

Unravelling the rapid range expansion in Senegal of the Nigerian gerbil (*Gerbillus nigeriae*) using a multifactorial modelling approach

Jean Le Fur^{1,3}, Françoise Duraffour², Laurent Granjon³

¹UMR-9220 ENTROPIE (Institut de Recherche pour le Développement, Université de la Réunion, Ifremer, CNRS, Université de la Nouvelle-Calédonie), 101, promenade Roger-Laroque Anse Vata, BP A5, 98848 Noumea, New Caledonia

² CNRS, UMR 8586 Prodig, Université Paris 1 Panthéon-Sorbonne, IRD, AgroParisTech, F-93322 Aubervilliers, France

³ CBGP, IRD, CIRAD, INRAE, Institut Agro, Univ Montpellier, Campus International de Baillarguet, Montferrier-sur-Lez, France

Corresponding author: Jean Le Fur (jean.lefur@ird.fr)

Keywords

Agent-based model, climate change, integrated approach, invasion, rodent, West Africa

Abstract

At the turn of the last century, Senegal experienced a spectacular invasion of the Nigerian gerbil (*Gerbillus nigeriae*). In less than 20 years, the species could be spotted in almost all areas of the northern half of the country, where it was previously undetected. In an effort to decipher the modalities of this invasion, we incorporated available information about the environment and gerbils' life traits into a simulation model and attempted to reproduce observations.

The model is agent-based. It formalises subpopulations of dispersing gerbil propagules that have the ability to settle in favourable habitats. The general and particular components of the model are described in detail, alongside with the sensitivity analyses conducted to calibrate

25 unknown parameter values pertaining to life traits, environmental drivers, and the origin of the
26 metapopulation.

27 Values obtained for each variation domain are discussed in view of understanding the given
28 invasion process. It is stressed that facets of the explanation are still speculative due to
29 unknowns regarding the invasion's history, the biological characteristics of the invading
30 populations or the imprecision of some environmental data.

31 A unique and comprehensive multifactorial invasion scenario emerges from the study. It
32 involves multiple entries of the invading population in Senegal combined with a set of physical,
33 physiological, and human-related consequences of the 1980s drought. Furthermore, the
34 scenario suggests both a restrictive and a facilitative effect of environmental drivers, as well as
35 phenotypic plasticity of the invasive species directed towards increased dispersal abilities.

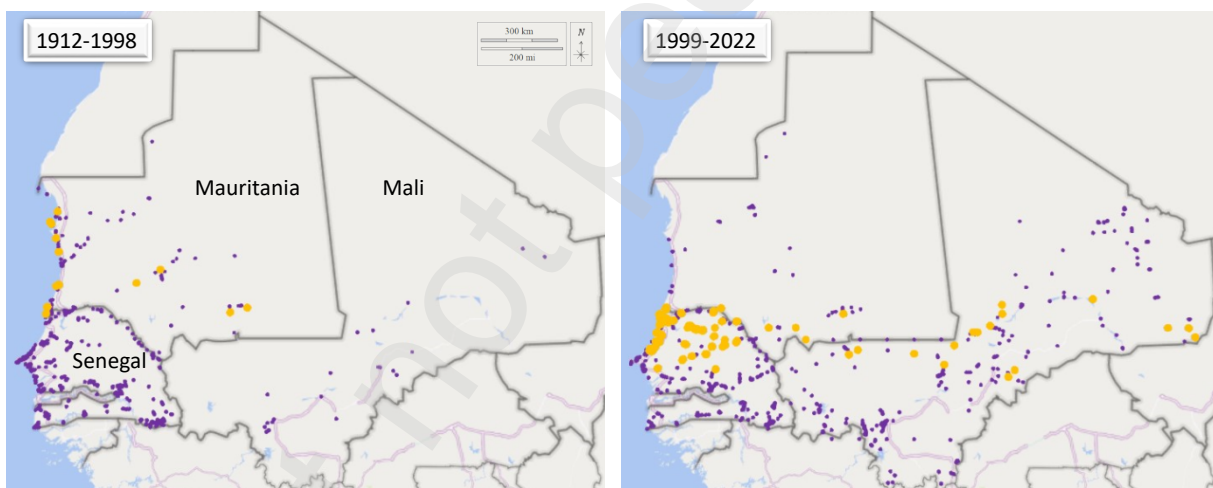
36 **1 Introduction**

37 Dispersal, defined as “any movement of individuals or propagules with potential consequences
38 for gene flow across space” (Ronce, 2007), represents a major process of population dynamics.
39 Such definition includes both natal dispersal (defined as the movement of a propagule between
40 its birthplace or natal group and its first breeding site or group) and breeding dispersal (defined
41 as ‘the movement between consecutive breeding sites or groups of adult breeders’; Greenwood
42 et al., 1979). Dispersal may take various forms, from small distance range shifts to long distance
43 one way movements, the latter (also referred as long distance dispersal) being especially
44 difficult to monitor (Koenig et al. 1996). This process has been the main topic of a variety of
45 studies and reviews, most of them focused on factors likely to influence the rate of dispersal,
46 the consequences of dispersal on population structure and genetics or the life-history correlates
47 of dispersal ability (see Ronce 2007, Clobert et al., 2012, Whitmee and Orme 2013 for reviews).

48 Until recently, dispersal was mainly studied in the context of populations with static ranges, or
49 supposed to be more or less in a relative steady state. The rise of invasion and range expansion
50 cases associated with the consequences of global changes has entailed a renewal of interest for
51 dispersal processes. In this frame, range shifts associated with either the introduction of
52 propagules into an entirely new area via human activities or the range expansion of populations
53 tracking evolving climatic and/or environmental conditions are considered to result mainly
54 from the interplay of two processes intrinsic to the population: dispersal and population growth
55 (Travis and Dytham 2002, Phillips 2015). Wilson et al. (2009) proposed to categorize major

56 pathways of extra-range dispersal as a frame for the study of dispersal and associated invasion
57 success. More specifically, various studies have concentrated on questions dealing with
58 disperser selection, phenotypic shifts as well as ecological / evolutionary trends in invading
59 populations of a variety of organisms (e.g. cane toads, Llewelyn et al. 2010 ; Lindström et al.
60 2013; bush crickets Thomas et al. 2001; ladybirds, Lombaert et al. 2015). Questions related to
61 dispersal itself (dispersal ability and rate, and factors influencing them at invasion fronts) have
62 mainly been tackled via theoretical and modelling approaches (Travis and Dytham 2002, Travis
63 et al. 2011, Ramanantoanina et al. 2014, Chuang and Peterson 2016).

64 However, few explicit/quantified estimations of spread rate associated with specific cases of
65 wide range expansion over a significant period have been produced to date (see however
66 Thomas et al. 2001 for butterflies and bush crickets, Pettit et al. 2016 for cane toads, Brzezinski
67 et al. 2019 for American minks). Such case of appearance and then rapid and extensive spread
68 occurred in Senegal (West Africa) for the Nigerian Gerbil *Gerbillus nigeriae*, an arid-adapted
69 species of murid rodent (Figure 1).



71 Figure 1. *Gerbillus nigeriae* observations before (left) and after (right) the first documented
72 occurrence in Senegal.

73 Recorded sites of rodent trapping (purple) and *G. nigeriae* catches (orange) in Mauritania,
74 Mali and Senegal (data from the database on Sahelo-Sudanian small mammals, [http://bpm-](http://bpm-cbgp.science)
75 [cbgp.science](http://bpm-cbgp.science)).

76 This Sahelian species is a major pest of standing or stored crops (Nomao and Gautun 2001). It
77 was unseen in Senegal in the end of 70s / early 80s, as shown in extensive trapping and owl
78 pellet data gathered by Poulet (1982, 1983) and Bâ et al. (2000). It was first unambiguously
79 documented in the country when several specimens were live-caught in 1999 in one site of the
80 Senegal River Valley (Bâ et al. 2006). This suggests that first settlers entered Senegal in the

81 course of the decades 1980-1990. Further analyses of owl pellet remains and trapping
82 campaigns along the 2000s and 2010s throughout Senegal confirmed that *G. nigeriae* has
83 become one of, if not the, dominant species of outdoor rodent communities in the northern part
84 of the country (Granjon and Duplantier 2009, Thiam et al. 2011, Granjon et al. 2019). This
85 species, although frequent in human-modified outdoor habitats such as fields and gardens, is
86 seldom found in the immediate vicinity of humans (buildings, villages, cities). Natural factors
87 should therefore rather be suspected as presumed preferential drivers of its invasion.

88 Data at hand show that the species has expanded southerly 200-250 km from its northern entry
89 sites into Senegal, along the Senegal River Valley, within a time window of around 20-25 years.
90 Roughly calculated, this would correspond to an average dispersal speed within a range of 600-
91 1000m per month sustained during the whole period. Such values appear especially puzzling as
92 beyond most, if not all those recorded for rodents of this size to date (Whitmee and Orme 2013).

93 The main question addressed here is the following: which drivers and especially what monthly
94 dispersal distance would be required, to make the invading population of *G. nigeriae* in Senegal
95 reach its current range in this country? The answer to this particular question requires
96 considering another one: What was (were) the introduction point(s) of the species in the country
97 (i.e., from where has the expansion started)?

98 In the present study, we take advantage of the dataset accumulated along the years on *G.*
99 *nigeriae* life traits and on its environment in Senegal to develop a model designed to answer
100 the aforementioned questions. The agent-based formalism (Grimm and Railsback, 2005) was
101 chosen to conduct this study. This computer simulation approach facilitates the taking into
102 account of multiple diverse factors likely to be involved in the phenomenon studied. It also has
103 the advantage of possibly capture any spatial or temporal singularities that could be important
104 in this population particular dynamics.

105 **2 Material and methods**

106 The description of the model conforms to the ODD protocol (Grimm et al. 2006, 2010) for
107 describing agent-based models. According to this scheme, an overview is first presented,
108 explaining the purpose of the model, its state variables, scales and process scheduling. The
109 design concepts are then described (emergence, fitness, interaction, etc.), followed by details
110 concerning its implementation (initialization, input, submodels).

111 **2.1 Model purpose**

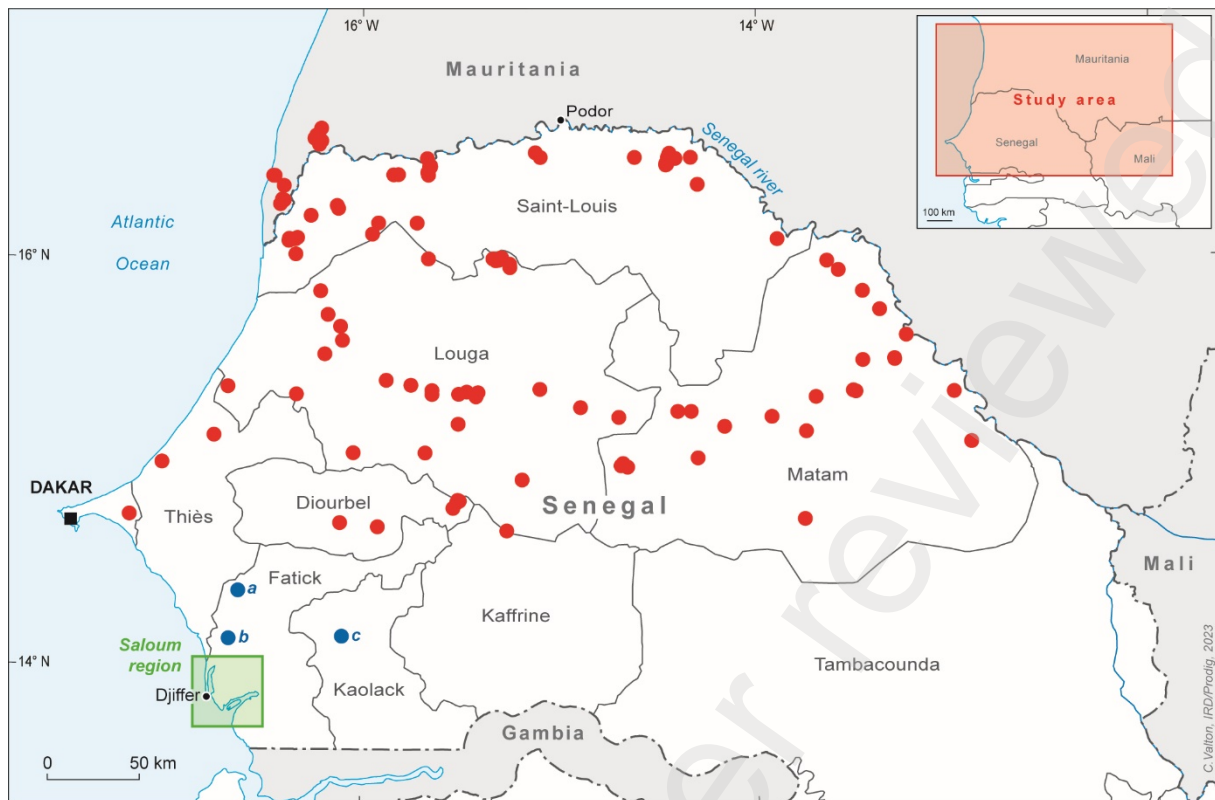
112 In a context where there is insufficient biological knowledge to determine the gerbil's rate of
113 progression and spatial expansion capabilities, it is proposed to use simulation to better identify
114 these parameters and report on the observed expansion of this species in its recent invasion area
115 in Senegal. We integrate in the same scheme the observed environmental constraints (soil,
116 rainfall, resources, landcover), and known biological drivers encapsulated within gerbil
117 population agents. The model will make it possible to reconstruct the most likely context and
118 then enable us to identify the plausible order of magnitude of parameters' set that could explain
119 observations.

120 2.2 State variables and scale

121 2.2.1 Environment

122 The temporal scope of the study is three decades (1982 to 2013), in agreement with observations
123 available on gerbils as well as with the time extent required to account for the expansion
124 phenomenon. Rainfall and vegetation index data are available on a monthly basis; it is the
125 temporal resolution that was chosen as it may be also relevant to simulate the metapopulation
126 trends over several decades.

127 The spatial scope simulated (Figure 2) includes southern Mauritania, West of Mali and the
128 northern part of Senegal, an area of 945 x 607 km ranging from 13.5°N / 18°W to 19°N / 9°W.
129 It is discretized using a grid of 38,403 square cells of 4 km side. Each cell, called a patch, is an
130 object characterized by three fixed attributes: coordinates, land cover and pedology, and three
131 dynamic attributes updated each simulated month: vegetation index, rainfall and habitat quality
132 (see input section). Vegetation index NOAA-AVHRR data were available at a scale of 8x8 km
133 before 1999 and land cover at 1x1 km; the 4x4 km granularity was chosen as a compromise
134 between these two resolutions.



135

136 Figure 2. Domain covered by the model and reference data utilized in the modelling study.
 137 Red and blue dots: observed occurrences of gerbils obtained from field trapping studies and
 138 examination of barn owl (*Tyto alba*) pellets in Senegal from August 1982 to December 2013.;
 139 (a) Ndiosmone (b) Fumela (c) Sing-Sing.

140 Among the 3,674 individuals recorded between 1992 and 2013, 16 individuals were recorded
 141 in barn owl pellets from 3 sites located farther south than the other observation records (blue
 142 dots Figure 2): Fumela (8 individuals in July 2004), Ndiosmone (2 individuals in July 2004),
 143 and Sing-Sing (6 individuals in July 2005). These three southernmost observations have been
 144 considered separately (see discussion).

145 2.2.2 Gerbil population agents

146 A specificity of this model is that agents themselves are not a representation of individual
 147 rodents but of groups of individuals (population) located on a space patch. Each population
 148 agent is individually described by its position in the patch, its age (time since the population
 149 creation) and its composition in males, females (including pregnant ones) and juveniles. Agents
 150 are also flagged with a "settled" attribute that declares if a population is installed or not. Each
 151 of these parameters is computed at each monthly time step.

152 Each settled population agent has the ability to produce monthly a new dispersing population
 153 agent called "propagule". These are mobile agents characterized by a set travelling speed. They

154 are able to perceive monthly their surrounding environment within a circle of radius equal to
155 the monthly distance they cover.

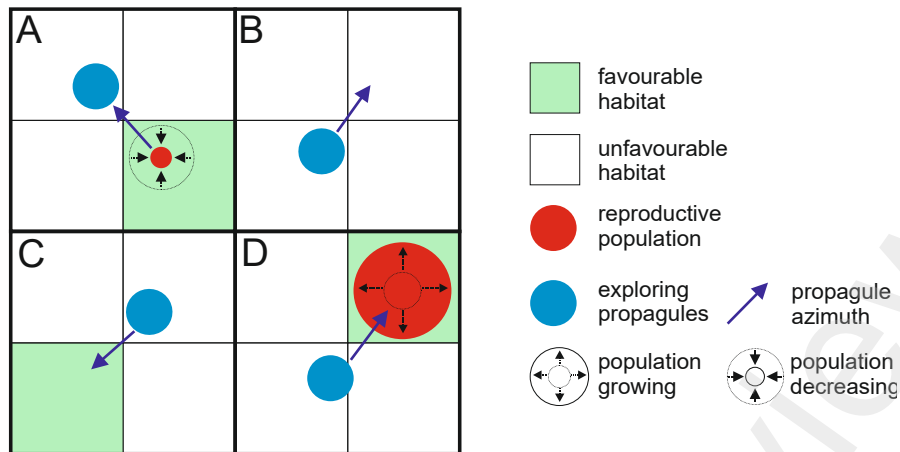
156 Each population agent is also characterized by one out of three possible ‘desires’ (Caillou et al.,
157 2017): reproduction, sexual rest or exploration. ‘Desires’ are selected depending on the agent
158 status and environmental parameters (life cycle, season).

159 Gerbil population agents are governed by a set of global parameters that are described in
160 following sections and include:

- 161 (1) The simulated initial metapopulation (sensu Hanski and Gilpin 1991) formalized here using
162 population number and individual population size,
- 163 (2) The reproductive life traits: pregnant female rate, litter size, reproduction season start and
164 end,
- 165 (3) The population ecology: propagule rate, propagule speed, survival rate.

166 2.3 Process overview

167 The model simulates a metapopulation expansion process based on the notion of propagules
168 leaving their native patch and population, exploring their distant environment and settling in
169 favourable locations. The environment in which populations evolve may be favourable to their
170 establishment or unfavourable as described further in the input section. Within a grid patch
171 there can only be one settled population that represents all individuals residing on that surface.
172 This situation reflects the granularity of the model where movement processes below this
173 resolution (conspecific meetings, local dispersal, foraging activities...) are not considered.
174 Settled populations are static within their patches and only undergo demographic changes
175 (reproduction/death, immigration, emigration). For gerbils, two “seasons” stand out in one year
176 (Sicard and Fuminier, 1996): i) a reproduction season that begins one month after the start of
177 the rainy season (usually in august) and stops one to five months after the end of the rainy
178 season ii) a non-reproductive period that extends over the remaining of the year. This situation
179 leads to three possible states (breeding, sexual rest, exploration) and four processes for the
180 population agents as represented in Figure 3.



181

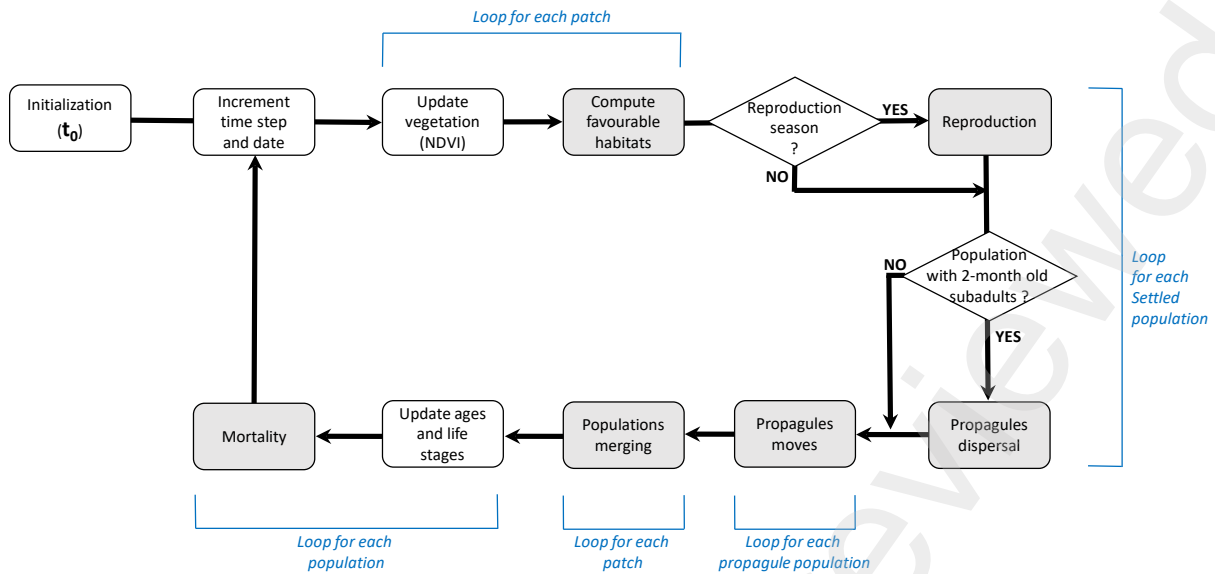
182 Figure 3. Synthetic scheme of the population states and processes formalized.

183 A) a population produces a propagule subpopulation and reduces accordingly in size. B)
 184 propagule exploration. C) a propagule selects and aims towards a preferential habitat. D) a
 185 propagule merges with an existing population which increases accordingly

186 During the breeding season, settled populations (red) reproduce. They can emit propagule
 187 population agents made up of subadult youngsters (A). When this dispersal occurs, the settled
 188 populations reduce in size. Propagules leave the mother population and explore space (B).
 189 When a propagule perceives a favourable habitat, it settles there (C). When the settling area is
 190 already occupied by a population, the agents merge (D).

191 2.4 Scheduling

192 The model hence formalizes four biological processes that are triggered at each monthly time
 193 step: propagule movements, merging of co-occurring populations (settled and/or propagule),
 194 population mortality and reproduction (Figure 4). Once a year, the end of the breeding season
 195 is scheduled according to the yearly rainfall value and the date of the last rain. Mortality,
 196 reproduction, fusion and (inter-patch) movement are then computed asynchronously for each
 197 agent. The order in which these four actions are triggered was found to have no impact on the
 198 expansion of the metapopulation.

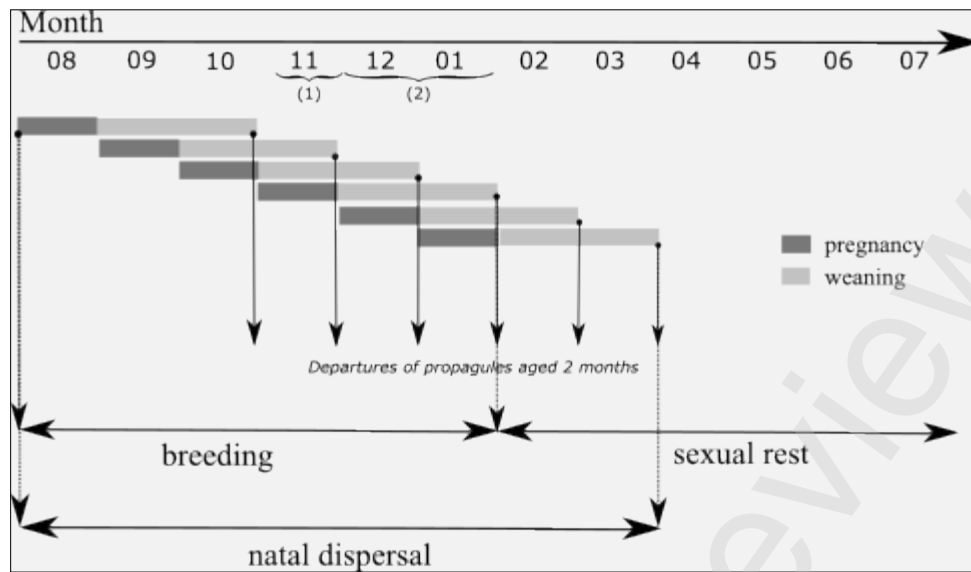


199

200 Figure 4. Simulation steps for the overall model. Grey boxes: procedures described in the sub-
 201 models section

202 2.5 Design concept

203 **Basic principles:** The gerbil life history is formalized using three major phases (Figure 5): (i)
 204 a breeding period that begins in August and ends 1 to 5 months after the first month without
 205 rain, depending on the quality (quantity and regularity) of rainfall; (ii) a sexual rest
 206 corresponding to a relative paucity of available food in the environment (Sicard and Papillon
 207 1996); (iii) a natal dispersal period starting ca. 3 months (one month of gestation plus two
 208 months before weaning/independence of the youngs) after the start of breeding period, when a
 209 fixed proportion of youngsters move until they find a favourable habitat where they settle.



210

211 Figure 5. Yearly reproduction cycle and dispersal scheduling.

212 (1) first month without rain (November or December depending on the year), (2) the length of
 213 the breeding period depends on the rainfall quality and rainfall quantity of the year. As a
 214 result, breeding period ends 1 to 5 months after the first month without rain.

215 During the breeding phase, populations reproduce every month. After three weeks of gestation,
 216 they produce newborns, which are weaned and completely independent 2 months later. Some
 217 of them, i.e. propagules, will then leave the population (natal dispersal).

218 The gerbil, a non-commensal species, is sensitive to the environment in which it evolves, feeds,
 219 moves and reproduces. It must be able to (i) dig burrows to hide, shelter, give birth and raise
 220 their young until weaning (ii) find suitable habitat areas in terms of land cover, (iii) get enough
 221 food and (iv) benefit from good breeding conditions. These four requirements lead to focus on
 222 three inputs: pedology, landcover and vegetation cover (measured by NDVI - Normalized
 223 Difference Vegetation Index).

224 **Emergence:** The model formalizes a metapopulation as a set of interconnected individualized
 225 and localized populations. Simulations generate two types of patterns: (i) a set of habitat
 226 patches, favourable or not, that evolve over time according to fluctuations in the environment,
 227 and that can shelter or not viable gerbil populations, (ii) the metapopulation dynamics, which
 228 evolves according to demography and dispersal, finally resulting in a moving colonization front
 229 which limits can be compared to field observations.

230 **Adaptation:** Adaptation varies according to the agents' type. The objective of propagules is to
 231 find a settling place favourable to their reproduction and their survival. Settled populations

232 persistence depends on their size, itself conditioned mostly by the length of their breeding
233 season, which is governed by the rainy season intensity (see suppl. mat.).

234 **Fitness:** The search for favourable conditions for life and reproduction is a key aspect of gerbil
235 populations' fitness. Each dispersing population or propagule looks for a location on which to
236 settle using three criteria: a soil configuration suitable for burrowing, a land cover that provides
237 favourable feeding and sheltering opportunities and a favourable NDVI that reflects the amount
238 of food available (details in "Submodels" section).

239 **Sensing:** In the model, space is perceived by propagules depending on the distance they travel
240 each month: from there, they will settle in any favourable patch lying within a circle of radius
241 equal to their monthly travel distance. In addition, they also perceive their close neighbours (i.e.
242 those located on the same patch) and will potentially merge with them at each step.

243 **Interaction:** Four types of interactions between populations and between population and the
244 environment they perceive are modelled explicitly : (i) populations merge when they are in the
245 same patch, (ii) the movement of simulated gerbil populations depends on the location of
246 favourable habitats when they perceive one; (iii) the percentage of pregnant females depends
247 on the month of the year (see Table 1), and (iv) the reproductive period ends 1 to 5 months after
248 the first month without rain (see Figure 5).

249 **Stochasticity:** the only stochastic variable involved is the direction of travel. Unless a
250 favourable patch has been found, propagule agents randomly select a direction between 0 and
251 359 degrees at each step before dispersing.

252 **Observation:** The model focuses on the (linear) distances travelled by gerbils after 3 decades
253 starting from August 82 and the conditions under which the simulated expansion corresponds
254 to the observed expansion. Thus, the model calculates 4 expansions: to the south, to the east, to
255 the west, to the north. An expansion is the linear distance (in meters) between the initial position
256 (in August 1982) and the final position (in December 2013). Given the most likely scenario of
257 a North-South expansion of the species once it entered Senegal, the study focuses on the
258 southern expansion observed.

259 2.6 Initialization

260 The initialization step consists of "loading" the environmental data, that is, soil composition,
261 land-cover, months of the beginning and end of the rainy season. The first step loads the first
262 NDVI dataset dated January 1982. These NDVI values are then updated every month.

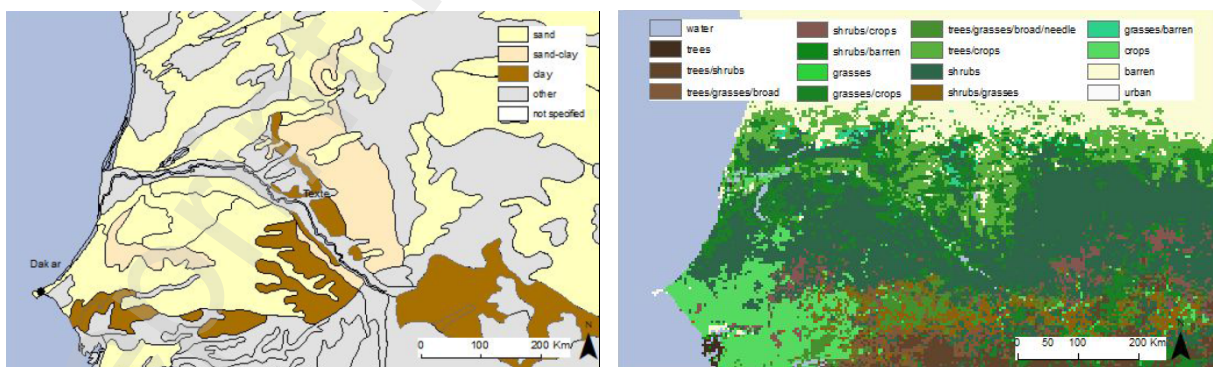
263 At the first step, the age of the population is one month. Populations have as many males as
264 females. Litter size, survival rate, propagule emission rate and propagule speed are fixed by
265 the interface parameters. The first reproductive cycle beginning in August 1982, the populations
266 are initialized as in sexual rest, i.e. there are no pregnant females.

267 The period from January to August 1982 is a period of "running-in" of the model, during which
268 there is no reproduction, no propagule departure and no expansion. Mortality (via the survival
269 rate, applied each month) is the only process acting on the populations.

270 The invading metapopulation is initialized as a fixed number of "founding" populations spread
271 along a start line. Each population is sized with an identical predetermined number of
272 individuals. The number, size and initial position of these populations are varied as described
273 in the sensitivity analysis subsection below.

274 2.7 Input

275 **Pedological data** (Figure 6 left) originate from the soil map of Boulet et al. (1971). The original
276 classification has been reworked by an expert (Y. Dewolf, pers. comm. 2017) following the
277 taxonomy in Mathieu and Lozet (2011) and Baize and Girard (2008), in order to retain soil
278 surface characteristics (sand, sandy-clay, clay and other) suitable or not for burrow digging and
279 foraging.



280
281 Figure 6. Left: reclassified soil map from Boulet et al. (1971). Right: SYNMAP reclassified
282 land cover map

283 We retrieved **landcover data** (Figure 6 right) at the required spatial (Sahelian West Africa) and
284 temporal (between 1982 and 2013) scales using the worldwide SYNMAP database
285 (https://webmap.ornl.gov/wcsdown/dataset.jsp?ds_id=10024), which provides a 10-year

286 consensus map based on various products depending on the year. Focusing on our study area,
287 we retained the 16 most significant classes (out of 48) reclassified at a 4 km resolution (from
288 an initial 1 km resolution).

289 **Vegetation cover** is updated monthly using an NDVI indicator. Input data come from NOAA
290 time series (James and Kalluri, 1994) that provide a complete time series from 1982 to 2013.
291 (<https://earth.esa.int/web/guest/missions/3rd-party-missions/current-missions/noaa-avhrr>).

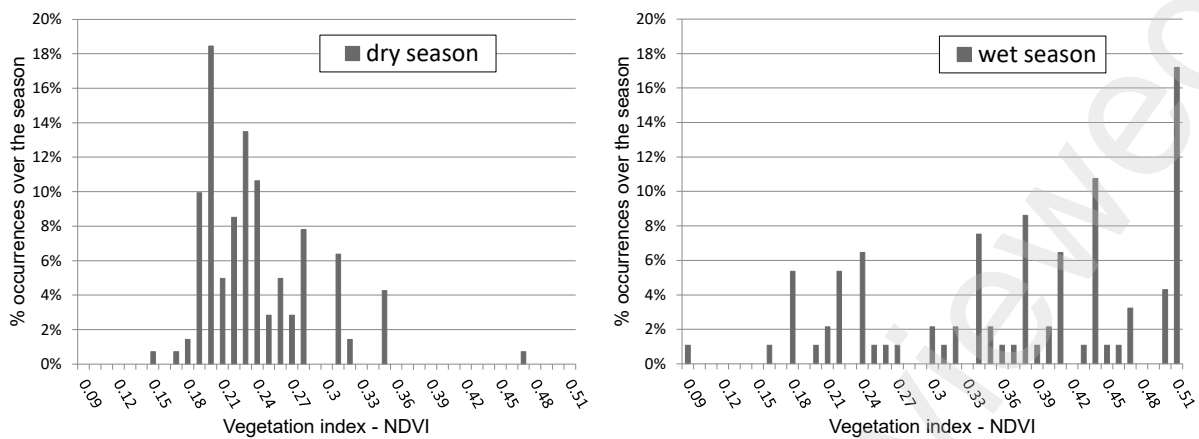
292 **Rainfall** input data are also updated monthly. We elaborated a data set on the area and the time
293 range of the study from the Global Precipitation Climatology Centre (GPCC;
294 <http://richardis.univ-paris1.fr/precip/index.html>). From 1998 onwards, GPCC data have been
295 replaced by TRMM 3B42 as a more relevant data source. A comparison of these two sources
296 for the years 1997 and 1998 showed that there is no bias induced by the change of data source.

297 2.8 Submodels

298 2.8.1 Preferential habitat computation

299 A favourable habitat is one that allows gerbil populations to dig their burrows, shelter, feed and
300 reproduce. They need a sufficiently loose, non-moist soil on which shrubs, grass or crops may
301 grow, enough vegetation to feed and a convenient substrate to dig their burrow. The preferential
302 habitat conditions for gerbils has been elaborated using (i) expert knowledge supported with
303 (ii) NDVI data, (iii) landcover and (iv) soil type maps (Figure 6) as well as (v) 2.056 gerbils
304 occurrences recorded in the so-called 'BPM' database on Sahelo-Sudanian rodents (Granjon
305 and Duplantier, 2009, <http://bpm-cbpg.science/>).

306 • **Food:** During the rainy season, vegetation grows sufficiently for gerbils almost
307 everywhere and is not a limiting factor, so NDVI was not accounted for during this
308 season. During the dry season, a NDVI range of 0.19-0.24 was selected as favourable
309 for gerbil settlement on the basis of observed data distribution (86% of the records found
310 in this NDVI range during this season; Fig.7).



311
 312 Figure 7. Gerbils occurrences as a function of vegetation index.
 313 Percentages of the overall seasonal observations within trapping sessions and owl pellets
 314 during the dry (november to june) and wet seasons from 1989 to 2013 as a function of NDVI.

- 315 • Soil type: from the 2.078 trapping occurrences, 62% of gerbils were found on sandy
 316 (40%) or sandy-clayed (22%) substrates and 38% scattered on "other" types of soil layer
 317 including indurated soils that are ill-suited for burrowing. Hence, 'sandy' and 'sandy-
 318 clayed' substrates were selected as preferential habitats for gerbils.
- 319 • Biotope: Based on the on the occurrence records, 84.5% of gerbils were trapped on grass
 320 (68.5%) or on shrub-grass (16%) areas. Gerbils seldom occur in areas classified as
 321 "crops" (10%) and are almost absent elsewhere. We thus selected the grass and shrub
 322 grass landcover areas as preferential habitats for gerbils.

323 Preferential habitats were computed using these three conditions of favourable soil, favourable
 324 NDVI and favourable landcover that must be simultaneously met, without any particular
 325 weighting for any of these factors.

326 2.8.2 Reproduction

327 Gerbil reproduction intensity is sensitive to food (plant) resources, themselves linked to rainfall
 328 (Sicard and Fuminier, 1996; Sicard and Papillon, 1996). The reproduction season begins one
 329 month following the regular occurrence of rain, usually in August. It ends 1 to 5 months after
 330 the last rains depending on the amount of rainfall (see suppl. mat). During this season, a
 331 percentage of pregnant females is first computed each simulated month and for each settled
 332 population as described below. Each resulting set of simulated pregnant females then produces
 333 a set of young viable individuals after pregnancy and a weaning latency period (see Figure 5),
 334 and depending on a fixed litter size.

335 The pregnant female rate (Table 1) is estimated on the basis of autopsies conducted over 470
 336 mature females caught in the field and including 70 pregnant females, 19 from Niger and 51
 337 from Senegal caught between May 1992 and July 2020.

338 Table 1. Pregnant female percentage used in the model (source <http://bpm-cbpg.science>)

	Jan.	Feb.	Mar.	Apr.	May.	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Nb females	6	36	101	80	10	17	34	67	22	32	51	14
Nb pregnant females	1	11	6	11	1	0	1	4	8	11	14	2
%	17	31	6	14	10	0	3	6	36	34	27	14

339

340 2.8.3 Propagule emission, dispersal and merging

341 Propagule emission starts 3 months after the beginning of the reproductive season in October
 342 and ends 3 months after the last month of reproduction (Figure 5). A subset of young subadults
 343 from each settled population gather to form a dispersing propagule, the others remaining in their
 344 natal population. The size of each propagule is obtained using a fixed percentage (propagule
 345 rate) of the subadults' population size.

346 Propagules move following a fixed speed that is equal to the radius length of their monthly
 347 perception circle. At the first step, the propagules move away from the burrow and travel in a
 348 random direction this monthly distance. If the place of arrival is a favourable habitat, they settle
 349 there. Otherwise, they move randomly, covering the monthly distance corresponding to their
 350 speed unless they perceive a favourable habitat. In this latter case they head towards it, settle
 351 and merge if relevant (see below).

352 When a propagule arrives in a patch already occupied with a population it merges with it. When
 353 populations merge, their numbers (females, males) are cumulated and their ages are averaged. If
 354 the new merged population is not yet established, its status is "exploring". If it is settled, its
 355 status changes to "breeding" during the breeding period or to "sexual rest" during the non
 356 reproductive period.

357 2.8.4 Mortality

358 Mortality is accounted for by applying a fixed parameter (survival rate) each month to each
 359 population agent. In addition, propagules that could not settle after one year are considered as
 360 no more viable and are discarded from the simulation.

361 2.9 Sensitivity analysis and parameters identification

362 Since the aim of the study was to report on the observed rapid southward expansion of this
 363 metapopulation, we selected the “maximum southward expansion” as one unique output
 364 indicator for the model’s calibration. This indicator is computed as the southernmost distance
 365 reached at the end of simulations in December 2013 relative to the initial northwestern position
 366 of August 1982.

367 2.9.1 Life-traits

368 Calibration and study of life-traits was realized by mean of a global sensitivity analysis
 369 involving a range of values for each model’s fixed parameter (Table 2).

370 Table 2. Driver variation ranges of the simulated gerbil metapopulation that have been
 371 successively explored to calibrate the model’s response

372

a)		
Parameter	Range of values explored	Nb values
1. propagule rate	[0.1-0.8, step 0.1]	8
2. survival rate	[0.50-0.85 step 0.5]	8
3. initial population number	5 ; 10 ; 100	3
fixed parameters : initial population size (10), litter size (3.4), monthly distance travelled (4000m) 192 simulations		

373

b)		
Parameter	Range of values explored	Nb values
1. initial population size	10; 100; 1000; 10000	4
2. initial population number	2 ; 5 ; 10 ; 100 ; 200	5
3. survival rate	0.2; 0.4; [0.50-0.85 step 0.5]	10
fixed parameters : propagules rate (0.50) and litter size (3.4), monthly distance travelled (4000m) 200 simulations		

374

c)		
Parameter	Range of values explored	Nb values
1. litter size	[3-5] step 0.2	11
2. survival rate	[0.50-0.85] step 0.5	8
fixed parameters : propagules rate (0.50), initial population number (5), initial population size (10), monthly distance travelled (4000m) 88 simulations		

d)		
Parameter	Range of values explored	Nb values
1. monthly distance travelled	[200-4,800 step 200] ; [5,000-7,500 step 500]	29

fixed parameters : propagules rate (0.50), initial population number (5), initial population size (10), litter size (3.4), survival rate (0.75) 29 simulations

375 For a fixed monthly distance travelled and given the large number of parameters and parameter
376 values to be tested, three sensitivity analyses were performed. The first one aimed to test the
377 influence of a variation in propagule rate and survival rate on expansion (Table 2a); the second
378 one focused on the impact of the size and number of initial populations as a function of survival
379 rate variation (Table 2b); the third one examined variations in litter size as a function of survival
380 rate (Table 2c). Based on these three analyses, we selected a combination of the parameters
381 with which we tested the influence of a variation in monthly distance travelled on expansion
382 (Table 2d). As a result, the model was run on a subset of 509 simulations

383 Using this set of outputs, the response curves of the model to the variation of each parameter
384 were then elaborated one at a time. The most plausible value for each single parameter has been
385 also extracted given model's response and biological expertise. The whole set of plausible, or
386 realistic values constitute a so-called 'most plausible/realistic scenario' that has been further
387 used to study the effect of environment and metapopulation origin.

388 2.9.2 Environmental drivers

389 Three major environmental drivers may influence the gerbil populations spread in this model:
390 (i) pedology as a proxy for digging ease (ii) land cover habitat suitability and (iii) effect of
391 temporal change of vegetation. We addressed these three drivers and their influence on the
392 simulated Sahelian gerbil invasion in Senegal using various combination, each defined on a
393 gradient of increasing environmental constraints (Table 3) to produce scenarios that illustrate
394 various patterns of preferential habitat for gerbil populations.

395 Table 3. Gradients of gerbil populations settlement constraints for the three environmental
396 drivers

397 **Pedology** imposed using three levels of constraint:

- 398 a) PEDO_0: no constraint (any configuration appropriate),
- 399 b) PEDO_1: medium constraint (sand, sandy clayey, indurated/hard grounds) corresponding
400 to the three soil classes where the majority of gerbils' occurrences were located during
401 surveys
- 402 c) PEDO_2: strong constraints where only sandy substrates were considered favourable for
403 settling

404 **Land cover** constrained using five levels of composition to define suitable habitats:

- 405 a) LC_0: no constraint (any configuration appropriate),
- 406 b) LC_1: smooth constraint with the 12 selected composition of relevant SYNMAP values of
407 the consensus map combining trees, shrubs, grass (broad and needle), crops, sand and crops
- 408 c) LC_2: medium constraint including only the three landcover classes where the majority of
409 gerbils' occurrences were located during surveys that is shrubs + grass, grass and crop.
- 410 d) LC_3 and LC_4: Strong constraints where only one of the preceding classes were
411 considered, namely, LC_3: shrub + grass only, LC_4: grass only

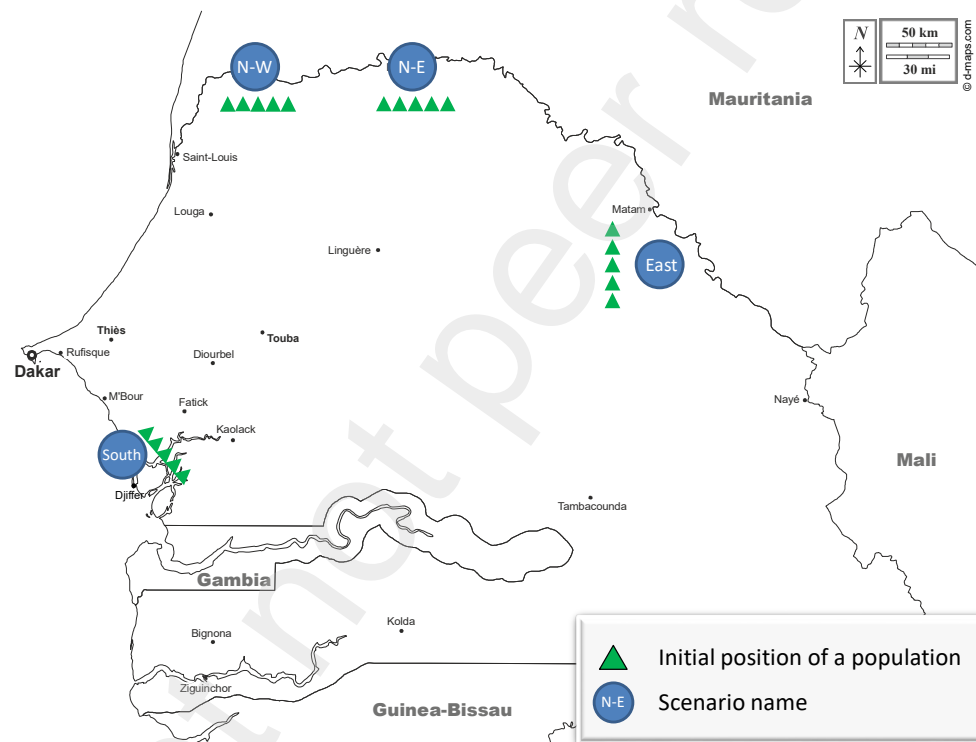
412 **Vegetation (NDVI) cover** constrained using three ranges of values conducive to settling:

- 413 a) NDVI_0: no constraint (any configuration appropriate),
- 414 b) NDVI_1: medium constraint using [0.19-0.28] suitable habitat during the dry season and
415 every configuration suitable during the wet season (see Figure 7)
- 416 c) NDVI_2: strong constraint using [0.19-0.24] suitable habitat during the dry season and
417 every configuration suitable during the wet season

418 The environmental scenario based on observation (submodels section - preferential habitat
419 computation), termed here "PEDO_1 / LC_2 / NDVI_2", has been utilized to generate the life
420 traits parameters set in the 'most plausible/realistic scenario'. With these parameters defined,
421 simulations were run using different combinations of pedology, landcover, and NDVI to
422 examine the impact of environmental signals on the spread of the gerbil invading
423 metapopulation.

424 2.9.3 Origin of the invading metapopulation

425 Nigerian Gerbils were first detected in the 1990s on the southern bank of Senegal River ($>16^{\circ}\text{N}$)
 426 and were shown to gradually spread southwards to a latitude of approximately 14°N in the
 427 2010s. Following this observation, two first starting positions might therefore been considered
 428 (Figure 8): south-west of the river bank (position N-W), and south-east of the river bank
 429 (position N-E). A supplementary scenario has been considered with initial populations spread
 430 along eastern border between Mauritania and Senegal (position East). This last scenario has
 431 been considered following a study based on species distribution model (Borner et al. unpubl.
 432 data) that suggests a favourable habitat corridor spreading between Mauritania and Senegal in
 433 this region and bolstered by the fact that the Senegal river is narrower here and hence more
 434 easily crossed.



435

436 Figure 8. Single introduction scenarios considered and combined to study the origin of the
 437 invading metapopulation

438 Several scenarios may therefore be plausible for the origin of the metapopulation and nine have
 439 been considered in this study: Three consider a unique introduction route (N-W, N-E and East,
 440 Figure 8) and three others propose a dual one that is a combination of the formers (N-W + N-
 441 E, N-W + East, N-E + East). Additionally, we explore three supplementary scenarios (South +
 442 N-W, South + N-E, South + East) including an introductory path from South to investigate
 443 potential explanation of three southernmost occurrences in this region evidenced from owl

444 pellet remains in 2005 (sites a, b, c Figure 2). In all cases, the starting populations are regularly
445 distributed along approximately 50km transects positioned in the corresponding regions (green
446 triangles on Figure 8).

447 In order to perform the life-trait parameters identification, we selected one unique scenario
448 among those nine with the initial metapopulation originating from the North-West of Senegal
449 (N-W on Figure 8) where the species was first observed.

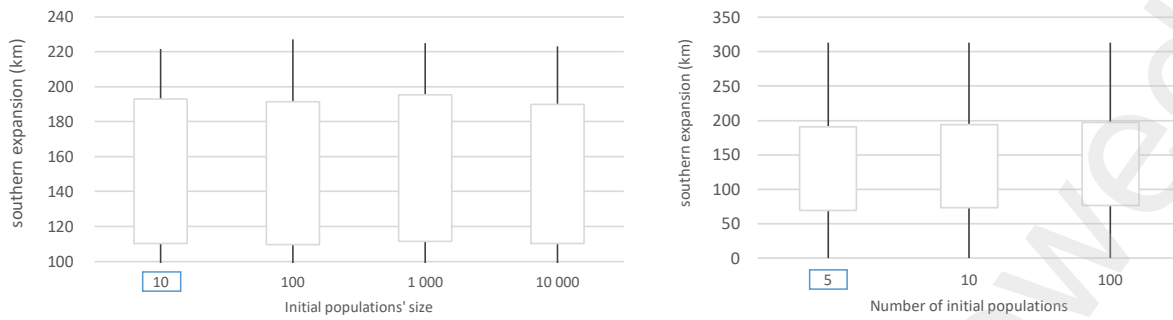
450 **3 Results (simulation results)**

451 The influence of stochasticity (i.e., choosing a location at random without using motivational
452 or driving factors, section Design concept) was quantified using the standard deviation from a
453 set of 100 identical simulations using the 'most plausible/realistic scenario' parameters set
454 (presented in the following sections). Following this pre-test, randomness produces 4.29%
455 variability for the southward expansion indicator, which e.g., results in 8.6 km lack of precision
456 for a 200.96 km mean expansion.

457 Using the selected combinations of parameters (Table 2), the simulated southern expansion
458 extends from 0 to 313 km, the latter distance corresponding to the southern limit of the
459 simulated domain. The details of this fluctuation range are presented below.

460 **3.1 Invading metapopulation composition**

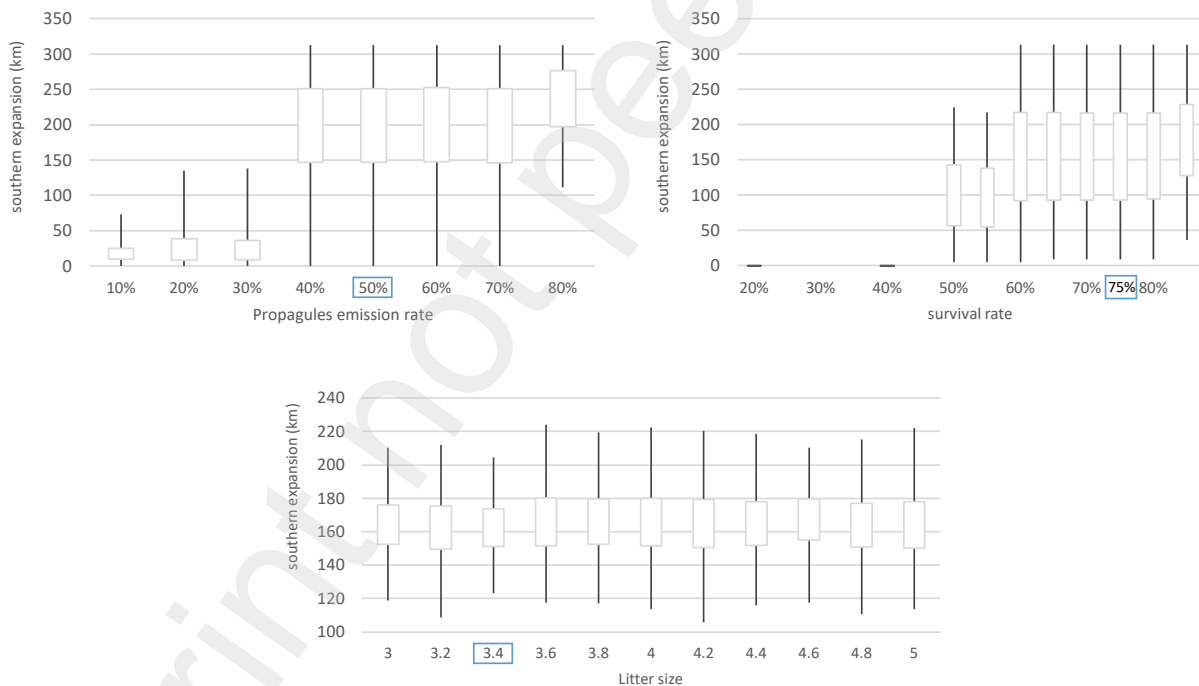
461 Among the set of variation studied, the composition of the initially 'invading' metapopulation
462 (size and number of populations) does not significantly influence the southern expansion
463 obtained at the end of the simulation in 2013 (Figure 9). The value of these parameters however
464 modify the demographic output resulting in denser populations when initial size of the invading
465 metapopulation grows (not figured). In the absence of concrete knowledge for these two
466 parameters, we have selected as plausible a set of 5 initial invading populations, each composed
467 of 10 individuals. These values are also intermediate in terms of metapopulation density (i.e.,
468 they lead neither to a pullulating nor a collapsing metapopulation).



469
 470 Figure 9. Model's southern expansion sensitivity to the starting conditions.
 471 Boxes stand for one standard deviation around the mean, lines indicate the maximum and
 472 minimum values, squared abscissa refer to the selected value for the 'most plausible/realistic
 473 scenario'.

474 **3.2 Life-trait calibration**

475 There is a clear threshold for the effect of propagule emission rate parameter on the southern
 476 expansion of the metapopulation (Figure 10 left): in this model, gerbils do not expand in
 477 Senegal below a dispersing fraction of 40% of the populations at each generation.



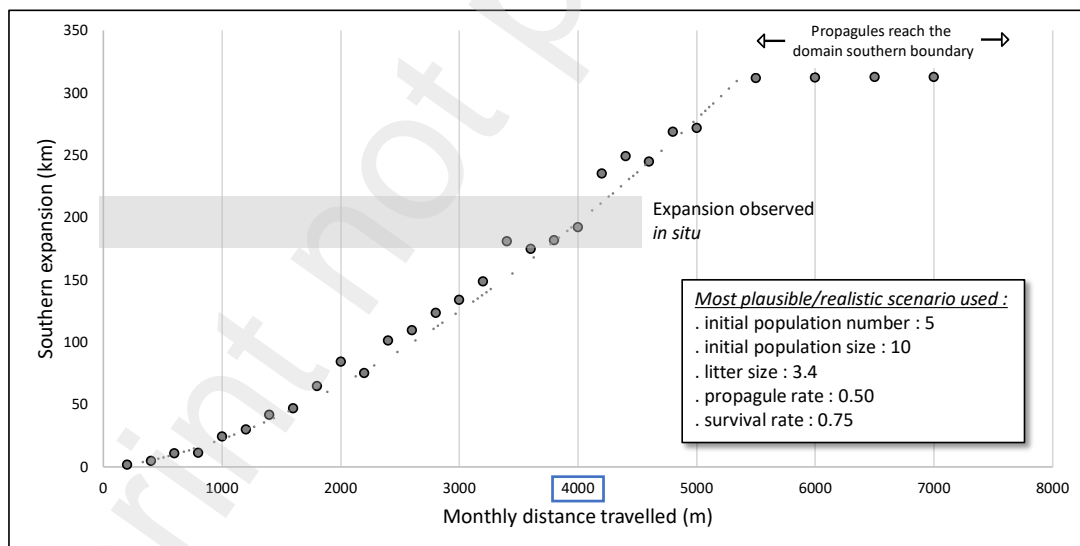
478
 479 Figure 10. Model's southern expansion sensitivity to selected life traits.
 480 Same caption as Figure 9.

481 Within the interval [40-70%] this rate does not influence the indicator. However, at a
 482 supposedly unrealistic value of 80% emigrating propagules, the model produces a further extent
 483 for the southward expansion. The expansion observed in the field in 2013 lies between 180 and
 484 220 km. We selected a 50% propagule emission rate as an intermediate value within the range
 485 that provides this expansion extent.

486 When the survival rate parameter (Figure 10 right) stands below 50%, the metapopulation
 487 simulated collapses. Beyond this threshold, survival rate parameter exerts a slight effect on
 488 southward expansion for the explored [20%-85%] survival rate range. It must be noticed that,
 489 for this parameter's value, beyond 85% (not figured) the model produces a pullulating
 490 metapopulation. A monthly survival rate of 75% has been selected as a value consistent with
 491 the few data at hand on similar-sized murid rodents from the same geographic area (e.g.
 492 *Mastomys* spp. from Senegal and Mali [Crespin et al. 2008, 2012], *Taterillus gracilis* from Mali
 493 [L. Granjon unpubl. data])

494 Litter size parameter (Figure 10 bottom) does not significantly influence the southern
 495 expansion; however, and as expected (not figured), it has an exponential effect on the mean size
 496 of settled populations as well as the number of adults. We selected a value of 3.4 corresponding
 497 to the one reported by Granjon and Duplantier (2009).

498 In contrast with the preceding parameters, the southern expansion is strongly correlated with
 499 the distance that can be travelled each month by the propagules. Given the importance of this
 500 parameter, we simulated in more detail the range of the parameter's value using the 'most
 501 plausible/realistic scenario' (Figure 11).



502
 503 Figure 11. Southern expansion in December 2013 as a function of propagules' monthly
 504 distance travelled.
 505 Dotted line: best fit of the ascending part (power function, $r^2=0.994$); squared abscissa:
 506 selected value for the 'most plausible/realistic scenario'.

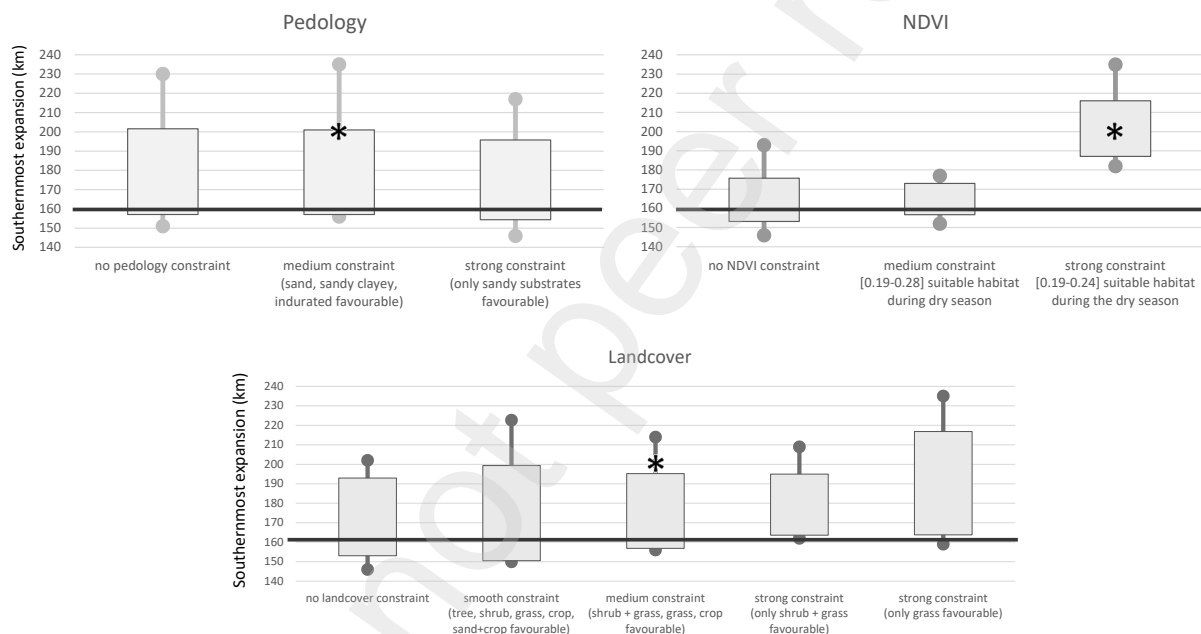
507 When the monthly dispersal increases the southern expansion also increases very regularly. The
 508 best interpolation of the simulated pattern is obtained using a power function that could be
 509 related to the occupation of the available surface by the exploring propagules. Only with an

510 (unrealistic) dispersal speed of 6km/month or higher does the metapopulation reach the
 511 southern boundary of the simulated domain which caps southward expansion (i.e. including the
 512 three south-westernmost sites where *G. nigeriae* was found in owl pellets in 2004)

513 The 200 km expansion observed in the years 2010 at the latitude of Dakar (see Figure 2) is
 514 obtained when the propagules travel 4,000 meters each month.

515 3.3 Sensitivity to the Environment

516 Following the schemes described in Table 3 we plotted the effect of various combinations of
 517 environmental constraints on the southward expansion of the simulated gerbil metapopulation
 518 (Figure 12).



519

520 Figure 12. Effect of environmental constraints on the souhtward expansion of the simulated
 521 metapopulation.

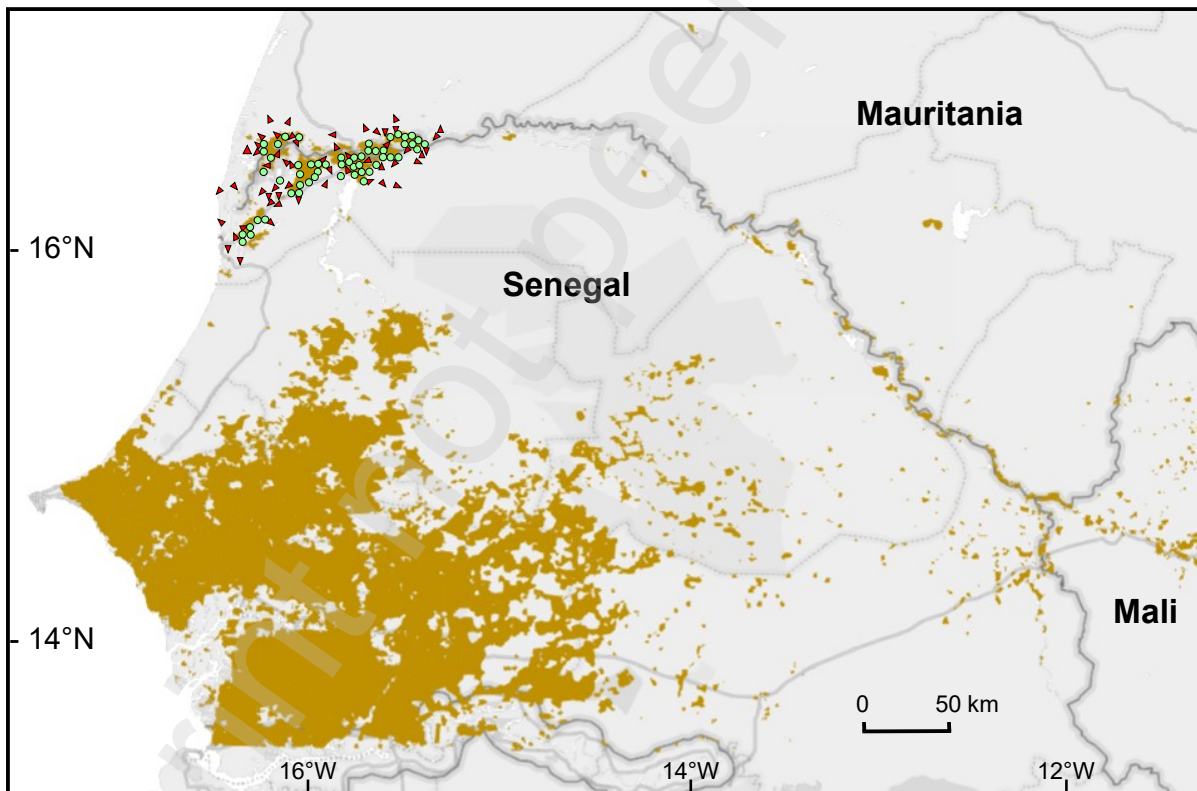
522 Boxes correspond to two standard deviations, vertical lines to maximum and minimum
 523 values, from all possible combinations of the “levels of constraint” listed in Table 3.

524 Horizontal thick line: ‘null’ scenario with no environmental driver (all cells favourable for
 525 settling). Initialization and life trait parameters conform to the ‘most plausible/realistic
 526 scenario’ (e.g., Figure 11). Star: southerly expansion using the ‘most plausible/realistic
 527 scenario’ selected value for the environment drivers.

528 Most scenarios result in a larger expansion than obtained using the ‘null’ scenario (thick line)
 529 that disregards environmental restrictions: it clearly appears that adding any combination of
 530 environmental constraints causes the metapopulation to spread farther south in the vast majority
 531 of cases. The landcover part of the chart also reveals a broad pattern whereby the southerly
 532 expansion is more pronounced when the environmental constraints are stronger. This effect of

533 constraining environment is particularly clear in the case of the NDVI constraint that produces
534 more expansion when the optimal window is narrowed. Using the ‘most plausible/realistic
535 scenario’, environmental constraints lengthens the southerly progression by about 40
536 kilometres.

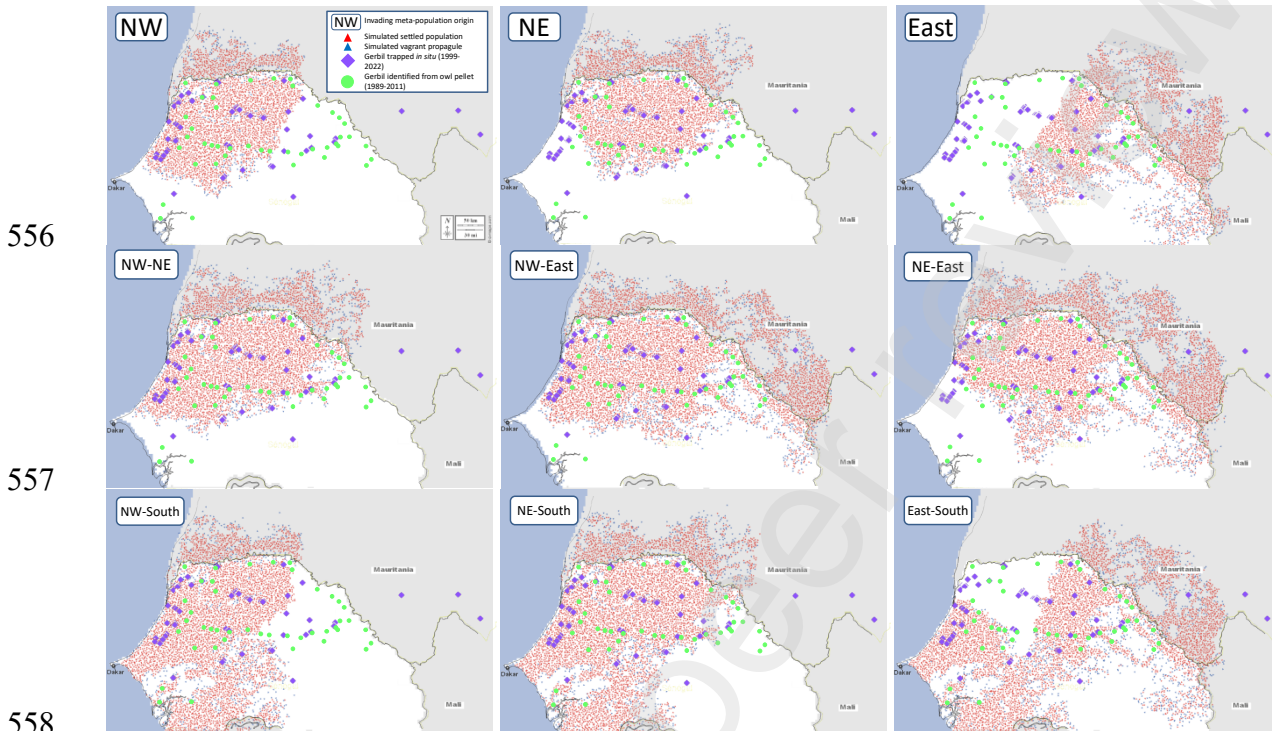
537 It has to be mentioned however that, when it comes to fixed values of environmental forcing
538 (pedology and land cover), the progression may be halted if the constraint is too severe and
539 does not allow access to areas further south. This is the case, as an illustrative example, when
540 the “crops” class is retained as the only favourable land cover category (Figure 13). In this
541 example, there is a divide between the northern and southern regions of the simulated zone. The
542 dispersing propagules cannot ‘sense’ and therefore reach the favourable zone further south, they
543 can only remain in the favourable zone near the place of introduction of the populations (North
544 West in the figured example).



545
546 Figure 13 Illustrative example of spread of the simulated population limited by an overly
547 stringent environmental constraint. Here, constraining favourable landcover type to crops only
548 clearly prevents gerbils’ propagation to the south. Green circles: settled populations, red
549 triangles: exploring propagules, brown areas: cultivation areas (crop layer of the SynMap
550 landcover.

551 3.4 Origin of the invading metapopulation

552 We examined the impact of the invading metapopulation origin on the pattern of expansion
553 following the suggested strategy (Figure 8 and text) and using parameters selected from the
554 "most plausible/realistic scenario". In order to achieve this, departure scenarios were simulated
555 beginning in 1982 and ending in 2013 (Figure 14).



556
557
558
559 Figure 14. Influence of initial position of the invading metapopulation on the simulated spread
560 of nigerian gerbils.
561 Introduction positions as on Figure 8; situation simulated on december 2013; parameters'
562 values are those of the 'most plausible scenario'.

563 The uniformly distributed pattern of *G. nigeriae* in northeastern Senegal cannot be accounted
564 for by the NW and NE scenarios alone. On the other hand, the western portion of its distribution
565 is not supported by the East scenario alone. None of the dual introduction scenarios leads to a
566 fully comprehensive description of the observed distribution, with incomplete coverage of the
567 eastern portion for the NW-NE scenario and of the western portion along the coast for the NE-
568 East scenario, respectively. Nevertheless, the combined NW-East introduction scheme provides
569 a rather satisfactory coverage, even though the southernmost simulated populations do not quite
570 reach the south westernmost observed positions. When incorporating a southern introduction
571 of a metapopulation (bottom three maps on Figure 14), the model can achieve these latter
572 positions, but at the cost of a prohibitive lack of cover of the north eastern (NW-South and NE-
573 South scenarios) or northern (East-South scenario) portions of the observed distribution.

574 4 Discussion

575 We examined the simulation outputs of a mechanistically rich deterministic model to decipher
576 the drivers underlying the spectacular phenomenon of invasion of Senegal by *G. nigeriae*
577 around the turn of the last century. The model developed incorporated available information
578 regarding biological traits and demography of gerbil populations evolving in a dynamic
579 multivariable environment generated from accessible data.

580 In the model proposed, randomness is restricted to determining the propagules' dispersal
581 direction when no favourable habitat is found or chosen between several equivalent habitats.
582 This results in a mean variation of 4.29% on simulated gerbils metapopulation spread in the
583 simulated domain. This distinction notwithstanding, the model is entirely deterministic. This
584 approach enables to better identify which factors may or may not have contributed to the
585 observed invasion: biological traits and demography, propagule dynamics and behaviour, the
586 effect of environmental constraints, potential invasion source(s) and routes.

587 4.1 Effect of invasive population density and demographics

588 Results indicate that a large original population is not required to achieve the metapopulation
589 spread throughout the entire colonized territory. In the present case, 5 populations of 10
590 individuals are sufficient to initiate the colonization process. This small number of pioneer
591 individuals seems realistic in the case of a species colonizing a new domain by its own means.
592 However, one could have expected that simulations initialized with a larger number of
593 populations and/or individuals per population would result in a quicker pace of colonization via
594 enhanced demographic effects. Even in simulations with high population size values (see Figure
595 9), the model did not produce this outcome.

596 The low importance of demography in explaining the colonization success of the simulated
597 species is also supported by the analysis of demographic life traits as such. For instance, one
598 could have anticipated that litter size would influence spatial colonization success by increasing
599 the number of individuals exploring the available habitat. This is not the case since here again,
600 increasing the litter size to excessive and even unrealistic levels produces no noticeable increase
601 in southward expansion of the metapopulation.

602 Literature most frequently reaches the conclusion that the initial invading propagule pressure is
603 decisive in the invasion success (e.g., Colautti et al., 2006, Blackburn et al., 2013). The model's
604 conclusions regarding the calibration of life attributes suggest, however, that the colonization
605 success is not determined by the number of individuals introduced into the new environment

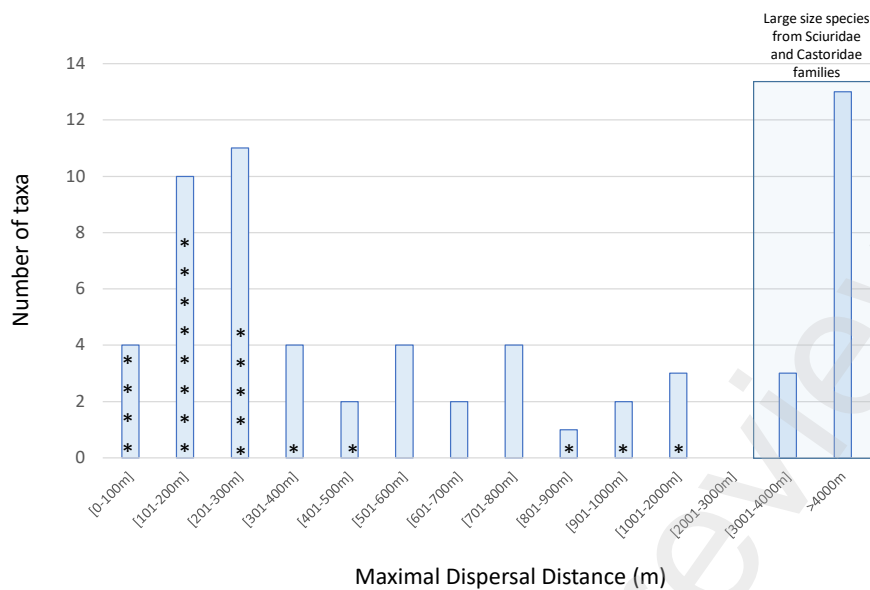
606 but by the subsequent dynamics of the propagules emitted through reproduction within the
607 invaded zone: the only biological features that influence propagation are those that affect the
608 propagules' dynamics. Indeed, the metapopulation does not spatially develop below a propagule
609 rate threshold neither below a survival rate threshold for populations.

610 4.2 Dispersion velocity

611 When survival rate, reproductive intensity, and propagule emission rate are held within
612 plausible ranges, the primary factor influencing colonization is clearly the movement intensity
613 of colonizing propagules.

614 4.2.1 Known dispersion rates

615 Comparing the outputs of the model with gerbil actual distribution (with a focus on its
616 southernmost limit) reveals that propagules require a mean displacement of 4,000 meters per
617 month (130 meters per day), sustained about six months per year for 20 years. Such a value of
618 monthly dispersal distances is far greater than previously recorded, and even imagined, in small
619 mammals of this size. In their meta-analysis of (natal) dispersal distances in mammals,
620 Whitmee and Orme (2013) used data coming from experimental / observational studies and
621 from reports of individual movement distances, to the exclusion of distances derived from
622 genetic information. Their analyses included data from 28 species of rodents. For some of them,
623 different studies were considered and for most of them male and female data were available
624 (see their Appendix S1). The distribution of maximal dispersal distances of the corresponding
625 63 cases is reported in Figure 15.



626

627 Figure 15 Compilation of maximal dispersal distance in rodent species using data from
 628 Whitmee and Orme, 2013, appendix S1. Stars refer to the number of examined rodent species
 629 of size close to those of *Gerbillus nigeriae*.

630 The dispersal distance modelled here in the expanding population of *G. nigeriae* falls in the
 631 upper range of maximal dispersal distances recorded, which characterized large species (ten to
 632 1000 times heavier than *G. nigeriae*) such as squirrels, marmots or beavers. Moreover, it is
 633 around 4 times higher than the highest value recorded for a small rodent the size of *G. nigeriae*
 634 (around 1km in female *Peromyscus maniculatus*; Whitmee and Orme, 2013).

635 The literature on invasive processes spanning various taxonomic groups (Estrada et al., 2015)
 636 or more specifically plants (e.g., Kupfer et al., 2006, Szabó et al., 2019) or animals (arthropods,
 637 fish, birds, mammals) including rodents (MacKay et al., 2019) points out that invasion events
 638 can be associated with changes in certain behavioural traits of colonising organisms. In
 639 particular, it appears that individuals at the vanguard of a range shift frequently have their
 640 phenotypes altered by a combination of behavioural traits that promote dispersal (Chuang and
 641 Peterson, 2016, Szabó et al. 2019, Daly et al., 2023) such as activity, aggressiveness, boldness,
 642 alertness, etc. (Malange et al., 2016). Traits such as speed (Phillips et al., 2006, 2010),
 643 endurance (Llewelyn et al., 2010) or the ability to maintain a direction (Lindström et al., 2013)
 644 can also be altered to favour a faster rate of colonisation. These traits express a phenotypic
 645 plasticity of invasive individuals, which frequently distinguishes them from settled populations'
 646 members. Furthermore, in certain cases, this plasticity can be rapidly selected within the
 647 propagules progeny, resulting in already pre-adapted colonisers with enhanced dispersal
 648 capabilities (Pettit et al., 2016). This possible heritability enables invading populations to spread
 649 even farther and faster and can further accelerate the invasive process (Phillips et al., 2010).

650 Here, we can hypothesize that invading gerbils demonstrated such phenotypic flexibility,
651 possibly heritable across the propagule offspring strain during the overall range shift,
652 contributing to the rapid range expansion throughout the entire colonisation period, hence
653 explaining the model-suggested 4000m mean monthly dispersal.

654 4.3 Influence of environmental constraints

655 Regarding the colonisation process, the environment appears to be both an impeding and a
656 helping force. Reaching the observed southern limit of *G. nigeriae* distribution in Senegal from
657 a northern introduction point at the Mauritania-Senegal border in a straight line within the same
658 time interval would correspond to a monthly dispersion of 600-1000m (see introduction). From
659 there, the environment first and foremost acts as a speed reducer, as it introduces constraints
660 against such a straight line dispersal. Instead, according to the model presented, 4000m/month
661 would correspond to the dispersal rate actually experienced by the gerbils to occupy Senegal's
662 unfilled niche.

663 Yet, the environment also aids in the invasion success. The investigation of the dispersal's
664 sensitivity to environmental forcing indeed shows that in the absence of environmental
665 constraints, the metapopulation's southern limit would be substantially less (by around 40 km)
666 than observed. Specifically, the results depicted in Figure 12 indicate a tendency whereby the
667 progression towards the south increases as the combination of environmental forcing factors
668 becomes more restrictive. In the absence of environmental limitation ("null scenario"), all cells
669 are equally favourable for propagule installation and the populations subsequently spread
670 tightly and isotropically around introduction spots, hence resulting in restricted dispersal.
671 Conversely, an increase in environmental restrictions results in the formation of privileged,
672 favourable "corridors" where propagule density rises, thereby encouraging the fusion and
673 settlement of new populations and thus generating additional dispersing propagules.

674 This trend is especially pronounced in relation to the monthly vegetation abundance constraint:
675 the narrower the favourable NDVI interval, the fewer favourable zones and the greater the
676 expansion. The monthly variation of NDVI favourable spots, moreover, ensures that there is
677 always a (southward) progression path available for gerbils.

678 In contrast, constraining too severely those environmental parameters that are temporally fixed
679 in the model may completely hinder the gerbil's southward progression. The
680 theoretical/unrealistic example on Figure 13 where crops constitute the only favourable habitat,

681 illustrates an environmental trap from which the species cannot escape. Such situation
682 corresponds to a strict habitat specialization but as such, is not representative of the ecology of
683 *G. nigeriae*, which does show a certain level of tolerance regarding habitat components' range
684 it can deal with (Granjon & Duplantier, 2009).

685 4.4 Origin of the invasive population

686 The different options simulated for the origin of the metapopulation (Figure 14) suggest that a
687 single source of introduction has not been sufficient for gerbils to expand over the entire area
688 where they are observed. This especially concerns the extreme west of Senegal where recent
689 surveys have confirmed their presence near the coast and in the east of the country where
690 individuals of this species are now regularly trapped (L. Granjon and colleagues, pers. obs.).
691 The most thorough coverage of the observed distribution would imply initial introductions of
692 gerbils to Senegal from both the North-West and the East. This double entry can be considered
693 realistic insofar, outside from Senegal, the presence of settled populations of *Gerbillus nigeriae*
694 has already been documented in south-western and south-central Mauritania (our data, Figure
695 1; see also Brito et al., 2022). If such a double-entry scenario suggested by the model turns out
696 to be accurate, it might be indicative of a widespread outbreak of colonisation in a region
697 (Senegal) unoccupied until the end of the 1970s / beginning of the 1980s that became an
698 available space to be filled.

699 The proposed model cannot be used to determine the nature of this potential trigger. However,
700 we can advance two non-exclusive hypotheses: first, climate-related alterations in northern
701 Senegal's habitats could have occurred following the severe drought observed during the
702 initiation stage of the invasion (Le Borgne, 1990), that may have facilitated gerbils' settlement.
703 Indeed, comparing physiological capacities of body water regulation in invading *Gerbillus*
704 *nigeriae* and two resident species of *Taterillus* (also belonging to the Gerbillinae subfamily)
705 from the same area of northern Senegal, Thiam et al. (2011) showed that *Gerbillus nigeriae*'s
706 better drought tolerance (capacity to conserve water) was probably a major element in their
707 successful colonisation of Senegal at the expense of *Taterillus* (especially *T. gracilis*) species.

708 Secondly and maybe more importantly, this potential trigger may be of physical order. Indeed,
709 in the configuration described, the Senegal River (Figure 2) constitutes for the gerbil a
710 significant barrier all along the entire potential area of entrance of the species in Senegal, i.e.,
711 from the Atlantic coast to Mali. According to diachronic monitoring of the Senegal River's flow
712 from 1900 to 2012 (Bader, 2015), the river experienced its lowest annual flow ever (7 km³/year

713 at the Bakel station) in the years 1983 and 1984 before rising gradually back to its average
714 historical mean flow (21 km³/year) over the next two decades.

715 Consequently, one probable scenario may be as follows: The very severe weakening of this
716 powerful barrier during the years 1983–1984 would have permitted gerbils cross the Senegal
717 River contemporaneously in several areas, along its northern and eastern course. Once the river
718 crossed, gerbils were placed in an open niche where climatic conditions of the former years had
719 provided very favourable habitats (including in terms of competitive release from other rodent
720 species), hence resulting in the rapid colonization southward of this incoming metapopulation.

721 4.4.1 The southern introduction issue

722 Even the “NW-East scenario”, which appears to best account for the observed distribution, does
723 not fully simulate the presence of the metapopulation in the three southernmost locations
724 (Fumela, Ndiosmone and Sing-Sing, blue dots on Figure 2) where the gerbil was detected in
725 owl pellet remains. This part of the distribution is very marginal, accounting for only 0.04% of
726 the records; yet it raises issues because a monthly distance of 4,000 m traveled by the propagules
727 does not allow these southern areas to be reached in time with, furthermore, unfavourable
728 clayey soil conditions to the north of Fumela, NDiosmone, and Sing-Sing.

729 To explain these extralimital points of presence relative to the rest of the distribution of the
730 species in Senegal, one could invoke the influence of a peculiar, historically well-documented,
731 anthropogenic factor. Following the extremely severe drought episode that occurred in Senegal
732 in 1983-1984 (Le Borgne, 1990), a large-scale human migratory movement began (Roquet,
733 2008). It involved in particular the Subalbe (Toucouleurs) ethnic group that was established in
734 the middle valley of the Senegal River (Podor region) and from which a portion migrated to the
735 Saloum region (Schmitz, 2007). This migratory movement was then consolidated in the
736 following decades with a strong intensification of mobility, in particular a difficult-to-quantify
737 but significant rise in canoe traffic from the North (Saint-Louis) to the South and in particular
738 the large Djiffer traditional fishing port in the Saloum (Figure 2), not far from where these
739 gerbils were observed (J.-Y. Weigel, comm. pers. 2022). This traffic is associated with artisanal
740 fishing and involves the practise of coastal trade between the north and the centre-west of
741 Senegal with food (rice, fish) transported by means of large canoes (20 metres in length). The
742 intensification of trade between the northern and central western regions of Senegal could have
743 resulted in the occasional transport of gerbils inadvertently trapped in food supplies (e.g. cereal

744 bags) to the Saloum region, thereby giving rise to a third, weaker but nonetheless
745 effective, route of colonisation via the Saloum region.

746 This explanation for the installation of gerbils in this southern area would appear unlikely in
747 normal circumstances since *Gerbillus nigeriae* is not known as a synanthropic species (Sicard,
748 2013). At the time when this phenomenon could have occurred, however, the extreme drought
749 episode led to a unique combination of conditions that both intensified human migration
750 towards the South and may have entailed food shortage for rodents, causing them to approach
751 humans and their resources. This could have enhanced the likelihood of gerbils accidentally
752 boarding in food being transported by canoe, rendering this explanation plausible although still
753 speculative.

754 **5 Conclusion**

755 Various sensitivity analyses have enabled us to explore which factors could have contributed
756 to *Gerbillus nigeriae*'s successful colonisation of Senegal. The insights provided by the model
757 can be considered at three levels of decreasing confidence: first, we get fairly clear clues such
758 as the possibly limited contribution of demography or the need for a multipoint entry of
759 populations into the invaded area. Then, we uncovered significant unexplored processes that,
760 despite being addressed, remain speculative, such as the possibility that human activities could
761 have influenced the introduction of gerbils in the southernmost part of their observed invaded
762 range. Finally, we emphasised that the success of the invasion needed processes (that may
763 involve phenotypic plasticity) that are still largely misunderstood, particularly large dispersal
764 distances in populations at the colonisation front sustained over several years. The non-
765 replicable uniqueness of such range expansion and the challenges faced by long-term
766 monitoring of wild rodents of this size make it difficult to envisage learn more about the latter
767 issue in real conditions. It may however stimulate experimental researches in more or less
768 controlled conditions regarding dispersal capacities of this important species in the Sahelian
769 context.

770 Nonetheless, the comprehensive examination of this model's outputs prompts the proposal of
771 an explanatory scenario for this quite unique example of fast and broad invasion of a new
772 territory by a rodent species of this size. Thus, the success of the Nigerian Gerbil's colonisation
773 of Senegal appears to have been made possible by a concomitant combination of (i)
774 multivariable synergetic environmental factors (environmental constraints that facilitate
775 progression), (ii) physical changes (relaxation of the Senegal River barrier after a sharp

776 drought), (iii) behavioural change (propagules dispersal capacities enhanced owing to
777 phenotypic plasticity), and possibly (iv) the intervention of unusual anthropogenic factors
778 (maritime transport of gerbils to the Saloum region).

779 **CRedit authorship contribution statement**

780 The study was conceptualized by all authors; Jean Le Fur and Françoise Duraffour designed
781 the model and analysed the simulation data; Françoise Duraffour carried out the coding and
782 simulation of the model. All authors participated in the discussion of the results, contributed to
783 the subsequent updates of the model, authored and reviewed the paper, and approved the final
784 manuscript.

785 **Declaration of competing interest**

786 We declare to have no conflict of interest.

787 **Data availability**

788 Data are available from international repositories and specific sources. Each is mentioned
789 alongside the corresponding texts.

790 **Acknowledgments**

791 The authors wish to thank C. Valton for reworking the map of Fig.2, Y.Dewolf for her expertise
792 on pedological data, J.-Y. Weigel for his expertise on fishers migration. This work was
793 supported the CERISE project funded by the Fonds Français pour l'Environnement Mondial
794 via the Fondation pour la Recherche sur la Biodiversité (AAP-SCEN-20B III).

795 **References**

- 796 Bâ K, Granjon L, Hutterer R, Duplantier JM (2000) Les micromammifères du Djoudj (Delta
797 du Sénégal) par l'analyse du régime alimentaire de la chouette effraie, *Tyto alba*. Bonner
798 zoologische Beiträge 49: 31–38. <https://www.documentation.ird.fr/hor/fdi:010026044>
- 799 Bâ K, Thiam M, Dobigny G, Granjon L, Mané Y, Volobouev V, Duplantier JM (2006)
800 Hypothesis on the origin of the invasion of Senegal by *Gerbillus nigeriae* based on
801 chromosomal data. Mammalia 70: 303–305. <https://doi.org/10.1515/MAMM.2006.047>
- 802 Bader JC (2015) Monographie hydrologique du fleuve Sénégal. De l'origine des mesures
803 jusqu'en 2011. IRD Éditions, Institut de Recherche pour le Développement, Marseille, 2015,
804 1-920. https://horizon.documentation.ird.fr/exl-doc/pleins_textes/divers16-01/010065190.pdf
- 805 Baize D, Girard MC (2008) Référentiel pédologique, Association Française pour l'étude du sol,
806 Quae: 1-423. [https://www.quae.com/produit/1011/9782759214884/referentiel-pedologique-](https://www.quae.com/produit/1011/9782759214884/referentiel-pedologique-2008)
807 [2008](https://www.quae.com/produit/1011/9782759214884/referentiel-pedologique-2008)

808 Blackburn TM, Prowse TAA, Lockwood JL, Cassey P (2013) Propagule pressure as a driver of
809 establishment success in deliberately introduced exotic species: Fact or artefact? *Biol Invasions*
810 15: 1459–1469. <http://dx.doi.org/10.1007/s10530-013-0451-x>

811 Boulet R, Fauck R, Kogaal B, Leprun JC, Vieilleron J, Riquier J (1971) Carte pédologique au
812 1/5.000.000 de l'Afrique de l'Ouest. In *Atlas International de l'Ouest africain*, O.U.A.,
813 Commission Scientifique, Technique et de la Recherche, pl. 9, 1 carte couleurs, légende 72
814 unités carto., notice explicative 15 p., table des unités cartographiques (correspondance avec
815 classification FAO).

816 Brito JC, Sow AS, Vale CG, Pizzigalli C, Hamidou D, Gonçalves DV, Fernando Martínez-
817 Freiria F, Santarém F, Rebelo H, Carlos Campos J, Pleguezuelos JM, Ferreira da Silva MJ, Naia
818 M, Tarroso P, Godinho R, Silva TL, Macedo T, Boratyński Z, El Abidine Sidatt Z, Álvares F
819 (2022) Diversity, distribution and conservation of land mammals in Mauritania, North-West
820 Africa. *PLoS ONE* 17(8) e0269870. <https://doi.org/10.1371/journal.pone.0269870>

821 Brzezinski M, Zmihorski M, Zarzycka A, Zalewski A (2019) Expansion and population
822 dynamics of a non-native invasive species: the 40-year history of American mink colonization
823 of Poland. *Biological Invasions* 21: 531–545. <https://doi.org/10.1007/s10530-018-1844-7>

824 Caillou P, Gaudou B, Grignard A, Truong CQ, Taillandier P (2017) A Simple-to-use BDI
825 architecture for Agent-based Modeling and Simulation. In: Jager W, Verbrugge R, Flache A,
826 de Roo G, Hoogduin L, Hemelrijk C (eds) *Advances in Social Simulation 2015*. *Advances in*
827 *Intelligent Systems and Computing*, 528 Springer, Cham. [https://doi.org/10.1007/978-3-319-](https://doi.org/10.1007/978-3-319-47253-9_2)
828 [47253-9_2](https://doi.org/10.1007/978-3-319-47253-9_2)

829 Chuang A, Peterson CR (2016) Expanding population edges: Theories, traits, and trade-offs.
830 *Global Change Biology*, 22(2): 494–512. <https://doi.org/10.1111/gcb.13107>

831 Clobert J, Baguette M, Benton TG, Bullock JM (2012) *Dispersal Ecology and Evolution*.
832 Oxford University Press (UK): 1-498. [https://global.oup.com/academic/product/dispersal-](https://global.oup.com/academic/product/dispersal-ecology-and-evolution-9780199608904?cc=nc&lang=en&#)
833 [ecology-and-evolution-9780199608904?cc=nc&lang=en&#](https://global.oup.com/academic/product/dispersal-ecology-and-evolution-9780199608904?cc=nc&lang=en&#)

834 Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: a null model for
835 biological invasions. *Biological Invasions* 8: 1023–1037. [https://doi.org/10.1007/s10530-005-](https://doi.org/10.1007/s10530-005-3735-y)
836 [3735-y](https://doi.org/10.1007/s10530-005-3735-y)

837 Crespin L, Duplantier JM, Granjon L (2012) Demographic aspects of the island syndrome in
838 two Afrotropical *Mastomys* rodent species. *Acta Oecologica* 39: 72-79.
839 <https://doi.org/10.1016/j.actao.2012.01.002>

840 Crespin L, Papillon Y, Abdoulaye D, Granjon L, Sicard B (2008) Annual flooding, survival
841 and recruitment in a rodent population from the Niger River plain in Mali. *Journal of Tropical*
842 *Ecology* 24: 375-386. <http://dx.doi.org/10.1017/S0266467408005105>

843 Daly EZ, Chabrierie O, Massol F, Facon B, Hess MCM, Tasiemski A, Grandjean F, Chauvat
844 M, Viard F, Forey E, Folcher L, Buisson E, Boivin T, Baltora-Rosset S, Ulmer R, Gibert P,
845 Thiébaud G, Pantel JH, Heger T, Richardson DM, Renault D (2023) A synthesis of biological
846 invasion hypotheses associated with the introduction–naturalisation–invasion continuum.
847 *Oikos* e09645. <https://doi.org/10.1111/oik.09645>

848 Estrada A, Morales-Castilla I, Caplat P, R Early (2015) Usefulness of Species Traits in
849 Predicting Range Shifts. *Trends Ecology Evolution* 31(3): 190-203.
850 <http://dx.doi.org/10.1016/j.tree.2015.12.014>

851 Granjon L, Bâ K, Diagne C, Ndiaye A, Piry S, Thiam M (2019) La communauté des petits
852 rongeurs du Ferlo : tendances historiques et caractéristiques du peuplement actuel. In Boëtsch

- 853 G, Duboz P, Guissé A, Sarr P (Eds.) La Grande Muraille Verte, une réponse africaine au
854 changement climatique. CNRS (Paris): 161-177.
- 855 Granjon L, Duplantier JM (2009) Les rongeurs de l'Afrique sahélo-soudanienne. IRD Editions,
856 Publications Scientifiques du Muséum - Collection Faune et Flore tropicales 43, ISBN 978-2-
857 7099-1675-2 :1-242. https://horizon.documentation.ird.fr/exl-doc/pleins_textes/ed-09-10/010048662.pdf
- 858
- 859 Greenwood PJ, Harvey PH, Perrins CM (1979) The role of dispersal in the Great Tit (*Parus*
860 *major*) : the causes, consequences and heritability of natal dispersal. Journal of Animal Ecology,
861 48: 123–142. <https://doi.org/10.2307/4105>
- 862 Grimm V, Berger U, Bastiansen F, Eliassen S, Ginot V, Giske J, Goss-Custard J, Grand T,
863 Heinz S, Huse G, Huth A, Jepsen J, Jorgensen C, Mooij W, Muller B, Pe'er G, Piou C,
864 Railsback S, Robbins A, Robbins M, Rossmannith E, Rnger N, Strand E, Souissi S, Stillman R,
865 Vabo R, Visser U, DeAngelis DL (2006) A standard protocol for describing individual-based
866 and agent-based models. Ecological Modelling, 198: 115–126.
867 <https://doi.org/10.1016/j.ecolmodel.2006.04.023>
- 868 Grimm V, Berger U, DeAngelis DL, Polhill JG, Giske J, Railsback SF (2010) The ODD
869 protocol: A review and first update, Ecological Modelling, 221: 2760–2768.
870 <https://doi.org/10.1016/j.ecolmodel.2010.08.019>
- 871 Grimm V, Railsback S (2005) Individual-based Modeling and Ecology. Princeton University:
872 1-485. [https://press.princeton.edu/books/paperback/9780691096667/individual-based-](https://press.princeton.edu/books/paperback/9780691096667/individual-based-modeling-and-ecology)
873 [modeling-and-ecology](https://press.princeton.edu/books/paperback/9780691096667/individual-based-modeling-and-ecology)
- 874 Hanski I, Gilpin M (1991) Metapopulation dynamics: brief history and conceptual domain. In:
875 Metapopulation Dynamics: Empirical and Theoretical Investigations (Gilpin M, Hanski I. eds.)
876 Academic Press (San Diego): 3–16. <https://doi.org/10.1111/j.1095-8312.1991.tb00548.x>
- 877 James ME, Kalluri SNV (1994) The Pathfinder AVHRR land data set: An improved coarse
878 resolution data set for terrestrial monitoring. International Journal of Remote Sensing 15(17):
879 3347-3363. <https://doi.org/10.1080/01431169408954335>
- 880 Jobard I, Chopin F, Berges JC, Roca R (2011) An intercomparison of 10-day satellite
881 precipitation products during West African monsoon, International Journal of Remote Sensing
882 32(9): 2353-2376. <http://dx.doi.org/10.1080/01431161003698286>
- 883 Koenig WD, VanVuren D, Hooge PN (1996) Detectability, philopatry, and the distribution of
884 dispersal distances in vertebrates. Trends in Ecology and Evolution 11: 514–517.
885 [https://doi.org/10.1016/S0169-5347\(96\)20074-6](https://doi.org/10.1016/S0169-5347(96)20074-6)
- 886 Kupfer JA, Malanson GP, Franklin SB (2006) Not seeing the ocean for the islands: the
887 mediating influence of matrix-based processes on forest fragmentation effects. Global Ecology
888 and Biogeography 15: 8 – 20. <https://doi.org/10.1111/j.1466-822X.2006.00204.x>
- 889 Le Borgne J (1990) La dégradation actuelle du climat en Afrique, entre Sahara et Équateur. In
890 Richard, JF La dégradation des paysages en Afrique de l'Ouest, La Documentation française-
891 PUD (Dakar) : 17-36. [https://horizon.documentation.ird.fr/exl-](https://horizon.documentation.ird.fr/exl-doc/pleins_textes/pleins_textes_7/b_fdi_03_01/35482.pdf)
892 [doc/pleins_textes/pleins_textes_7/b_fdi_03_01/35482.pdf](https://horizon.documentation.ird.fr/exl-doc/pleins_textes/pleins_textes_7/b_fdi_03_01/35482.pdf)
- 893 Lindström T, Brown GP, Sisson SA, Phillips BL, Shine R (2013) Rapid shifts in dispersal
894 behavior on an expanding range edge. Proceedings of the National Academy of Sciences
895 110(33): 13452-13456. <https://www.pnas.org/doi/full/10.1073/pnas.1303157110>
- 896 Llewelyn J, Phillips BL, Alford RA, Schwarzkopf L, Shine R (2010) Locomotor Performance
897 in an Invasive Species: Cane Toads from the Invasion Front Have Greater Endurance, but Not

- 898 Speed, Compared to Conspecifics from a Long-Colonised Area. *Oecologia*, 162(2): 343–348.
899 <http://www.jstor.org/stable/40540172>
- 900 Lombaert E, Estoup A, Facon B, Joubard B, Gregoire JC, Jannin A, Blin A, Guillemaud T
901 (2015) Rapid increase in dispersal during range expansion in the invasive ladybird *Harmonia*
902 *axyridis*. *Journal of Evolutionary Biology* 27: 508–517. <https://doi.org/10.1111/jeb.12316>
- 903 MacKay JWB, Russell JC, Clout MN, Murphy, EC, Hauber ME (2019) See how they run:
904 increased ranging behavior counters potential Allee effects in experimentally introduced house
905 mice on an island. *Biological Invasions* 21: 1669–1681. <https://doi.org/10.1007/s10530-019-01927-9>
- 906
- 907 Malange J, Izar P, Japyassú H (2016) Personality and behavioural syndrome in *Necromys*
908 *lasiurus* (Rodentia: Cricetidae): Notes on dispersal and invasion processes. *Acta Ethologica*
909 19(3): 189–195. <https://doi.org/10.1007/s10211-016-0238-z>
- 910 Mathieu C, Lozet J (2011) Dictionnaire encyclopédique de science du sol, Lavoisier (Paris) :1-
911 733.
- 912 Nomao A, Gautun JC (2001) Dynamique de l'abondance et reproduction de *Gerbillus nigeriae*
913 (Rodentia, Gerbillinae) dans la ferme de Kollo (Niger). In Denys C, Granjon L, Poulet A (eds)
914 African Small Mammals, IRD coll. Colloques et séminaires (Paris): 481-498.
915 <https://www.documentation.ird.fr/hor/fdi:010028478>
- 916 Pettit LJ, Greenlees MJ, Shine R (2016) Is the enhanced dispersal rate seen at invasion fronts a
917 behaviourally plastic response to encountering novel ecological conditions? *Biology Letters* 12
918 20160539. <https://doi.org/10.1098/rsbl.2016.0539>
- 919 Phillips BL, Brown GP, Shine R (2010). Evolutionarily accelerated invasions: the rate of
920 dispersal evolves upwards during the range advance of cane toads. *Journal of Evolutionary*
921 *Biology* 23(12): 2595-2601. <https://doi.org/10.1111/j.1420-9101.2010.02118.x>
- 922 Phillips BL, Brown GP, Webb JK, Shine R (2006) Invasion and the evolution of speed in toads.
923 *Nature* 439: 803–803. <https://doi.org/10.1038/439803a>
- 924 Phillips BL (2015) Evolutionary processes make invasion speed difficult to predict. *Biological*
925 *Invasions* 17: 1949–1960. <http://dx.doi.org/10.1007/s10530-015-0849-8>
- 926 Poulet AR (1982) Pullulation de rongeurs dans le Sahel: mécanismes et détermination du cycle
927 d'abondance de *Taterillus pygargus* et d'*Arvicanthis niloticus* (Rongeurs, Gerbillidés et
928 Muridés) dans le Sahel du Sénégal de 1975 à 1977. PHD thesis, Université Paris VI (Paris).
- 929 Poulet AR (1983) Influence de la prédation sur la dynamique de population de *Taterillus*
930 *pygargus* dans la savane arbustive sèche du nord du Sénégal. *Annales du Musée royal de*
931 *l'Afrique centrale, Sciences Zoologiques* 237: 179-191.
- 932 Ramanantoanina A, Ouhinou A, Hui C (2014) Spatial assortment of mixed propagules explains
933 the acceleration of range expansion. *PLoS ONE* 9(8): e103409.
934 <https://doi.org/10.1371/journal.pone.0103409>
- 935 Ronce O (2007) How does it feel to be like a rolling stone? Ten Questions about Dispersal
936 Evolution. *Annual Review of Ecology, Evolution, and Systematics* 38: 231-253.
937 <https://doi.org/10.1146/annurev.ecolsys.38.091206.095611>
- 938 Roquet D (2008) Leaving to Last Better: Migration as an Answer to the Drought in Senegal?
939 *Space Population Societies* 2008/1: 37-53. <https://doi.org/10.4000/eps.2374>
- 940 Schmitz J (2007) Les migrations saisonnières des pêcheurs subalbe dans la réserve de biosphère
941 du delta du Saloum. In Weigel JY, Féral F, Cazalet B Sci Eds. *Les aires marines protégées*

942 d'Afrique de l'Ouest. Gouvernance et politiques publiques. Presses Universitaires de Perpignan
943 :76-82. <https://core.ac.uk/download/pdf/39839902.pdf>

944 Sicard B, Papillon Y (1996) Water redistribution and the life cycle of Sahelian rodents.
945 Mammalia 60: 607-617.
946 [https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=d2e767ec2a3e6b92fe7ac7](https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=d2e767ec2a3e6b92fe7ac7674561ff1009b692bf)
947 [674561ff1009b692bf](https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=d2e767ec2a3e6b92fe7ac7674561ff1009b692bf)

948 Sicard B (2013) *Gerbillus nigeriae*, Nigerian Gerbil. In Happold DCD (Ed.) Mammals of Africa
949 (III) Bloomsbury (London) : 120-121.

950 Sicard B, Fuminier F (1996) Environmental cues and seasonal breeding patterns in Sahelian
951 rodents. Mammalia 60(4): 667-675.
952 [https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=e3a9f75b58e7d793f9cf3eb](https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=e3a9f75b58e7d793f9cf3eb7885a1e9e80a359cf)
953 [7885a1e9e80a359cf](https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=e3a9f75b58e7d793f9cf3eb7885a1e9e80a359cf)

954 Szabó S, Peeters ETHM, Várbiro G, Borics G, Láukács BA (2019) Phenotypic plasticity as a
955 clue for invasion success of the submerged aquatic plant *Elodea nuttallii*. Plant Biology 21: 54–
956 63. <https://doi.org/10.1111/plb.12918>

957 Thiam M, Atteynine SA, Traoré S, Duplantier JM, Maurel D, Sicard B (2011) Capacity for
958 water conservation in invasive (*Gerbillus nigeriae*) and declining rodents (*Taterillus pygargus*
959 and *Taterillus gracilis*) that exhibit climate-induced distribution changes in Senegal. Journal of
960 Arid Environments 75(11) : 998-1007. <http://dx.doi.org/10.1016/j.jaridenv.2011.04.029>

961 Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, Musche M, Conradt L
962 (2001). Ecological and evolutionary processes at expanding range margins. Nature 411: 577–
963 581. <https://doi.org/10.1038/35079066>

964 Travis MJJ, Dytham C 2002 Dispersal evolution during invasions. Evolutionary Ecology
965 Research, 4: 1119-1129.

966 Travis MJJ, Harris CM, Park KJ, Bullock JM (2011) Improving prediction and management of
967 range expansions by combining analytical and individual-based modelling approaches.
968 Methods in Ecology and Evolution 2: 477–488. [https://doi.org/10.1111/j.2041-](https://doi.org/10.1111/j.2041-210X.2011.00104.x)
969 [210X.2011.00104.x](https://doi.org/10.1111/j.2041-210X.2011.00104.x)

970 Whitmee S, Orme CDL (2013) Predicting dispersal distance in mammals: a trait-based
971 approach. Journal of Animal Ecology 82: 211–221. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2656.2012.02030.x)
972 [2656.2012.02030.x](https://doi.org/10.1111/j.1365-2656.2012.02030.x)

973 Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM (2009) Something in the way
974 you move: dispersal pathways affect invasion success. Trends in Ecology and Evolution 24:
975 136-144. <https://doi.org/10.1016/j.tree.2008.10.007>

976

977 **Supplementary material: Estimation of the length of the breeding season based on rainfall**
978 **from 1982 to 2013**

979 Gerbil reproduction is sensitive to food (plant) resources, themselves linked to rainfall (Sicard
980 and Fuminier, 1996; Sicard and Papillon, 1996) that directly influences the duration of the
981 breeding season at the population scale. We connected the length of the breeding season with
982 the rainfall intensity using five categories of yearly raining intensity (Table 4).

983 Table 4 Intervals used to estimate the length of the breeding season according to annual
984 rainfall.

Rainfall (mm / year)	< 250	[250, 319]	[320, 399]	[400,499]	>= 500
Length of the breeding season (months)	1	2	3	4	5

985
986 Following this partition we computed the length of the breeding season during the study period
987 (Table 5) using the observed rainfall databases from GPCC and TRM 3B82 (Jobard et al., 2011)
988 available at <http://richardis.univ-paris1.fr/precip/index.html>.

989 Table 5 Estimation of the length of the breeding season based on rainfall from 1982 to 2013

year	first month without rain (GPCC/TR M 3B82)	rainfall (mm)	estimated length of breeding period	Estimated end of breeding period
1982	nov.	274	2	jan.
1983	nov.	210	1	dec.
1984	nov.	254	1	dec.
1985	nov.	319	2	jan.
1986	nov.	311	2	jan.
1987	nov.	302	2	jan.
1988	nov.	371	3	feb.
1989	nov.	382	3	feb.
1990	nov.	270	2	jan.
1991	nov.	273	2	jan.
1992	dec.	305	2	feb.
1993	dec.	361	3	mar.
1994	nov.	355	3	feb.
1995	nov.	382	3	feb.
1996	nov.	307	2	jan.
1997	nov.	297	2	jan.
1998	nov.	313	2	jan.
1999	nov.	445	4	mar.
2000	dec.	380	3	mar.
2001	dec.	337	3	mar.
2002	nov.	260	2	jan.
2003	nov.	458	4	mar.
2004	dec.	327	3	mar.
2005	nov.	453	4	mar.
2006	nov.	344	3	feb.
2007	dec.	318	2	feb.
2008	nov.	400	4	mar.
2009	dec.	454	4	apr.
2010	oct.	511	5	mar.
2011	nov.	297	2	jan.
2012	nov.	455	4	mar.
2013	dec.	412	4	apr.

990

991