)	241 (46.7%)	734 (73.3%)	1,210 (64.8%)
M. huberti	68 (19.4%)	207 (40,1%)	251(25.1%)	526 (28.2%)
Taterillus sp.	46 (13.1%)	67 (13.0%)	14 (1.4%)	127 (6.8%)
X. erythropus	1 (0.3%)	1 (0.2%)	2 (0.2%)	4 (0.2%)
Total	350 (100%)	516 (100%)	1,001 (100%)	1,867 (100%)
Number of trap.nights; trap.days	1,645; 989	9,323; 6,087	6,988; 4,414	17,956; 11,490

Effects of environmental changes on the dynamics of rodent abundance, age structure and adult breeding pattern

We first analysed rodent indices of abundance using a generalized linear mixed modelling (GLMM) approach with a negative binomial distribution, with the log-transformed number of (trap.nights + trap.days) for *A. niloticus* and of trap.nights for *M. huberti* as an offset variable in the linear predictor function in order to correct for variations in sampling effort, and the year as a random effect to account for the temporal aspect of our survey. The dataset used for these analyses is presented in Table S1. For each GLMM, we presented estimates of partial regression coefficients as well as the corresponding adjusted incidence rate ratios (AIRR).

We then analysed separately age structure and adult reproductive patterns of both rodent species using logistic regression models. The dataset used for these analyses is presented in Table S2. We used a binomial distribution, the log-transformed number of (trap.nights + trap.days) for *A. niloticus* and of trap.nights for *M. huberti* as an offset variable in the linear predictor function to correct for variations in sampling effort, and year as random effect. For the logistic regression models, we presented adjusted odds ratios (AOR).

For each of the two species and for both GLMM and logistic regressions, bivariate analyses were first performed to identify eligible variables for the full models (results not shown), followed by multivariate analyses. In the multivariate analyses we (i) did not consider the trap line as an additional random factor as we were not able to set the trap lines at exactly the same locations from year to year over the whole survey period, and (ii) tested the following explanatory variables: the total amount of rainfall in the previous year (expressed in mm), the percentage of traps with the presence of water and the percentage of plant cover within a radius of five meters around each trap, as well as the following categorical variables: land use (i.e. rice fields, vegetable gardening fields, uncultivated plots) and irrigation management program (i.e. experimental area pre-2015, positive control area pre-2015, experimental area post-2015, positive control area post-2015). The categorical variables were tested in separate models as changes in the irrigation infrastructure were accompanied by changes in land use, and we thus expected strong collinearity if both variables were simultaneously considered, which also precluded consideration of a "model selection" strategy. In the same vein, we decided to not include any interaction in our models, given no clear underlying expectation without potential confounding effects. For instance, including an interaction between "rainfall of the previous year" and "plant cover" would have been irrelevant here, because our sampling design include both non-irrigated and irrigated areas — in the latter areas, this likely buffers the impact of the previous rainfall season on the plant cover compared with the former areas. These analyses were performed using R software version 4.1.0 and R Studio version 1.4.1717 with the package lme4 v1.1-27.1 (functions glmer.nb and glmer). All *P*-values are two-tailed.

Results

Occurrence of rodent species depending on land-use

A total of 1,867 rodent individuals were captured in lowland areas of the lower delta from 2008 to 2019, on 324 trap lines (= samples) totalling 17,956 trap.nights and 11,490 trap.days (Tables 1 and 2). Specimens were identified as belonging to *A. niloticus*, *M. huberti*, *Taterillus* sp. and the striped ground squirrel *Xerus erythropus*. Molecular

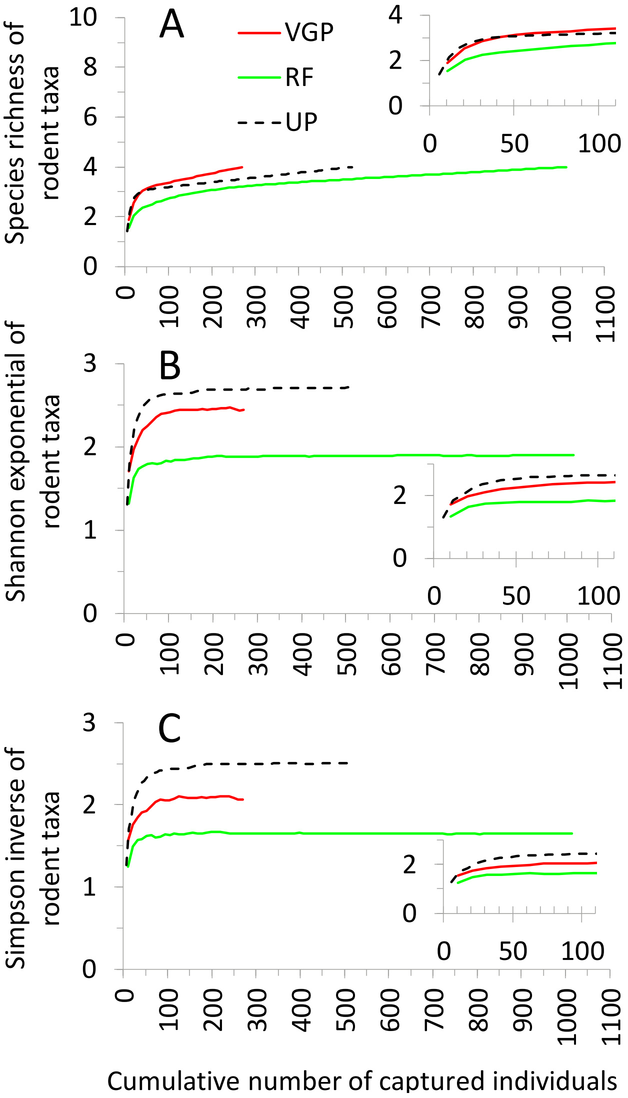

Fig. 2. Sample-based rarefaction curves rescaled by individuals representing three biodiversity indicators for rodent fauna in lowland agroecosystems of the lower delta of the River Senegal, 2008-2019: A – Species richness; B – Shannon exponential; C – Inverse of Simpson; i.e. expressed as Hill numbers of orders 0, 1, 2 that quantify diversity in units of equivalent numbers of equally abundant species; for a given number of captured individuals over all trapping lines of the three types of habitats: vegetable gardening plots (VGP), rice fields (RF) and uncultivated plots (UP). Small inset figures give an overview on the relationship up to rarefied subsamples of ca. a hundred individuals as indicated in the text.

identification within *Mastomys* spp. individuals showed that only *M. huberti* was detected in the delta of the River Senegal (109 sequences from individuals collected each year in 2007-2011 and 2014-2018 in the two study areas), while an additional sample from the middle valley of the River Senegal, more than 200 km from the study areas, was assigned to *M. erythroleucus* (110 sequences from individuals collected each year in 2007-2011 at MO6bis, 16.511° N, 14.449° W; unpublished data). All investigated *Taterillus* sp. individuals showed typical karyotypes of *T. pygargus* (Ndour 2011), however, given the modest sample (n = 9) this taxon will be hereafter conservatively referred to as *Taterillus* sp. *Arvicanthis niloticus* was the most frequently captured species, followed by *M. huberti* and then by a few *Taterillus* sp. (Tables 1 and 2). In terms of occurrence, rodents were detected in 216 of the 324 trap lines (66.7%): *M. huberti* in 137 of them (42.3%), *A. niloticus* in 135 (41.7%) and *Taterillus* sp. in 55 (17.0%). Rodents were detected in 31 of 33 trap lines in vegetable crops (93.9%), 94 of 128 trap lines in rice fields (73.4%) and 91 of 163 trap lines in uncultivated plots (55.8%) and showed a significant heterogeneous rodent distribution according to land use ($\chi^2_2 = 22.3$, $P < 0.001$). The occurrence of rodent taxa varied among land-use categories for the main taxa: *A. niloticus* (90.9% vegetable plots, 50.8% rice fields and 24.5% uncultivated; $\chi^2_2 = 57.0$, $P < 10^{-3}$), *M. huberti* (48.5% vegetable plots, 52.1% rice fields and 32.5% uncultivated; $\chi^2_2 = 13.1$, $P = 0.002$) and *Taterillus* sp. (39.4% vegetable plots, 6.3% rice fields and 20.9% uncultivated; $\chi^2_2 = 24.0$, $P < 10^{-3}$).

Rodent species diversity depending on land-use

We used three different estimates (species richness, Shannon exponential, inverse of Simpson) to assess specific diversity of the samples (Table 3). These results showed that the most common taxa have been sampled in all investigated habitats as a sample-based rarefaction curve, rescaled by individuals, approached a plateau (Fig. 2A, B, C). Two species, *A. niloticus* and *M. huberti*, were numerically dominant in rice fields while three taxa (*A. niloticus*, *M. huberti* and *Taterillus* sp.) were more evenly encountered both in vegetable gardening fields and in uncultivated plots.

Co-occurrence patterns of rodent species

The null model used to test species co-occurrence patterns at the trap-line level for all habitats combined showed that *M. huberti* and *A. niloticus* were significantly aggregated, *M. huberti* and *Taterillus* sp. were significantly segregated, and the association between *A. niloticus* and *Taterillus* sp. was not statistically different from random expectations (Table 4).

Environmental changes and rodent population abundance dynamics

Arvicanthis niloticus (n = 1,210 individuals; 64.8 % of the captures) and *M. huberti* (n = 526; 28.2%) were more frequently trapped than *Taterillus* sp.

Table 3. Rodent species diversity estimated for a sample of ca. 105 trapped individuals according to land-use in lowland agroecosystems of the lower delta of the River Senegal, 2008-2019. Mean ± standard error (SE), 95% confidence interval (95% CI) and 84% confidence interval (84% CI) of species richness – ${}^0D$, exponential Shannon entropy – ${}^1D$, and inverse form of Simpson index – ${}^2D$, i.e. expressed as Hill numbers of orders 0, 1 and 2, respectively, that quantify diversity in units of equivalent numbers of equally abundant species.

	Uncultivated plots	Rice fields	Vegetable gardening fields
${}^0D$ ± SE	3.20 ± 0.69	2.72 ± 0.73	3.30 ± 0.60
95% CI	1.85-4.56	1.29-4.16	2.12-4.48
84% CI	2.23-4.17	1.69-3.75	2.45-4.15
${}^1D$ ± SE	2.65 ± 0.18	1.85 ± 0.23	2.25 ± 0.25
95% CI	2.30-3.00	1.40-2.30	1.76-2.74
84% CI	2.40-2.90	1.53-2.17	1.90 - 2.60
${}^2D$ ± SE	2.45 ± 0.21	1.65 ± 0.25	1.91 ± 0.27
95% CI	2.04-2.86	1.16-2.14	1.38-2.44
84% CI	2.15-2.75	1.30-2.00	1.53-2.29

Table 4. Patterns of co-occurrence of rodent species in lowland agroecosystems of the lower delta of the River Senegal, 2008-2019. The standardized C-score (SCS) measured the extent to which pairwise species co-occur significant negative and positive SCS indicates aggregation and segregation, respectively, whereas SCS that does not deviate significantly from the null distribution suggests random associations. Results are presented for a null model with fixed row – fixed column randomizations. Significant SCS and *P*-values, using the 95% confidence limit criterion, are in bold. n = 216 trapping lines with at least one individual captured.

Species 1	Number of occurrences	Species 2	Number of occurrences	Number of joint occurrences	Model result SCS	*P*
M. huberti	138	*A. niloticus*	136	80	–3.18	**0.001**
M. huberti	138	*Taterillus* sp.	55	22	2.62	**0.009**
A. niloticus	136	*Taterillus* sp.	55	26	0.87	0.39

(n = 127; 6.8%) in this study. This result justified restricting population dynamics and breeding pattern analyses to these two former species.

The results of generalized linear mixed model (GLMM) multivariate analyses showed that abundance indices of *A. niloticus* and *M. huberti* during the hot-dry season were significantly influenced by total rainfall in the previous year ($P < 0.05$; Fig. 3A, B), plant cover ($P < 0.001$) and, for *A. niloticus*, by land use (Table 5, model 1). In terms of AIRR, the abundance of *A. niloticus* and *M. huberti* increased by a factor of 1.06 (95% CI = 1.01; 1.11) and 1.07 (95% CI = 1.02; 1.13) every millimetre of rainfall, and by a factor of 1.02 (95% CI = 1.01; 1.03) and 1.02 (95% CI = 1.01; 1.02) every percent of plant cover, respectively. *Arvicanthis niloticus* was more abundant in rice fields and in vegetable gardening fields than in uncultivated plots (all $P < 0.001$). In this sample, we did not detect any significant difference in *A. niloticus* indices of abundance between rice fields and vegetable gardening fields in multivariate analyses ($P = 0.11$) though there was a marginally non-significant effect ($P = 0.066$) in bivariate analyses, with a trend of higher abundance in vegetable gardening than in rice fields. Overall, GLMM multivariate analysis with this sample showed a significantly higher abundance of *A. niloticus* rodents in cultivated fields than in uncultivated plots ($P < 0.001$). Open water had no significant effect on trap success of *A. niloticus* ($P = 0.14$), but favoured *M. huberti* ($P < 0.001$), which resulted in the AIRR of its abundance increasing by a factor of 4.21 (95% CI = 2.63; 6.75) every percent of trap with open water in a trapping line. For samples of *M. huberti*, we did not detect any statistical effect of land use on trap success with multivariate analyses, though bivariate analyses suggested a lower abundance in uncultivated plots as compared to rice fields ($P = 0.036$) as well as compared to cultivated fields considered as a whole ($P = 0.016$). For *M. huberti*, we did not detected an

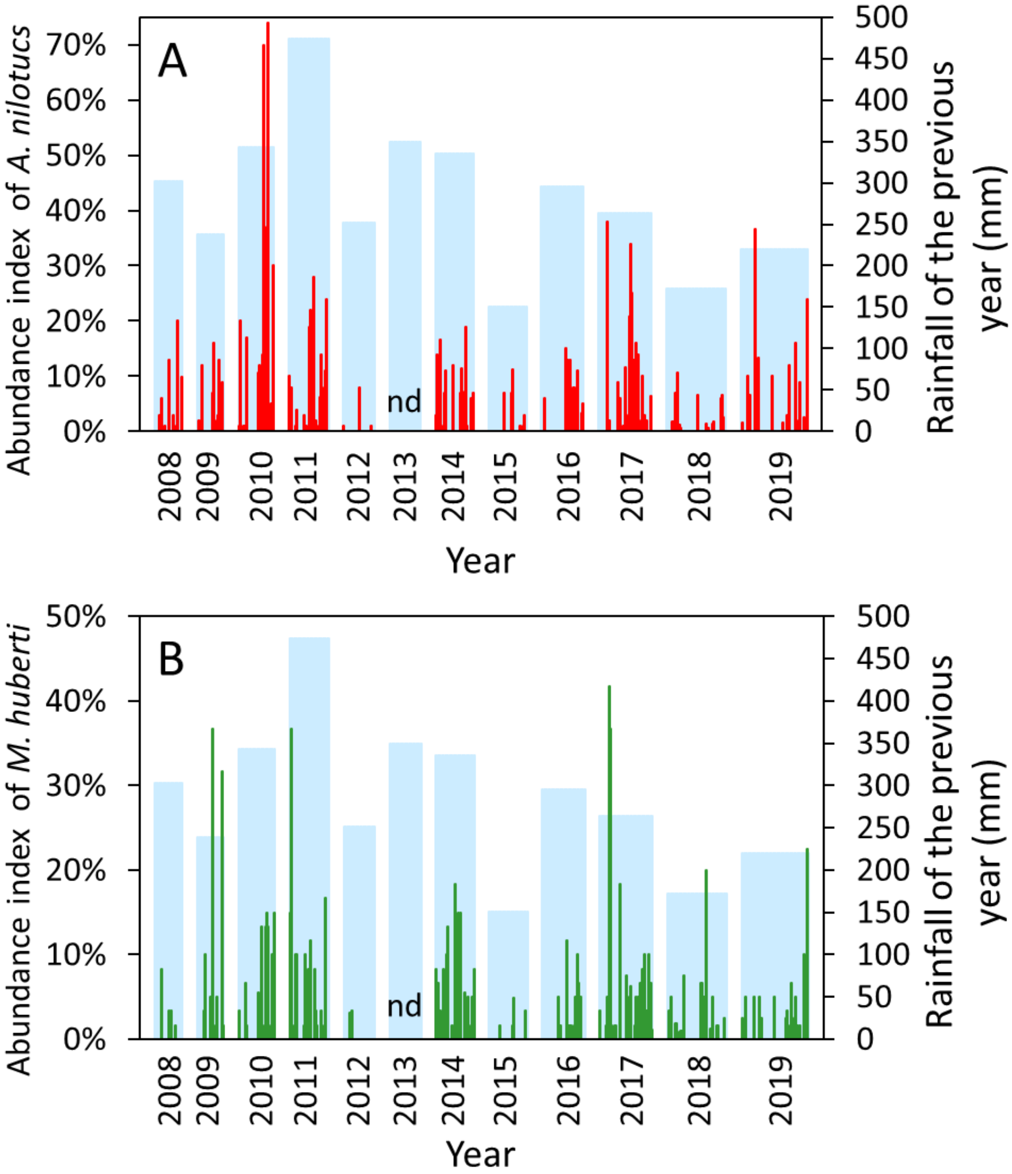

Fig. 3. Abundance indices of *A. niloticus* (A – in red) and *M. huberti* (B – in green) rodents during the hot-dry season and total rainfall of the previous year (in blue) in lowland agroecosystems of the lower delta of the River Senegal, 2008-2019. Abundance was illustrated by vertical bars for each trap line (n = 324) and expressed as trap success indices: number of captures/(number of trap.days + number of trap.nights) for *A. niloticus* and number of captures/(number of trap.nights) for *M. huberti*. "nd" indicated no trapping data in 2013. The width for each year varies with the number of samples (i.e. trap lines).

impact of hydroagricultural program between the positive control area and the experimental area through time. Before implementation of the irrigation and water resource management project (2009-2014), there was a significant difference of *A. niloticus* trap success between studied areas ($P < 0.001$, Table 5, model 2) where the AIRR of the abundance of this species was higher by a factor of 3.49 (95% CI = 1.79; 6.78) in the positive control area (Savoigne) compared to the experimental area (lower Lampsar-Djeuss). Notably, this difference between areas was no more significant after the management project was completed (2015-2019) (AIRR = 0.45, 95% CI = 0.18; 1.10, $P = 0.080$), even though we did not detect statistical differences in *A. niloticus* abundance within the experimental area before and after 2015 (AIRR = 1.78, 95% CI = 0.62; 5.10, $P = 0.28$). Comparatively, in the positive control area, *A. niloticus* trap success did not change before and after 2015 (AIRR = 1.13, 95% CI = 0.37; 3.43, $P = 0.83$). These results suggest that the abundance of *A. niloticus* increased consequently to the hydro-agricultural rehabilitation of irrigation and drainage infrastructure.

Table 5. Multivariate analyses of the generalized linear mixed model (GLMM) to predict indices of abundance (trap success) for two rodent species, *A. niloticus* and *M. huberti*, in lowland agroecosystems of the lower delta of the River Senegal, 2008-2019. GLMM with a negative binomial distribution, the log-transformed sampling effort as an offset variable in the linear predictor function, and year as random effect. For pairwise comparisons, the categorical variable of reference is indicated after *vs.* b_{yi}, partial regression coefficient; SE – standard error of b_{yi}; AIRR – adjusted incidence rate ratio; 95% CI – 95% confidence interval of AIRR. Significant values ($P < 0.05$) are shown in bold.

Models	*Arvicanthis niloticus*					*Mastomys huberti*				
	b_{yi}	SE	AIRR	95% CI	*P*	b_{yi}	SE	AIRR	95% CI	*P*
Model 1: rainfall + plant cover + open water + land use										
Intercept	–6.16	0.82	0.00	0.00; 0.01	< 0.001	–7.84	0.89	0.00	0.00; 0.00	< 0.001
Rainfall	0.06	0.02	1.06	1.01; 1.11	**0.017**	0.07	0.03	1.07	1.02; 1.13	**0.008**
Plant cover	0.02	0.00	1.02	1.01; 1.03	**< 0.001**	0.02	0.00	1.02	1.01; 1.02	**< 0.001**
Open water	–0.19	0.29	0.83	0.47; 1.47	0.52	1.44	0.24	4.21	2.63; 6.75	**< 0.001**
Land use										
Vegetable gardening fields *vs.* rice fields	0.76	0.48	2.14	0.84; 5.45	0.11	0.24	0.40	1.28	0.59; 2.76	0.54
Uncultivated plots *vs.* rice fields	–1.46	0.28	0.23	0.13; 0.40	**< 0.001**	–0.26	0.23	0.77	0.49; 1.22	0.28
Vegetable gardening *vs.* uncultivated plots	2.22	0.46	9.21	3.76; 22.57	**< 0.001**	0.51	0.38	1.66	0.79; 3.47	0.18
Model 2: rainfall + plant cover + open water + irrigation management program										
Intercept	–6.01	0.90	0.00	0.00; 0.01	< 0.001	–8.58	1.01	0.00	0.00; 0.00	< 0.001
Rainfall	0.07	0.02	1.07	1.02; 1.12	**0.008**	0.09	0.03	1.09	1.03; 1.15	**0.003**
Plant cover	0.01	0.01	1.01	1.00; 1.02	**0.027**	0.02	0.00	1.02	1.00; 1.02	**0.001**
Open water	0.18	0.31	1.20	0.66; 2.20	0.55	1.54	0.25	4.65	2.89; 7.49	**< 0.001**
Irrigation management program										
Positive control post-2015 *vs.* positive control pre-2015	0.12	0.57	1.13	0.37; 3.43	0.83	0.85	0.59	2.34	0.74; 7.45	0.15
Experimental post-2015 *vs.* positive control pre-2015	–0.67	0.53	0.51	0.18; 1.45	0.21	0.58	0.58	1.78	0.57; 5.62	0.32
Experimental post-2015 *vs.* positive control post-2015	–0.80	0.45	0.45	0.18; 1.10	0.080	–0.27	0.37	0.76	0.36; 1.59	0.47
Experimental post-2015 *vs.* experimental pre-2015	0.58	0.54	1.78	0.62; 5.10	0.28	0.55	0.58	1.72	0.55; 5.38	0.35
Positive control post-2015 *vs.* experimental pre-2015	1.37	0.56	3.95	1.30; 11.93	**0.015**	0.82	0.59	2.26	0.71; 7.19	0.17
Positive control pre-2015 *vs.* experimental pre-2015	1.25	0.34	3.49	1.79; 6.78	**< 0.001**	–0.03	0.28	0.97	0.55; 1.68	0.90

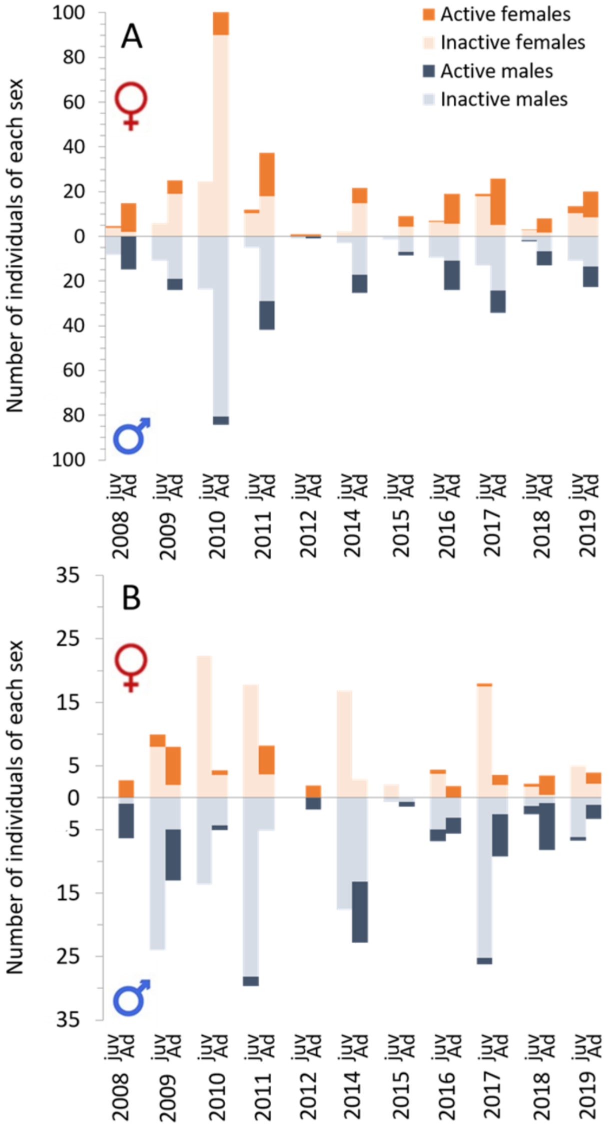

Fig. 4. Number of trapped individuals, illustrating age structure and breeding pattern of two rodent species in lowland agroecosystems of the lower delta of the River Senegal, from 2008 to 2019. A – for *A. niloticus*, corrected for a minimal trapping effort of 1,800 (trap.nights + trap.days); B – for *M. huberti*, corrected for a minimal trapping effort of 1,080 trap.nights. "Ad" – adult individuals, "juv" – juvenile and sub-adult individuals. The weight limit between these two age classes was established for each species by Granjon & Duplantier (2009) and corresponds to the weight at which 50% of the individuals show signs of sexual maturity, which explains why a small proportion of "juv" individuals may be reproductively active.

Dynamics of rodent age structure and breeding pattern

Rodent age structure

At the period of trapping (February-May), the proportion of adult *A. niloticus* were globally higher than those of juvenile and subadult individuals (Fig. 4A) while the age structure of *M. huberti* showed an opposite trend of higher proportions of juvenile and subadult than adult individuals (Fig. 4B).

Results of multivariate logistic analyses for age structure are summarized in Table 6. The results show that in this sample the age structure of both species was not significantly influenced by precipitation of the previous year (*A. niloticus*: $P = 0.81$; *M. huberti*: $P = 0.36$). The age structure of *Mastomys huberti* was not influenced by the impact of hydroagricultural change. However, the probability of a captured *A. niloticus* individual being juvenile or subadult was higher in the lower Lampsar-Djeuss area than in the Savoigne area before 2015 (AOR = 0.57, $P = 0.014$), but a marginally non-significant difference was observed on *A. niloticus* age structure after 2015 between the two study areas (AOR = 0.59, $P = 0.070$). The probability of a captured *A. niloticus* individual being juvenile or subadult increased significantly after 2015 in the Savoigne area (AOR = 2.14, $P = 0.041$). There was not significant effect of plant cover (AOR = 0.99, $P = 0.34$) and open water (AOR = 0.90, $P = 0.61$) for *A. niloticus*. For *M. huberti* the probability of a captured individual being juvenile or subadult was negatively influenced by open water (AOR = 0.27, $P < 10^{-3}$) and to a lesser extent by plant cover (AOR = 0.98, $P < 10^{-3}$). For both species, land use significantly affected age structure with the proportion of juvenile or subadult individuals higher in rice-cultivated fields than vegetable gardening fields (*A. niloticus*: AOR = 0.46, $P = 0.002$; *M. huberti*: AOR = 0.43, $P = 0.027$) and uncultivated plots (*A. niloticus*: AOR = 0.50, $P = 0.001$; *M. huberti*: AOR = 0.53, $P = 0.021$).

Rodent breeding pattern

Breeding pattern was investigated for adults, both in males and females for each species. Results of multivariate logistic analyses of breeding pattern are summarized in Table 7. For *M. huberti*, the adult breeding pattern was not significantly influenced by land use or open water (all $P > 0.05$). The probability of a captured *M. huberti* adult individual to be non-active was high following years with high rainfall (AOR = 1.08, $P = 0.005$) and when plant cover was high (AOR = 1.04, $P = 0.022$). Before 2015, the probability of a captured *M. huberti* adult individual being non-active was significantly lower in the Savoigne than the lower Lampsar-Djeuss area (AOR = 0.32, $P = 0.017$). We did not detect any effect of rainfall from the previous year on the breeding pattern of adult *A. niloticus* (AOR = 1.01, $P = 0.91$). The probability of capturing an adult *A. niloticus* that was sexually non-active was low when there was less open water (AOR = 0.39, $P < 10^{-3}$); it was significantly lower in vegetable

Table 6. Multivariate analyses of the logistic regression model to predict age structure, expressed as the probability of a captured individual to be juvenile or subadult, of two rodent species, *A. niloticus* and *M. huberti*, in lowland agroecosystems of the lower delta of the River Senegal, 2008-2019. Logistic regressions with a binomial distribution, the log-transformed sampling effort as an offset variable in the linear predictor function, and year as random effect. For pairwise comparisons, the categorical variable of reference is indicated after *vs.* AOR, adjusted odds ratio; SE – standard error; 95% CI – 95% confidence interval. Significant values ($P < 0.05$) are shown in bold.

	Arvicanthis niloticus				*Mastomys huberti*			
Models	AOR	SE	95% CI	*P*	AOR	SE	95% CI	*P*
Model 1: rainfall + plant cover + open water + land use								
Intercept	0.61	0.42	0.15; 2.38	0.48	5.96	8.60	0.35; 100.86	0.22
Rainfall	1.00	0.02	0.96; 1.03	0.81	1.04	0.05	0.95; 1.14	0.36
Plant cover	1.00	0.01	0.99; 1.01	0.63	0.98	0.01	0.97; 0.99	**0.006**
Open water	0.73	0.13	0.50; 1.04	0.084	0.30	0.10	0.16; 0.56	**< 0.001**
Land use								
Vegetable gardening fields *vs.* Rice fields	0.46	0.11	0.28; 0.76	**0.002**	0.43	0.16	0.21; 0.91	**0.027**
Uncultivated plots *vs.* Rice fields	0.50	0.10	0.33; 0.75	**0.001**	0.53	0.14	0.30; 0.90	**0.021**
Vegetable gardening *vs.* Uncultivated plots	0.92	0.27	0.51; 1.63	0.77	1.90	0.53	1.10; 3.28	**0.021**
Model 2: rainfall + plant cover + open water + irrigation management program								
Intercept	0.31	0.22	0.07; 1.32	0.11	4.29	6.58	0.21; 86.4	0.34
Rainfall	1.00	0.02	0.96; 1.04	0.96	1.06	0.04	0.97; 1.15	0.21
Plant cover	0.99	0.00	0.98; 1.00	0.34	0.98	0.01	0.96; 0.99	**0.001**
Open water	0.90	0.18	0.61; 1.33	0.61	0.27	0.10	0.14; 0.54	**< 0.001**
Irrigation management program								
Positive control post-2015 *vs.* Positive control pre-2015	2.14	0.80	1.03; 4.44	**0.041**	1.25	1.08	0.23; 6.82	0.80
Experimental post-2015 *vs.* Positive control pre-2015	1.26	0.51	0.57; 2.80	0.56	1.48	1.28	0.27; 8.07	0.65
Experimental post-2015 *vs.* Positive control post-2015	0.59	0.17	0.33; 1.04	0.070	1.18	0.58	0.45; 3.08	0.73
Experimental post-2015 *vs.* Experimental pre-2015	0.73	0.31	0.31; 1.69	0.46	1.95	1.70	0.35; 10.74	0.44
Positive control post-2015 *vs.* Experimental pre-2015	1.23	0.48	0.57; 2.65	0.59	1.65	1.42	0.30; 8.97	0.56
Positive control pre-2015 *vs.* Experimental pre-2015	0.57	0.13	0.37; 0.89	**0.014**	1.32	0.43	0.69; 2.50	0.40

Table 7. Multivariate analyses of the logistic regression model to predict breeding pattern among adult individuals, expressed as the probability of a captured adult individual to be sexually non-active, of two rodent species, *A. niloticus* and *M. huberti*, in lowland agroecosystems of the lower delta of the River Senegal, 2008-2019. Logistic regressions with a binomial distribution, the log-transformed sampling effort as an offset variable in the linear predictor function, and year as random effect. For pairwise comparisons, the categorical variable of reference is indicated after *vs.* AOR, adjusted odds ratio; SE – standard error; 95% CI – 95% confidence interval. Significant values ($P < 0.05$) are shown in bold.

	Arvicanthis niloticus				*Mastomys huberti*			
Models	AOR	SE	95% CI	*P*	AOR	SE	95% CI	*P*
Model 1: rainfall + plant cover + open water + land use								
Intercept	5.91	8.80	0.32; 109.22	0.23	0.00	0.00	0.00; 0.06	**< 0.001**
Rainfall	1.01	0.05	0.92; 1.10	0.91	1.08	0.03	1.02; 1.14	**0.005**
Plant cover	0.99	0.01	0.98; 1.01	0.26	1.04	0.02	1.00; 1.07	**0.022**
Open water	0.39	0.09	0.24; 0.61	**< 0.001**	0.95	0.57	0.29; 3.08	0.93
Land use								
Vegetable gardening fields *vs.* Rice fields	0.25	0.07	0.15; 0.42	**< 0.001**	1.74	0.98	0.57; 5.27	0.33
Uncultivated plots *vs.* Rice fields	0.34	0.08	0.22; 0.54	**< 0.001**	1.03	0.45	0.44; 2.43	0.94
Vegetable gardening *vs.* Uncultivated plots	0.75	0.21	0.43; 1.29	0.30	1.69	0.82	0.64; 4.41	0.29
Model 2: rainfall + plant cover + open water + irrigation management program								
Intercept	10.07	17.38	0.34; 296.70	0.18	0.00	0.01	0.00; 0.26	**0.009**
Rainfall	0.99	0.05	0.90; 1.09	0.92	1.09	0.04	1.02; 1.16	**0.011**
Plant cover	0.98	0.01	0.97; 0.99	**0.012**	1.03	0.02	1.00; 1.07	**0.042**
Open water	0.48	0.12	0.29; 0.77	**0.002**	0.76	0.51	0.20; 2.84	0.68
Irrigation management program								
Positive control post-2015 *vs.* Positive control pre-2015	0.76	0.76	0.10; 5.44	0.78	0.77	0.53	0.20; 2.99	0.71
Experimental post-2015 *vs.* Positive control pre-2015	0.27	0.27	0.04; 1.98	0.20	0.60	0.45	0.14; 2.57	0.49
Experimental post-2015 *vs.* Positive control post-2015	0.36	0.13	0.17; 0.73	**0.005**	0.78	0.60	0.17; 3.48	0.74
Experimental post-2015 *vs.* Experimental pre-2015	0.39	0.40	0.05; 2.93	0.36	1.90	1.44	0.42; 8.45	0.40
Positive control post-2015 *vs.* Experimental pre-2015	1.08	1.11	0.14; 8.04	0.94	2.44	1.73	0.61; 9.80	0.21
Positive control pre-2015 *vs.* Experimental pre-2015	1.43	0.389	0.83; 2.43	0.19	0.32	0.15	0.12; 0.81	**0.017**

gardening and in uncultivated fields than in rice cultivated fields (AOR = 0.25, $P < 0.001$; and AOR = 0.34; $P < 0.001$, respectively). We did not detect temporal differences within each of the two areas for either species before and after 2015 (all $P > 0.05$). Between areas, the probability of a captured adult *A. niloticus* individual being non-active was lower in the lower Lampsar-Djeuss area than in the Savoigne area after 2015 (AOR = 0.36, $P = 0.005$).

Discussion

Rodent community in lowland hydro-agricultural landscape of the River Senegal delta

The results from this ten-year study showed that on the clay soils characteristics of irrigated crops in the lowlands of the River Senegal delta, four rodent taxa were found: *A. niloticus*, *M. huberti*, *Taterillus* sp. and, very occasionally, *X. erythropus* (see also Duplantier 1990, Duplantier & Sène 2000, Bâ 2002, Catalano et al. 2018, 2019). *Arvicanthis niloticus* and *M. huberti* were the two main species captured in the hydro-agricultural context of the lower delta of the River Senegal. The two other species are less well represented. *Taterillus* sp., belonging to the Gerbillinae subfamily, is more frequently found in or close to sandy areas. Accordingly, in our study, it was more frequently captured in uncultivated plots and market garden fields with sandy-clay soils (and even more in the nearby upland "Diery" sandy area, beyond the scope of this study), some of which were adjacent to rice plots. The diurnal *X. erythropus*, although regularly seen, was rarely caught, at least partly because the traps used here were not suitable for its capture. Indeed, this species has been poorly represented in previous studies in the area (Poulet 1982, Duplantier & Sène 2000, Granjon & Duplantier 2009). These results are consistent with those of Poulet (1980) who showed in Savoigne that *A. niloticus* and *M. huberti* were the only species present at high densities in irrigated fields during the 1975-1976 rodent outbreak. These two species, belonging to the subfamily Murinae, are especially well adapted to this ecosystem where they constituted in the present study more than 90% of captured individuals. Our results show a significant aggregation trend at the trap-line level between *A. niloticus* and *M. huberti*, which confirms that they share similar habitats in lowland ecosystems. Mainly herbivorous, *A. niloticus* is the most ubiquitous of Sahelo-Sudanese rodents in western Africa (Granjon & Duplantier 2009). This species occurs in wetlands, especially in rice fields and irrigated crops where it may find both food and shelter (Poulet 1980), but also in human settlements and in dry areas, vegetable gardens or temporary ponds (Granjon & Duplantier 2009, Dobigny et al. 2013). *Mastomys huberti* is a Sahelian species, limited to West Africa (Mouline et al. 2008) where it is tightly linked to humid habitats such as marshes and flood-prone agricultural lands (Duplantier & Granjon 1988, Granjon et al. 2005). Its diet is predominantly seeds, grains and tubers (Granjon & Duplantier 2009). Thus, in lowland agroecosystems, the "pest couple" *A. niloticus* – *M. huberti* appears to be of particular concern for rice cultivation because at high population densities *A. niloticus* may start to damage crops as soon as they begin the vegetative growth, while damage by *M. huberti* may be more severe during heading and harvest. *Mastomys huberti* has been found to be locally more abundant than *A. niloticus* in the River Senegal delta in previous studies based on nocturnal trapping (Poulet 1982, Duplantier 1990) while we frequently observed the opposite during this study: our trapping protocol performed during night and day bring results probably closer to reality as *A. niloticus* has an important diurnal activity. However, this result should be confirmed by accounting for detection probability of the different species (MacKenzie et al. 2006).

A previous three-years bimonthly survey of rodents as potential reservoirs of intestinal schistosomiasis established *A. niloticus* (60% of captures) and *M. huberti* (37%) as the main species in the hydro-agricultural schemes of the River Senegal upper delta at Richard-Toll, ca. 80 km north-east from our study sites (Duplantier & Sène 2000). The same two species were also the major rodent species identified in rice fields of the inner delta of the River Niger in Mali (Granjon et al. 2005). Rodent biodiversity in the lowlands of the River Senegal Valley is low (Poulet 1982, Duplantier 1990, Bâ 2002); a pattern that may be typical of rodent communities in open agroecosystems in sub-Saharan Africa. Indeed, the combination of a small number of dominant taxa, including one species of *Mastomys* and one of *Arvicanthis*, both associated with crop damage, has been observed in other tropical African agroecosystems (e.g. Makundi et al. 1991, Granjon et al. 2005, Leirs et al. 2010, Rabiu 2017, Welegerima et al. 2020). We note that other combinations of a low number of dominant rodent species, typically including *Mastomys* species, may also occur (e.g. Mulungu et al. 2013, 2015, Mayamba et al. 2020). However, we suggest that the numerical dominance of diurnal *Arvicanthis* species in rodent communities may have been underestimated because it has frequently been based solely on night trapping and on the use of Sherman LFA live traps, which may be poorly effective in detecting this taxon. To correct for this potential bias, we advocate that future studies of rodent communities should take into account the probability of detection of the different species, according to the heterogeneity of sampling protocol, using occupancy modelling (MacKenzie et al. 2006).

Population dynamics mainly driven by rainfall, land use and hydro-agricultural developments

Population dynamics, age structure and adult reproductive parameters have been evaluated in *A. niloticus* and *M. huberti*; the main species in the lowlands of the River Senegal delta. Our study shows that the abundances of both rodent species during the hot-dry season were significantly correlated with the cumulative rainfall of the previous year and with plant cover. Their abundances were also higher in cultivated plots than uncultivated. As expected, based on *M. huberti's* ecological requirements, the presence of open water had a significant influence on its abundance, even when controlling for the effect of rainfall variation. More particularly, in an area affected by the hydro-agricultural infrastructures developed within the framework of the Millennium Challenge Account program-Senegal (MCA-Senegal), the abundance of the grass-rat *A. niloticus* significantly increased consequent to these hydro-agricultural developments. Several studies have shown a link between rodent reproduction and rainfall in sub-Saharan Africa (Taylor & Green 1976, Neal 1981, Poulet 1982, Leirs et al. 1989, 1996, Sicard & Fuminier 1996, Stenseth et al. 2003, Mayamba et al. 2021). In the Sahelian zone, outdoor rodent reproduction is seasonal and tightly linked to the rainfall cycle. This does not act directly on the physiology of reproduction (see Sicard & Fuminier 1996), but it conditions the importance of plant biomass production and, therefore, of food resources (Hubert 1982, Duplantier 1998, Granjon & Duplantier 2009). In this context, the period from February/March to June/July, corresponding with the late phase of the dry season, is generally a period of reproductive rest in Sahelian rodents, whose population abundance is thus tightly dependant of the population level they reached earlier in the year. The latter is closely linked to the intensity and distribution of rainfall of the previous year: when the rains from mid-July to September/October are abundant and regularly distributed, the animals survive better, grow faster and reproduce better and for longer in response to abundant food resources.

Well-distributed rainfall over time and space could also reduce the transhumance movements of livestock, which graze in and around the rice fields before and after cultivation. Abundant vegetation in the upland "Diery" sandy agro-sylvo-pastoral areas flanking the lowland "Walo" clay cultivated areas would also cause livestock to remain longer in sandy pastures, which would thus lead to a reduction in competition between rodents and livestock in terms of food resources in the irrigation scheme. We thus expect an interaction effect of rainfall and live-stock grazing intensity on rodent abundance. However, it is difficult to explore this hypothesis because of a lack of information on the number of head of cattle per herd or their daily movements in our sampling localities, which precludes any accurate estimation of herbivore pressure by these herds in and around the rice fields (see for instance Vial et al. (2011) and Young et al. (2017) for studies in sub-Saharan Africa).

Concerning the hydro-agricultural developments, they most likely resulted in an increase in cultivated areas (hence resources for rodents), a permanent availability of water and higher plant cover. Duplantier (1998) already showed that the ongoing development of irrigated agriculture along the River Senegal caused a significant extension of the distribution of *M. huberti* eastward. More generally, Delattre et al. (1998) suggested that the creation or extension of habitats favourable to a species are environmental modifications that cause outbreaks. In agricultural lands, the density of rodents is higher than in uncultivated areas, likely because food is available most of the year, and this rodent density decreases rapidly when food is no longer available (Poulet 1980). In crops, the breeding season can be extended due to the greater availability of food resources. Irrigation networks, dikes, piles of thorny branches enclosing fields, vegetation (cultivated and spontaneous) provide dense vegetation cover that serves both as shelter for rodents and as food. For example, Rabiu & Rose (2004) observed a greater extent of rodent damage as the rice crop matures and its seed and plant cover value increases. In irrigated rice systems in Tanzania, reproduction of *Mastomys natalensis* occurs throughout the year when food and water availability is not limiting, resulting in an increase of rodent abundance in the dry season (Mulungu et al. 2013, 2016). Thus, extended reproduction during the dry period would be responsible for high abundances of rodents in crops. Our results are in agreement with those previously published: before 2015, rodent abundances were significantly higher in the formerly rehabilitated plots than in the unrehabilitated plots. However, after the irrigation and water resource management project ended in 2015, this statistical difference disappeared. This result suggests that the agricultural intensification associated with the MCA-Senegal management project has played a major amplification role on rodent abundances. This is plausible as the succession of vegetable crops in the cold dry off-season, followed by rice crops in the hot dry off-season and during the rainy season results in year-round availability of resources. *Mastomys natalensis* has been shown in Tanzania to have higher food preferences for plant vegetative biomass and seeds (Mlyashimbi et al. 2018). The proportion of available vegetative biomass can also be positively correlated with reproductive activity. In particular, it has been reported that plant compounds such as 6-methoxy-2-benzoxazolinone (6-MBOA) trigger reproductive activity in rodents (Neal 1981, Sicard et al. 1999, Rose et al. 2008, Dai et al. 2016, Mlyashimbi et al. 2018). *Arvicanthis niloticus* and *M. huberti* being predominantly herbivorous and granivorous, respectively, spontaneous vegetation and crops may biosynthesize 6-MBOA with a potential effect on reproduction of both species as reported for *M. natalensis* on which most of the above-mentioned studies focused. This would support the hypothesis of rodent communities of the River Senegal Valley becoming active throughout the year, leading to a chronic increase in abundance or even outbreaks, with potential critical consequences in terms of human health and crop damage.

Age structure and adult breeding pattern

Our results did not show any statistical effect of cumulative rainfall in the previous year on the age structure of either rodent species, contrary to our original expectations, although land use was a driving factor. The proportion of juvenile or subadult individuals of both species was significantly higher in rice-cultivated fields than in vegetable gardening fields and uncultivated plots. In *A. niloticus*, the proportion of reproductively active rodents among the adults was significantly lower in rice plots than in vegetable gardening and uncultivated plots. In contrast, we did not detect any statistical effect of land use on adult *M. huberti* reproductive patterns. This breeding pattern in *A. niloticus* could be explained by the fact that plots in the delta form a complex mosaic, which means that cultivated fields (rice, vegetable gardening) and uncultivated plots are relatively close to each other, which could therefore favour coarse-grained dispersal of rodents between them. This supports the hypothesis that rodents take shelter in the dikes surrounding the rice fields and also in the uncultivated plots and market gardens located in their immediate vicinity, which serve as refuges and breeding grounds. At the same time, the rice fields would be mainly feeding places. Mulungu et al. (2015) reported that rodents have an aggregated distribution in rice fields. *Arvicanthis niloticus* being diurnal, gregarious and living in colonies (Granjon & Duplantier 2009), we believe that this behaviour and an aggregated distribution in rice fields would make this species apparently more abundant but also easier to detect and capture than *M. huberti*. With a proposed movement distance up to a few tens of meters (and likely less than a few hundred of meters) in irrigated fields (Poulet 1982, Granjon & Duplantier 2009), *A. niloticus* could therefore move between rice fields to feed, and nearby uncultivated plots and vegetable gardening fields (some of those being permanent plots) to shelter and breed. This observation would explain the pattern of the higher proportion of reproductively active adult individuals in uncultivated habitats and vegetable gardening fields where they could spend most of their time. However, data on individual movements and dispersal of *A. niloticus* in anthropized landscapes of in northern Senegal are lacking and testing this hypothesis is, therefore, an area for future research.

The breeding patterns of adult *A. niloticus* and *M. huberti* appear different with respect to the irrigation and water resource management project. Indeed, before the rehabilitation, the probability of capturing a reproductively active adult *M. huberti* as compared to a non-active adult during the hot dry season was significantly higher in non-rehabilitated than in rehabilitated plots, whereas there was no significant difference for *A. niloticus*. However, after 2015 and the implementation of the rehabilitation, the previously observed difference in *M. huberti* was negated and the probability of capturing a reproductively active adult *A. niloticus* in comparison with a non-active adult individual increased. The rehabilitation work generates more areas for cultivation and at the same time reduces uncultivated areas such as fallow land, wasteland, etc. It was proposed above that those rodents would preferentially breed in uncultivated habitats and market garden fields. Thus, the reduction of wasteland and fallow land due to the rehabilitation program would contribute to the reduction of the probability of capturing active adult *M. huberti* individuals in the newly managed areas. This observation further encourages, in terms of rodent control strategy, the avoidance or reduction of fallow land near cultivated fields, which can be a starting point for the re-invasion of fields. As for *A. niloticus*, increased resources, agricultural intensification or a combination of underlying factors would explain this change in pattern. Further studies are needed in this respect in order to have at our disposal all the elements to help set strategies for management of these two crop pest species.

Conclusion

Our study has shown that environmental change related to land use and development programs in the River Senegal delta have an impact on the population dynamics of rodent crop pests. More periods of high rodent densities are likely to occur as crop area, rice production and water availability increase. We established that rodent abundance was related to rainfall in previous years and land use, but also to plant cover. The factors tested also showed that age structure, for *A. niloticus* and *M. huberti*, and adult breeding patterns, for *A. niloticus*, were also modified, with uncultivated areas and vegetable fields being identified as potential refuges for adults and likely to prolong breeding during the dry season, making these habitats potential starting points for new infestations in rice plots that are more disturbed by human activities, including tillage and flooding. Our results suggest that the risks of recurrent rodent outbreaks and the possible emergence of associated zoonotic diseases are of paramount importance in the River Senegal delta. Thus, we urgently recommend implementing regular rodent monitoring as well as efficient and sustainable control strategies at the national and community levels to maintain pest populations within tolerable limits.

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Author Contributions

Design of the study: C. Noûs, K. Bâ, A. Dalecky; sampling: C.T. Niang, M. Kane, Y. Niang, C. Tatard, E. Artige, J.-F. Mauffrey, K. Bâ, A. Dalecky; data processing and analysis: C.T. Niang, N. Sarr, E. Artige, L. March, C. Diagne, V. Moron, A. Dalecky; molecular biology: C.T. Niang, C. Tatard; paper writing: C.T. Niang, I. Laffont-Schwob, A.B. Bal, A. Dalecky; all authors read, revised and approved the final manuscript.

Data Availability Statement

The data that support the findings of this study are available in the FigShare repository under the name "Niang et al. 2022 J. Vertebr. Biol. 2022, 71: 22015_Datasets_Tables S1 & S2": http://dx.doi.org/doi:10.6084/m9.figshare.19747666.

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Supplementary online material

Table S1. Dataset at the trap line level in lowland agroecosystems of the lower delta of the River Senegal, 2008 to 2019 (https://www.ivb.cz/wp-content/uploads/JVB-vol.-71-2022-Niang-et-al.-Table-S1.pdf).

Table S2. Dataset at the rodent individual level in lowland agroecosystems of the lower delta of the River Senegal, 2008 to 2019 (https://www.ivb.cz/wp-content/uploads/JVB-vol.-71-2022-Niang-et-al.-Table-S2.pdf).

Appendix S1. French version of manuscript “Socio-environmental changes and rodent populations in lowland agroecosystems of the lower delta of the River Senegal, West Africa: results of observations over a decade, 2008-2019” (https://www.ivb.cz/wp-content/uploads/JVB-vol.-71-2022-Niang-et-al.-Appendix-S1.pdf).