View metadata, citation and similar papers at core.ac.uk

brought to you by CORE

provided by HAL-CIRAD

Host habitat patchiness and the distance decay of similarity among gastro-intestinal nematode communities in two species of Mastomys (southeastern Senegal)

Carine Brouat, Jean-Marc Duplantier, A. Loiseau, M. Kane, K. Bâ

► To cite this version:

Carine Brouat, Jean-Marc Duplantier, A. Loiseau, M. Kane, K. Bâ. Host habitat patchiness and the distance decay of similarity among gastro-intestinal nematode communities in two species of Mastomys (southeastern Senegal). Oecologia, Springer Verlag, 2007, 152 (4), pp.715-720. <10.1007/s00442-007-0680-8>. <ird-00195246>

HAL Id: ird-00195246

http://hal.ird.fr/ird-00195246

Submitted on 10 Dec 2007

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Population genetic structure of two ecologically distinct multimammate rats: the commensal *Mastomys natalensis* and the wild *M. erythroleucus* in south-eastern Senegal

C. BROUAT[1], A. LOISEAU[1], M. KANE[2], K. BÂ[2], J.-M. DUPLANTIER[2]

[1] UMR *IRD (UR 022)-INRA-CIRAD, Centre de Biologie et de Gestion des Populations, Campus International de Baillarguet, CS 30016, 34988 Montferrier/ Lez cedex, France*

[2] *IRD (UR 022), Centre de Biologie et de Gestion des Populations, BP 1386, Dakar, CP 18 524, Senegal*

Keywords: Mastomys; rodent; habitat patchiness; genetic structure; commensal habitat; microsatellite

Corresponding author: C. Brouat, CBGP, Campus International de Baillarguet, CS 30016, 34988 Montferrier/ Lez cedex, France; Fax: +33 4 99 62 33 45; E-mail: brouat@mpl.ird.fr

Running title: Population genetic structure of *Mastomys*

17 **Abstract**

18 Using the same set of microsatellite markers, we compared the population genetic structure of two
19 *Mastomys* species, one being exclusively commensal in south-eastern Senegal, and the other being
20 continuously distributed outside villages in this region. Both species were sampled in the same
21 landscape context and at the same spatial scale. According to the expectations based on the degree of
22 habitat patchiness (which is higher for commensal populations in this rural area), genetic diversity was
23 lower and genetic differentiation was higher in commensal populations of *M. natalensis* than in wild
24 populations of *M. erythroleucus*. Contrasting estimates of effective dispersal and current migration
25 rates corroborates previous data on differences in social structure between the two species. Isolation by
26 distance analyses showed that human-mediated dispersal is not a major factor explaining the pattern of
27 genetic differentiation for *M. natalensis*, and that gene flow is high and random between *M.*
28 *erythroleucus* populations at the spatial scale considered.

29 **Introduction**

30

31 Numerous interacting ecological and evolutionary processes determine genetic diversity and structure
32 in natural populations. Habitat characteristics may influence genetic structure *via* their effects on gene
33 flow among populations (Frankham *et al.* 2002), and on effective population sizes (*Ne*; Wright 1931)
34 and thus the strength of genetic drift. Considered in their environmental context, species characteristics
35 such as dispersal abilities, mating system or sex-ratio determine the impacts of mutation, genetic drift
36 and selection on genetic structure.

37 Habitat characteristics are so different in commensal and non-commensal environments that
38 synanthropic mammals are expected to have particular life-history traits in order to persist (Pocock *et*
39 *al.* 2004). Although several species of small mammals intermittently make use of the shelter or food
40 provided by living commensally (e.g. Marsh & Harris 2000), only a very few can persist entirely in
41 human settlements (Pocock *et al.* 2004). Among rodents, they include some of the world's most
42 cosmopolitan species, such as the house mice (*Mus musculus domesticus* Rutty) and the rats (*Rattus*
43 *rattus* L. and *R. norvegicus* Berkenhout), but also the multimammate rats of the genus *Mastomys* in
44 Africa (Granjon *et al.* 1987; Leirs in press). One important habitat characteristic of human settlements
45 in rural areas is their patchy distribution in the landscape. The expected outcomes of various island or
46 metapopulation models diverge in their conclusions about the effect of patchiness on genetic structure
47 (Aars *et al.* 2006). In most cases however, subdivision of natural populations is likely to induce some
48 loss of intra-population genetic variability, but the magnitude of the negative effects would be heavily
49 dependent on local demography (Whitlock & Barton 1997). In commensal populations, the few
50 existing data do not give a clear picture about the effect of patchiness on genetic structure. The
51 commensal habitat is considered to be an environment of high quality in which food is constantly

52 provided and the habitat protected, that is where interspecific competition, predation and climatic
53 pressures are strongly reduced (Boursot *et al.* 1993). Environmental stability and resource permanence
54 may imply higher densities than in wild populations, such as in house mice (Pocock *et al*. 2005). High
55 patch quality may reinforce the effects of habitat patchiness in reducing dispersal rates and increasing
56 philopatry (Lin *et al.* 2006). Alternatively, human transports sometimes increase migration for
57 commensal species between distant human settlements (Britton-Davidian 1990; McKinney 2006).
58 Only few studies have empirically investigated the effect of patchiness in synanthropic populations
59 on population genetic structure (Pocock *et al.* 2004). Two alternative empirical approaches may be
60 chosen to this end. One may be to work on commensal and wild populations of the same species, but in
61 different locations in order to ensure that wild and commensal populations are not connected by gene
62 flow. In this case, landscape contexts are not rigorously comparable. The other approach may be to
63 work on two closely related species living in the same area, one having commensal and the other
64 having wild populations. The effects of commensalism and of species identity are thus not formally
65 disentangled, and the observed differences in genetic structure between both species may result from a
66 complex interplay with population history or biogeography. Separating these effects is challenging but
67 the comparative analysis of genetic structure may be a first step to carefully examine each alternative
68 hypothesis (population history, geography, or habitat) that explain genetic patterns, and thus to provide
69 demographic and ecological hypotheses that can be further tested (Matocq *et al.* 2000). Another
70 challenge in species comparison is to have common genetic markers on both species, to avoid locus
71 effects on genetic structure. This implies cross-priming which can lead to null alleles in one or both
72 species when using microsatellites. Nevertheless, recent methods have been developed to account for
73 the effects of null alleles in genetic analyses (Chapuis 2006; Chapuis & Estoup 2006; Wagner *et al.*
74 2006).

75 We examine population genetic diversity and structure of two closely related species that coexist in
76 the same region, one being exclusively commensal, and the other living outside villages. *Mastomys*
77 *natalensis* and *M. erythroleucus* are morphologically similar, but chromosomally well differentiated
78 species (Granjon *et al.* 1997). These sibling species diverged during the last 3 Myr (Lecompte *et al.*
79 2002). In south-eastern Senegal, *M. natalensis* is commensal, living exclusively inside villages
80 (Duplantier *et al.* 1997). Commensal specialization in *M. natalensis* seems to be associated with
81 extreme locations inside its geographic range (Duplantier *et al.* 1990b). South-eastern Senegal
82 represents the northern limit of the distribution area of this species (Figure 1), which is largely
83 distributed all over sub-Saharan Africa (Granjon *et al.* 1997), being either commensal or wild.
84 *Mastomys erythroleucus* is distributed in sahelian regions (Leirs in press), and is found in various kinds
85 of habitats (including villages) everywhere in Senegal (Figure 1). In the south-eastern part of the
86 country, *M. erythroleucus* has a continuous distribution across wild habitats but is present only
87 occasionally inside villages (Duplantier *et al.* 1997). The ecology of both species is well known due to
88 the considerable work conducted since the eighties on their population dynamics (Hubert 1982; Leirs *et*
89 *al.* 1993**;** Leirs *et al.* 1997; Julliard *et al.* 1999), and ecology (Granjon *et al.* 1987; Granjon &
90 Duplantier 1993; Duplantier *et al.* 1996), but the only available studies on their population genetic
91 structure are based on allozyme markers (Duplantier *et al.* 1990a; Smit *et al.* 2001). Both are small
92 rodents (mean adult weight of 40-50 g), with short generation time (individuals rarely live for more
93 than 12 months), high reproductive rates (mean litter size of 10-12 for *M. erythroleucus* and *M.*
94 *natalensis* respectively in Senegal and in Tanzania; mean litter size of 6.5 for commensal *M. natalensis*
95 in Senegal [Duplantier *et al.* 1996; Leirs in press]) and a seasonal reproduction in wild populations
96 (Leirs in press). Previous behavioural and ecological studies suggested that commensal and wild
97 populations of *Mastomys* may differ in their social structure (Granjon, Duplantier & Cassaing 1987;

98 Granjon & Duplantier 1993). Commensal populations of *M. natalensis* were characterized by a
99 strongly female-biased sex ratio and males were very aggressive toward each others compared to wild
100 populations of *M. erythroleucus* (Granjon & Duplantier 1993).

101 As well as habitat patchiness, unbalanced sex-ratio and mating systems can lower the effective
102 population size (Futuyma 1986; Storz *et al.* 2001). Basic population genetics theory also predicts that
103 the effective population size will tend to be smaller in edge than in core populations of a given species,
104 because of lower abundance and higher temporal variability in abundance at extreme locations
105 representing less favourable environments (Vucetich & Waite 2003). We thus made the prediction that
106 genetic diversity would be lower, and mean relatedness and genetic differentiation would be higher in
107 commensal populations of *M. natalensis* than in wild populations of *M. erythroleucus*. We expected to
108 find an isolation by distance pattern in *M. erythroleucus*, due to frequent genetic exchange between
109 neighbouring subpopulations in this continuously distributed species, and no pattern of isolation by
110 distance in *M. natalensis* due to reduced or distance-independent (in the case of human transport)
111 dispersion events between human settlements. We examined genetic structure using F_{ST} measures for
112 long-term gene flow (effective dispersal) and assignment tests for current first-generation migrants
113 (Wilson & Rannala 2003). Using the same set of microsatellite markers, and carefully taking into
114 account the problem of null alleles, our research provides a statistical comparison of population genetic
115 structure of both species at the same spatial scale and in the same landscape context.

116

117 **Materials and methods**

118

119 *Study area and sampling*

120 The study area is located in south-eastern Senegal, inside the soudano-guinean biogeographic zone,
121 and covers about 1300 km² around the town of Kedougou (12°33'23"N; 12°10'17"W). The landscape of
122 this low altitude area (60-450 m high) mainly comprises large areas of cattle-grazed savannas,
123 interrupted by riparian forests along the streams. Near the villages, temporary fields (millet, sorghum)
124 are cultivated during the rainy season, and at a distance large areas are now cultivated with cotton. The
125 mean annual rainfall is 1200 mm (period 1991-2000), with one annual rainy season from June to
126 October.

127 Fieldwork was conducted during three weeks in January 2001 in the middle of the dry season.
128 Rodents were live-caught using Sherman and wire-meshed traps, and around 20 individuals of each
129 focus species were collected per trapping site. Ten villages (including a district of Kegoudou) were
130 chosen as trapping sites for *M. natalensis* (Fig. 1). Chosen villages had between 500 and 3000
131 inhabitants. The residential unit is a compound housing containing several huts distributed around a
132 court. The vast majority of dwellings are huts covered with thatched roofs. Inside the villages, traps
133 were set inside houses (two traps per house: one Sherman and one wire-meshed). Chosen villages were
134 separated from other human settlements by at least 5 km of wild habitat. In the fields or savannas
135 around each of these villages and at a maximum distance of 5 km from them, one trapping site was also
136 chosen for *M. erythroleucus* (Fig. 1). There, twenty wire-meshed traps were set along lines with a 10
137 meter-interval between consecutive traps (one to five lines of twenty traps per site, in order to catch at
138 least 20 individuals in three nights). The only potential barriers between trapping sites for *M.*
139 *erythroleucus* may be the Gambia River and its riparian forests (Fig. 1). Trapping sites, hereafter
140 referred to as "populations", were distant from each other's by 3.9 to 69 km for both species.
141
142 *Laboratory methods*

143

144 DNA was extracted from ear tissue using the PUREGENE DNA purification kit. Quantification of
145 genetic variation for each species was performed using the same 15 microsatellites (MH1, MH10,
146 MH188, MH3, MH39, MH80, MH105, MH133, MH146, MH174, MH206, MH216, MH30, MH52,
147 MH60) cloned from *Mastomys huberti* (Loiseau *et al.* in press). The polymerase chain reaction (PCR)
148 amplifications and electrophoresis of the fragments on polyacrylamide gels were carried out as
149 described in Loiseau *et al.* (in press).

150

151 *Detection of null alleles*

152 Deviations from Hardy-Weinberg Equilibrium (HWE) and genotypic linkage disequilibria were
153 tested by locus and by population using the Markov chain method implemented in GENEPOP 3.4
154 (Raymond and Rousset 1995). Corrections for multiple tests were performed using the false discovery
155 rate (fdr) approach according to Benjamini & Hochberg (1995), and implemented in the QVALUE
156 package of R.

157 As null genotypes were found in each species, the presence of null alleles was suspected. Every
158 individual that was successfully genotyped at some loci but not at some others was re-amplified once
159 by simple PCR (to avoid primer competition) for each failed locus. We used MICRO-CHECKER 2.2.3
160 (Van Oosterhout *et al.* 2004) to evaluate whether heterozygote deficiencies may be explained by the
161 existence of null alleles. We then used the software FREENA (available at
162 http://www.montpellier.inra.fr/URLB; Chapuis & Estoup 2006) to estimate null allele frequencies (*a*)
163 for each population and locus following Dempster *et al.* (1977). Null allele frequencies per population
164 were compared between species with a generalized linear model (binomial distribution and logit link)
165 sing the software SAS v. 9.1 (SAS 2002).

166

167 *Intrapopulation genetic diversity*

168 Mean numbers of alleles per locus, observed (H_O) and expected (H_E) heterozygosities (Nei 1987)
169 were calculated over all loci at each sampling location using the program POP100GENE 1.1.02
170 (http://www.ensam.inra.fr/URLB) on the original data sets, excluding null genotypes. The allelic
171 richness (*r*, a measure of the number of alleles independent of sample size) was calculated using the
172 rarefaction procedure implemented in FSTAT 2.9.3.2 (Goudet 2001) for a minimum sample size of 16
173 diploid individuals in both species. Null alleles can result in an underestimation of statistics
174 traditionally used to summarize genetic variation within populations. However, H_E and *r* are little
175 affected by mean null allele frequencies ($\bar{a}$) below 0.15 (Chapuis 2006) such as those that we obtained
176 (see results), rendering possible their comparison between species using FSTAT (1 000 permutations).

177 Failure to correct for the presence of null alleles in microsatellite data can produce badly biased
178 estimates of relatedness. Alternatively, dropping data from problem loci altogether can significantly
179 discard valuable information (Wagner et al. 2006). A new approach has been proposed for estimating
180 relatedness from data sets that include null alleles, which was implemented in the software *ML-Relate*
181 (Kalinowski *et al.* 2006). This approach was shown to perform well on simulated data, and better than
182 the alternative strategies of excluding loci or not correcting data (Wagner et al. 2006) for mean null
183 allele frequencies up to 0.4. We thus calculated maximum likelihood estimates of relatedness (ML-*R*)
184 accommodated for null alleles using the software *ML-Relate*. A Wilcoxon test was then performed to
185 compare ML-*R* values between species using the software SAS.

186

187 *Population differentiation*

188 Genotypic divergence among populations for all loci and population pairs was tested using Markov
189 chain methods in GENEPOP 3.4 (Raymond and Rousset 1995) on the original datasets. Corrections for
190 multiple tests were performed using the fdr approach.

191 Null allele frequencies may conduct to an overestimation of population differentiation (Chapuis &
192 Estoup, 2006). F_{ST} were estimated following Weir (1996) using FREENA, with the so-called ENA (for
193 Excluding Null Alleles) method described in Chapuis & Estoup (2006). This method was found to
194 efficiently correct for the bias induced by null alleles and provide unbiased estimates of F_{ST}, whatever
195 the mean null allele frequency. F_{ST} estimated with FREENA will be called hereafter F_{ST}^{ENA}. Ninety-five
196 percent confidence intervals (CI) for mean F-statistics were generated by bootstrap resampling across
197 loci.

198 Theoretical considerations showed that the level of genetic differentiation between populations is
199 maximized by homozygosity (Hedrick 1999). For each species, a standardized measure for F_{ST} was
200 calculated by using the software RecodeData v. 0.1 (Meirmans 2006), which permit to recode the data
201 such that every population of each species only contains unique alleles (no shared alleles between
202 populations). The recoded datasets were then used to calculate the $F_{ST(max)}^{ENA}$ for each species.
203 Standardized F'_{ST}^{ENA} were then calculated following Hedrick (2005) as $F'_{ST}^{ENA} = F_{ST}^{ENA} / F_{ST(max)}^{ENA}$.

204 Under a model of isolation by distance, genetic distance between populations is expected to
205 increase with geographical distance. Isolation by distance was analysed by regressing pairwise
206 estimates of F_{ST}^{ENA} /(1 .- F_{ST}^{ENA}) against ln-distance between trap sites (Rousset 1997). Mantel tests
207 were performed to test the correlation between matrices of genetic differentiation and Euclidean
208 geographical distance between sampled populations using GENEPOP 3.4. (10 000 permutations)
209 (Raymond & Rousset 1995). Ninety-five percent confidence intervals for slopes of the relationships

210 were obtained using an adapted (Leblois *et al.* 2003) nonparametric ABC bootstrap procedure from
211 DiCiccio & Efron (1996).
212
213 *Assignment tests*
214 The effect of null alleles on assignment tests has never been investigated. We have thus decided
215 to perform assignment tests on both the original datasets and the datasets that had been corrected for
216 null alleles using the so-called INA (for including null alleles) traditional method described in Chapuis
217 & Estoup (2006) and implemented in FREENA. Whereas null alleles can involve several alleles, the
218 INA method attributes them a single allelic state (the same for all the loci and all the populations).
219 Individual assignment tests using the frequency method of Paetkau *et al.* (1995) were performed
220 using the software GENECLASS2 (Piry *et al.* 2004). The frequency method is the most frequently
221 employed in empirical studies against other assignment criterions (Guinand *et al.* 2002). GENECLASS2
222 uses multilocus genotypes to identify putative first-generation immigrants within each sampled
223 population and the most likely source of these immigrants, on the basis of the likelihood that the
224 individual's genotype originated in the population from which it was sampled. The statistical criterion
225 computed was the likelihood of the individual genotype within the population where the individual has
226 been sampled (L_home), as recommended when all putative source populations for immigrants have
227 not been sampled (Piry *et al.* 2004). A probability of belonging to each of the potential population was
228 calculated for every individual sampled (10 000 simulated individuals) following the simulation
229 algorithm of Paetkau *et al.* (2004), and using the critical probability value $\alpha = 0.01$. This resampling
230 method was found to perform better than other ones that generally result in an excess of resident
231 individuals being excluded (Piry *et al.* 2004). Relative migrant rates were compared between both
232 species for each type of dataset using an exact test of Fisher. The estimated migration rate was

233 calculated as in Paetkau *et al.* (2004) by dividing the total number of individuals falling past the critical
234 value minus the number of expected errors by the total number of sampled individuals. The genetic
235 distance D_{LR} (Paetkau *et al.* 1997) was also calculated for each pair of sampled populations in each
236 species, as this distance was shown to perform best at predicting power of assignment tests (Paetkau *et*
237 *al.* 2004).
238
239 **Results**
240
241 A total of 225 *M. natalensis* and 310 *M. erythroleucus* were collected at the 20 trap sites. One
242 locality (FA) was largely over-sampled for *M. erythroleucus* (80 sampled individuals), as we wanted to
243 find another morphologically sibling species of *Mastomys* (*M. huberti*) that was expected in this site on
244 the basis of previous sampling (Duplantier *et al.* 1990b). Nevertheless, all the *Mastomys* sampled in
245 this locality and submitted to a molecular test for species identification (Lecompte *et al.* 2002) were
246 determined as *erythroleucus*, except one individual in FAe (probably hybrid) that has been excluded
247 from the analyses.
248
249 *Null alleles*
250 Among the 15 loci, seven (MH1, MH10, MH80, MH105, MH146, MH206 and MH30) for *M.*
251 *natalensis* and ten (MH1, MH10, MH3, MH80, MH105, MH133, MH146, MH30, MH52, and MH60)
252 for *M. erythroleucus* showed significant heterozygote deficiencies (Table 1). Using MICRO-CHECKER,
253 we showed that the most probable hypothesis to explain heterozygote deficiencies in these loci was the
254 existence of null alleles. Mean estimated null allele frequencies were moderate in both species (*M.*
255 *natalensis*: mean frequency = 0.09 on loci not in HWE; mean frequency overall loci = 0.06; *M.*

256 *erythroleucus*: mean frequency = 0.05 on loci not in HWE; mean frequency overall loci = 0.04) (Table
257 2), however some loci have relatively strong mean null allele frequencies (0.14 for MH1 and 0.27 for
258 MH10 in *M. natalensis*, 0.10 for MH146 in *M. erythroleucus*). Null allele frequencies were not
259 significantly different between species with all loci taken into account ($\chi^2(1) = 0.0007$; $P = 0.98$), or
260 with only loci with significant heterozygote deficiencies ($\chi^2(1) = 1.14$; $P = 0.28$).
261
262 *Intrapopulation genetic diversity*
263 Basic statistics summarizing genetic diversity observed at each trapping site for the two *Mastomys*
264 species are presented in Table 2. Although all microsatellite loci were polymorphic in all local samples,
265 genetic variability differed among loci. The number of alleles per locus over all populations ranged
266 from five to 26 for *M. natalensis* (mean number of alleles per locus = 13.0 ± 6.4) and from eight to 47
267 for *M. erythroleucus* (mean number of alleles per locus = 23.4 ± 11.7). Genetic diversity was higher for
268 *M. erythroleucus* than for *M. natalensis* (r, H_E, $P = 0.001$). Mean ML-*R* per population was higher in
269 *M. natalensis* (mean ML-*R* = 0.066 ± 0.017) than in *M. erythroleucus* (mean ML-*R* = 0.037 ± 0.012)
270 ($\chi^2(1) = 11.6$; $P = 0.0007$).
271 Of the 1050 exact tests performed in each species for genotypic disequilibria, eight for *M.*
272 *natalensis* and 35 for *M. erythroleucus* were significant at the 0.05 level after fdr correction. Significant
273 values involved different pairs of loci and occurred in different populations.
274
275 *Population differentiation*
276 Microsatellites revealed significant genotypic differentiation among populations both in *M.*
277 *natalensis* and *M. erythroleucus* ($P < 0.0001$ for each locus). After fdr correction, every pair of

278 sampled populations differed by at least 10 (for *M. natalensis*) or three (for *M. erythroleucus*)
279 significant (P < 0.05) pairwise genotypic tests of frequency differences by locus (Table 3). Pairwise
280 F_{ST}^{ENA} estimates ranged from 0.07 to 0.18 for *M. natalensis* (Table 3A), and from 0.01 to 0.07 for *M.*
281 *erythroleucus* (Table 3B). As indicated by the mutually exclusive 95% CI of the F_{ST}^{ENA} estimates, the
282 level of differentiation was significantly higher in *M. natalensis* (mean F_{ST}^{ENA} = 0.129; CI =[0.11;
283 0.14]) than in *M. erythroleucus* (mean F_{ST}^{ENA} = 0.027 CI =[0.02; 0.031]).
284 Standardized genetic differentiation was higher in *M. natalensis* ($F'_{ST}{}^{ENA}$ = 0.41; $F_{ST(max)}{}^{ENA}$=
285 0.31, CI = [0.25; 0.38]) than in *M. erythroleucus* ($F'_{ST}{}^{ENA}$ = 0.17, $F_{ST(max)}{}^{ENA}$= 0.15; CI = [0.10; 0.22]).
286
287 No pattern of isolation by distance was apparent for *M. erythroleucus* (Fig. 2; Mantel test: P = 0.44;
288 slope = 0.002). For *M. natalensis*, genetic differentiation was positively correlated with geographical
289 distance (Fig. 2; Mantel test: P = 0.0003; slope = 0.03). ABC bootstrap procedures gave non-
290 overlapping 95% CI for slopes between the two species (Figure 2).
291
292 *Assignment tests*
293 Thirteen (original dataset) and seven (INA correction) detected migrants were detected among the
294 225 individuals from *M. natalensis*, and 23 (original dataset) and 13 (INA correction) among the 310
295 individuals from *M. erythroleucus*. For both species, first-generation immigrants were thus less
296 numerous when the analysis was performed on the datasets corrected for null alleles. Nevertheless, all
297 the individuals detected in these analyses were also detected in those performed on the original
298 datasets, suggesting that the most conservative analyses were those realised on the corrected datasets.
299 Migration rate estimates (m) was lower in *M. natalensis* (original dataset: m = 0.048; INA correction:
300 m =0.021) than in *M. erythroleucus* (original dataset: m = *0.*064; INA correction: m = 0.032) (ratio

301 close to 3/4 for original data, close to 2/3 for the INA-corrected data). However, the proportions of
302 migrants were not significantly different between species (Test de Fisher: original dataset: $P = 0.60$;
303 INA correction: $P = 0.64$).

304 For every populations pairs, D_{LR} values were always higher in *M. natalensis* (mean $D_{LR} = 27.7$)
305 than in *M. erythroleucus* (mean $D_{LR} = 16.4$) indicating a better power to detect first-generation
306 migrants in the commensal species.

307

308 **Discussion**

309

310 Null alleles are frequent in cross-priming experiments, because of divergence time between species,
311 leading to mutations in the flanking microsatellite regions and thus poor primer annealing (Paetkau &
312 Strobeck 1995). Null alleles may overestimate population differentiation by reducing the estimates of
313 genetic diversity within populations (e.g., Paetkau and Strobeck 1995; Chapuis & Estoup 2006). We
314 have thus carefully taken into account all the possible bias relative to null alleles, particularly by using
315 recent methods developed to account for null alleles in genetic analyses. In our datasets, there is clearly
316 a locus effect on null allele frequencies per population (Table 2). The high variation of null allele
317 frequencies per locus per population could have been problematic if the aim of the study was to
318 conduct inter-population comparisons within species. This is however not the case as we have focused
319 our study on the interspecific comparison of the genetic estimates (and thus on mean values per
320 species).

321 Our main result is that genetic diversity was lower and that genetic differentiation was higher in *M.*
322 *natalensis* than in *M. erythroleucus*. Higher null allele frequencies in *M. natalensis* may not explain
323 the differences in genetic diversity, as the maximum decrease of genetic diversity related to null alleles

324 was shown to be only about 0.02 on H_E and r for mean null allele frequencies around 0.05 (Chapuis
325 2006). The ENA correction permitted us to have unbiased estimates of F_{ST} for both species (Chapuis &
326 Estoup 2006), and thus unbiased results concerning genetic differentiation and isolation by distance.
327 Assignment tests performed on datasets including or excluding null alleles showed the same tendencies
328 in species comparisons. Moreover, mean null allele frequencies were not significantly different
329 between species. All these reasons make us to feel confident about the robustness of our species
330 comparison.

331

332 The goal of this study was to examine the relationship between habitat type (wild/ commensal) and
333 the patterns of genetic diversity and structure across populations of two closely related *Mastomys*
334 species. In particular, we predicted that genetic diversity would be lower and differentiation would be
335 higher in commensal populations of *M. natalensis* than in wild populations of *M. erythroleucus*.

336 Population genetic diversity was high in both species, reaching the upper values of diversity levels
337 found in other Muridae with microsatellite markers (e.g., Dallas *et al.* 1995; Ehrich *et al.* 2001; Peakall
338 *et al.* 2003; Karanth *et al.* 2004; Berthier *et al.* 2005). The same tendency was observed with enzymatic
339 markers (Duplantier *et al.* 1990a). Most population genetic studies performed on rodents concerned
340 Arvicolinae species of the temperate life zone (but see Dallas *et al.* 1995 and Peakall *et al.* 2003 for
341 studies on Murinae). Various ecological and populational factors are supposed to influence genetic
342 diversity (Nevo 1985), such as social system (Lacey *et al.* 2001), but the relative influence of these
343 factors is difficult to assess in a comparative analysis of studies performed in different geographic area
344 and for different taxa.

345 According to our prediction, we found that genetic diversity was lower and that genetic
346 differentiation was higher in *M. natalensis* than in *M. erythroleucus*. As we compare genetic structure

347 between species, higher levels of genetic drift due to reduced effective population sizes, increased
348 levels of inbreeding and/or reduced gene flow between populations of *M. natalensis* may result from a
349 complex interplay between population history, biogeography and habitat characteristics. It is not
350 possible to determine for how long either *M. natalensis* or *M. erythroleucus* has been resident in south-
351 eastern Senegal. The region is well included in the distribution area of *M. erythroleucus*, and recent
352 colonization by this species is thus unlikely. South-eastern Senegal represents the north-western limit
353 of the distribution range of *M. natalensis* (Granjon *et al.* 1997). Recent colonization of this area, with
354 founder effects that would explain the lower genetic diversity in *M. natalensis* are however difficult to
355 envisage as the isolation by distance pattern (Fig. 2) exhibited by this species suggests that sufficient
356 time has elapsed to reach an equilibrium between genetic drift and migration. Tests for detecting recent
357 founder effects in *M. natalensis* were moreover not significant (results not shown: BOTTLENECK
358 software, Cornuet & Luikart 1996). Lower genetic diversity in *M. natalensis* could also reflect the edge
359 location of south-eastern Senegal in the distribution area of this species. Smaller effective population
360 sizes may be expected in edge locations that represents unfavourable environments (Vucetich & Waite
361 2002).Trap success was higher in *M. natalensis* than in *M. erythroleucus* populations in south-eastern
362 Senegal (Brouat *et al.* in press), suggesting high population abundances and that commensal habitats
363 are not so unfavourable for the first species (perhaps being even the only favourable habitats in these
364 extreme locations of the distribution area because of resource permanence and environmental stability).
365 Indeed, genetic diversity levels estimated using enzymatic markers were similar between studies
366 performed on populations of *M. natalensis* from Senegal (Duplantier *et al.* 1990a) and South Africa
367 (Smit *et al.* 2001). Nevertheless, geography and commensal specialization are nowadays impossible to
368 disentangle in this species. The only microsatellite data that we know concerning *M. natalensis* are
369 unpublished but revealed a higher genetic diversity in a wild population from Tanzania (P. van Hooft

370 and J.-F. Cosson, pers. comm.: average number of alleles per locus: 17.3; H_O: 0.86) than in south-
371 eastern Senegal.

372 Commensalism may explain by itself the differences in population genetic structure between *M.*
373 *natalensis* and *M. erythroleucus*. In house mice, population densities were higher in commensal
374 populations than in wild ones (Pocock *et al.* 2005) due to resource permanence and environmental
375 stability that lead to continuous reproduction all over the year. In *Mastomys* species, reproduction is
376 also continuous in commensal populations and interrupted during the dry season in wild ones
377 (Duplantier, unpublished data). If mean population size is higher in commensal than in wild
378 populations, effective size may however be smaller due to biased sex-ratio or strong social structure
379 (Storz *et al.* 2001). The strongly female-biased sex-ratio (that was not significant on our dataset: only
380 20 trapped individuals per population) and the high level of aggressiveness between males found by
381 previous studies in commensal populations of *M. natalensis* suggested a polygynous mating system
382 with a dominant male living with gregarious females and offspring (Granjon & Duplantier 1993), as in
383 commensal house mouse populations (Boursot *et al.* 1993; Pocock *et al.* 2005). This may be reflected
384 in our study by the higher levels of within population mean relatedness in *M. natalensis* than in *M.*
385 *erythroleucus*.

386 Social structure in commensal populations fits with the hypothesis that high patch quality increases
387 the likelihood of social units becoming groups with reduced dispersal rates and increased philopatry
388 (Lin *et al.* 2006). Populations of the commensal *M. natalensis* were more spatially structured than those
389 of *M. erythroleucus*, suggesting lower gene flow levels. F_{ST} estimates (even when corrected for
390 homozygosity) and the number of pairs of genotypically-differentiated populations were higher for *M.*
391 *natalensis* than for *M. erythroleucus*. Traditional attempts to relate estimates of regional F_{ST} to gene
392 flow and drift uses the Wright's (1931) equation $F_{ST} = 1/(4N_em + 1)$. Mean F_{ST} values obtained for both

393 species led to estimate that N_em in *M. erythroleucus* could be at least five times higher than in *M.*
394 *natalensis*. However, the number of first-generation migrants was not significantly different between
395 *M. erythroleucus* and *M. natalensis*, and the ratio between migration rates calculated from assignment
396 tests was clearly lower than that between N_em estimates based on F_{ST}. The discordance in the estimates
397 of effective dispersal and migration rates may first suggest higher effective population sizes in *M.*
398 *erythroleucus* than in *M. natalensis*. Preliminary tests have shown that our intra-population sampling
399 was not sufficient to permit a valid calculation of N_e using the linkage disequilibrium method (Waples
400 2006). As direct estimates of population size via mark-capture-release studies are ethically difficult to
401 conduct in villages (because of the need to release animals that are potential vectors of severe human
402 diseases [see Gratz *et al.* 1997 for data on African rodents]), temporal genetic surveys would be useful
403 to compare effective population sizes in commensal and wild *Mastomys*. Temporal changes towards an
404 increase of gene flow in *M. natalensis* may also imply a discrepancy between F_{ST}-based migration
405 estimates and migration rates calculated from the number of detected first-generation migrants. This
406 could be related with the development of roads and human traffic in this region during the last fifty
407 years. Finally, the number of detected first-generation migrants may over-estimate gene flow in *M.*
408 *natalensis* more than in *M. erythroleucus*. This may be expected again in the case of a stronger social
409 structure in *M. natalensis* than in *M. erythroleucus*, with weak acceptance of immigrants as potential
410 mates in the first species, such as in commensal house mice (Boursot *et al.* 1993). Discriminating
411 between the two last hypotheses requires fine-scale studies of the relative importance of active versus
412 passive dispersal in among-population variation.

413 Understanding how genetic differentiation between populations varies with geographical distance
414 can help to determine whether genetic differentiation is primarily due to limited dispersal or to more
415 complex demographic processes (e.g. Leblois *et al.* 2000). At mutation–migration–drift equilibrium,

416 and for species with relatively limited dispersal in space such as those studied here, genetic
417 differentiation is expected to increase with geographical distance (Slatkin 1993; Rousset 1997).
418 However, only one of the two species that we studied clearly conformed to these theoretical
419 expectations. Against our expectations, results of Mantel tests and bootstrap confidence intervals
420 suggested that isolation by distance is more clearly implicated in population genetic differentiation for
421 *M. natalensis* than for *M. erythroleucus*. This was confirmed by comparison of regression slopes
422 obtained for each species between genetic differentiation and geographical distance. Genetic diversity
423 levels such as those obtained for the two species (i.e. H_O between 0.6 and 0.85) are not likely to bias
424 the estimation of slopes in isolation by distance analyses (Leblois *et al.* 2003). The observed difference
425 in the regression slopes between the two species cannot therefore be explained by differences in genetic
426 diversity.

427 For the wild *M. erythroleucus*, no relationship was found between genetic differentiation and
428 geographical distance. The absence of an observable pattern of isolation by distance may suggest that
429 populations of *M. erythroleucus* have not yet reached a drift–migration equilibrium (Hutchinson &
430 Templeton 1999). Whereas recent colonization of the species in this area is unlikely, temporal
431 fluctuations in density in a context of fragmented distribution may conduct to a disruption of the drift-
432 migration equilibrium and temporal absence of isolation by distance, with very low dispersion rates and
433 high genetic drift (Berthier *et al.* 2005). However, very low dispersion rates should have given higher
434 levels of genetic differentiation and less first-generation migrants between populations of *M.*
435 *erythroleucus* compared with those observed in *M. natalensis*. As *M. erythroleucus* was known to be
436 continuously distributed outside villages (Duplantier *et al.* 1997), we thus suggest that the absence of
437 an isolation by distance pattern in *M. erythroleucus* rather reflects high gene flow and random dispersal
438 between populations at a range equivalent to the geographical scale that we considered.

439 For the commensal species *M. natalensis*, there was a clear pattern of isolation by distance between
440 populations, suggesting first that savannas and fields are partial barriers to gene flow for this species, as
441 already shown by genetic differentiation levels. Dispersal of *M. natalensis* through non-commensal
442 areas may be limited by physical properties of the surrounding environment, but also by inter-specific
443 competition or predation pressures that may be higher in outdoor environments (Boursot *et al.* 1993).
444 It is not clear whether dispersal was limited in this species by patchiness, by the effects of resource
445 permanence and stability on social structure (Lin *et al.* 2006), or by both factors. Evaluating the effects
446 of population density on dispersal rates would help to evaluate the mechanisms that explain population
447 structure in this species. Secondly, the isolation by distance pattern showed that dispersal occur
448 primarily between neighbouring villages, and not at random or towards the town of Kedougou, as it
449 could be expected in the case of a major human-mediated dispersal. In the eastern Senegal, human
450 transport that often explain the homogenisation of commensal faunas (McKinney 2006) was not
451 sufficiently implicated for *M. natalensis* to counteract the effects of patchiness and of geographic
452 proximity. Whereas historical factors related to man may explain colonization patterns in commensal
453 rodents, Britton-Davidian (1990) had also shown that dispersal by man would not be a prominent
454 feature moulding microgeographic population structure in house mice.
455
456 **Conclusion**
457
458 Genetic structure was clearly different between the commensal populations of *M. natalensis* and the
459 wild populations of *M. erythroleucus* in south-eastern Senegal, with a higher genetic differentiation
460 between populations in *M. natalensis* and a higher genetic diversity within populations in *M.*
461 *erythroleucus*. Most of our results conformed to the expectations based on the effect of habitat

462 characteristics on genetic structure, but confounding factors such as the geographic location of the
463 study site in the distribution area of *M. natalensis*, or biological differences between species cannot be
464 ruled out. This is clearly the limit of such approach using two different species, even closely related, to
465 look at the effects of habitat characteristics on genetic differentiation. Further explanations will depend
466 on the outcome of follow-up studies focusing on temporal surveys of genetic variations in *M.*
467 *natalensis* and *M. erythroleucus*. Other comparative studies in other landscape contexts and African
468 regions (dealing with the commensal populations of *M. erythroleucus* in northern Senegal for example,
469 or wild populations of *M. natalensis* in East Africa) are necessary to disentangle the effects of host
470 species and commensal habitat patchiness in population genetic structure.

471

472 **References**

473

474 Aars J, Dallas JF, Piertney SB, *et al.* (2006) Widespread gene flow and high genetic variability in
475 populations of water voles *Arvicola terrestris* in patchy habitats. *Molecular Ecology*, **15**, 1455-1466.
476 Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful
477 approach to multiple testing. *Journal of the Royal Statistical Society B*, **57**, 289–300.
478 Berthier K, Galan M, Foltete JC, Charbonnel N, Cosson JF (2005) Genetic structure of the cyclic
479 fossorial water vole (*Arvicola terrestris*): landscape and demographic influences. *Molecular Ecology*,
480 **14**, 2861-2872.
481 Boursot P, Auffray J-C, Britton-Davidian J, Bonhomme F (1993) The evolution of house mice. *Annual*
482 *Review of Ecology and Systematics*, **24**, 119-152.

483 Britton-Davidian J (1990) Genic differentiation in *M. m. domesticus* populations from Europe, the
484 Middle East and North Africa: geographic patterns and colonization events. *Biological Journal of the*
485 *Linnean Society*, **41**, 27-45.
486 Brouat C, Kane M, Diouf M *et al.* Host ecology and variation in helminth community structure in
487 *Mastomys* rodents from Senegal. *Parasitology*, in press.
488 Chapuis MP (2006) *Génétique des populations d'un insecte pullulant, le criquet migrateur,* Locusta
489 migratoria. PhD thesis, Montpellier II University, Montpellier.
490 Chapuis MP, Estoup A (2006) Microsatellite null alleles and estimation of population differentiation.
491 *Molecular Biology and Evolution* Advance access published December 5, doi:
492 10.1093/molbev/msl191.
493 Cornuet JM, Luikart G (1996) Description and power analysis of two tests for detecting recent
494 population bottlenecks from allele frequency data. *Genetics*, **144**, 2001-2014.
495 Dallas JF, Dod B, Boursot P, Prager EM, Bonhomme F (1995) Population subdivision and gene flow in
496 Danish house mice. *Molecular Ecology*, **4**, 311-320.
497 Dempster AP, Laird NM, Rubin DB (1977) Maximum likelihood from incomplete data via the EM
498 algorithm. *Journal of the Royal Statistical Society* B, **39**, 1-38.
499 DiCiccio TJ, Efron B (1996) Bootstrap confidence intervals (with discussion). *Statistical Science*, **11**,
500 189–228.
501 Duplantier JM, Granjon L, Mathieu E, Bonhomme F (1990a) Structures génétiques comparées de trois
502 espèces de rongeurs africains du genre *Mastomys* au Sénégal. *Genetica*, **81**, 179-192.
503 Duplantier JM, Britton-Davidian J, Granjon L (1990b) Chromosomal characterization of three species
504 of the genus *Mastomys* in Senegal. *Zeitschrift für Zoologische Systematik und Evolutionsforschung*,
505 **28**, 289-298.

506 Duplantier J-M, Granjon L, Bâ K (1997) Répartition biogéographique des petits rongeurs au Sénégal.
507 *Journal of African Zoology*, **111**, 17-26.
508 Duplantier JM, Granjon L, Bouganaly H (1996) Reproductive characteristics of three sympatric species
509 of *Mastomys* in Sénégal, as observed in the field and in captivity. *Mammalia*, **60**, 629-638.
510 Ehrich D, Krebs CJ, Kenney AJ, Stenseth NC (2001) Comparing the genetic population structure of
511 two species of arctic lemmings: more local differentiation in *Lemmus trimucronatus* than in
512 *Dicrostonyx groenlandicus*. *Oikos*, **94**, 143-150.
513 Frankham R, Ballou JD, Briscoe DA (2002) *Introduction to Conservation Genetics*. Cambridge
514 University Press, Cambridge, UK.
515 Futuyma DJ (1986) Evolutionary Biology, 2nd edition. Sinauer Associates, Sunderland,
516 Massachussets, USA.
517 Goudet J (2001). *FSTAT, a program to estimate and test gene diversities and fixation indices (version*
518 *2.9.3)*. Available from http://www.unil.ch/izea/softwares/fstat.html. Updated from Goudet (1995).
519 Granjon L, Duplantier J-M (1993) Social structure in synanthropic populations of a murid rodent
520 *Mastomys natalensis* in Senegal. *Acta Theriologica*, **38**, 39-47.
521 Granjon L, Duplantier J-M, Cassaing J (1987) Etude des relations sociales dans plusieurs populations
522 du genre *Mastomys* (rongeur, Muridé) au Sénégal: implications évolutives. Actes du Colloque
523 National "Biologie des Populations". Lyon, Septembre, 1986.
524 Granjon L, Duplantier J-M, Catalan J, Britton-Davidian J (1997) Systematics of the genus *Mastomys*
525 (Thomas, 1915) (Rodentia: Muridae). *Belgian Journal of Zoology*, **127**, S7-S18.
526 Gratz N (1997) The burden of rodent-borne diseases in Africa South of the Sahara. *Belgian Journal of*
527 *Zoology* (suppl.), **127**, 71-84.

528 Guinand B, Topchy A, Page KS *et al.* (2002) Comparison of likelihood and machine learning methods
529 of individual classification. *Journal of Heredity*, **93**, 260–269.
530 Hamilton WD (1971) Selection of selfish and altruistic behavior in some extreme models. In: *Man and*
531 *Beast: Comparative Social Behavior (eds.* Eisenberg and Dillon), pp. 57-91. Smithsonian Inst. Press,
532 Washington, USA.
533 Hardy O, Vekemans X (1999) Isolation by distance in a continuous population: reconciliation between
534 spatial autocorrelation analysis and population genetics models. *Heredity*, **83**, 145-154.
535 Hardy OJ, Vekemans X (2002). SPAGeDi: a versatile computer program to analyse spatial genetic
536 structure at the individual or population levels. *Molecular Ecology Notes*, **2**, 618-620.
537 Hedrick PW (1999) Perspective: highly variable loci and their interpretation in evolution and
538 conservation. *Evolution*, **53**, 313-318.
539 Hedrick PW (2005) A standardized genetic differentiation measure. *Evolution*, **59**, 1633–1638.
540 Hubert B (1982) Dynamique de populations de *Mastomys erythroleucus* et de *Taterillus gracilis* au
541 Sénégal. *Mammalia*, **46**, 137-166.
542 Hutchinson DW, Templeton AR (1999) Correlation of pairwise genetic and geographic distance
543 measures: inferring the relative influences of gene flow and drift on the distribution of genetic
544 variability. *Evolution*, **53**, 1898-1914.
545 Julliard R, Leirs H, Stenseth NC *et al.* (1999). Survival-variation within and between functional
546 categories of the African multimammate rat. *Journal of Animal Ecology*, **68**, 550-561.
547 Kalinowski ST, AP Wagner, ML Taper (2006) *ML-Relate*: a computer program for maximum
548 likelihood estimation of relatedness and relationship. *Molecular Ecology Notes*, **6**,576-579.

549 Karanth KP, Avivi A, Beharav A, Nevo E (2004) Microsatellite diversity in populations of blind
550 subterranean mole rats (*Spalax ehrenbergi* superspecies) in Israel: speciation and adaptation.
551 *Biological Journal of the Linnean Society*, **83**, 229-241.

552 Lacey EA (2001) Microsatellite variation in solitary and social tuco-tucos: molecular properties and
553 population dynamics. *Heredity*, **86**, 628-637.

554 Leblois R, Estoup A, Rousset F (2003) Influence of mutational and sampling factors on the estimation
555 of demographic parameters in a 'continuous' population under isolation by distance. *Molecular*
556 *Biology and Evolution*, **20**, 491-502.

557 Leblois R, Rousset F, Tikel D, Moritz C, Estoup A (2000) Absence of evidence for isolation by
558 distance in an expanding cane toad (*Bufo marinus*) population: an individual-based analysis of
559 microsatellite genotypes. *Molecular Ecology*, **9**, 1905-1909.

560 Lecomte E, Granjon L, Denys C (2002) The phylogeny of the *Praomys* complex (Rodentia: Muridae)
561 and its phylogenetic implications. *Journal of Zoological Systematics and Evolutionary Research*, **40**,
562 8-25.

563 Leirs H, Stenseth NC, Nichols JD *et al.* (1997) Stochastic seasonality and nonlinear density-dependent
564 factors regulate population size in an African rodent. *Nature*, **389**, 176-180.

565 Leirs H, Verhagen R, Verheyen W (1993) Productivity of different generations in a population of
566 *Mastomys natalensis* rats in Tazania. *Oikos*, **68**, 53-60.

567 Leirs H (in press) *Mastomys erythroleucus*, *M. natalensis*, in *Mammals of Africa*, Volume 4: Rodentia,
568 D.C.D. Happold Ed., Academic Press.

569 Lin YK, Keane B, Isenhour A, Solomon NG (2006) Effects of patch quality on dispersal and social
570 organization of prairie voles: an experimental approach. *Journal of Mammalogy*, **87**, 446–453.

571 Loiseau A, Konecny A, Galan M *et al.* New polymorphic microsatellite loci for rodents of the genus
572 *Mastomys* using PCR multiplexing, and cross-species amplification in *Myomys* and *Praomys*.
573 *Molecular Ecology Notes*, in press.
574 Marsh A, Harris S (2000) Living with yellow-necked mice. *British Wildlife*, **11**, 168–174.
575 Matocq MD, Patton JL, da Silva MNF (2000) Population genetic structure of two ecologically distinct
576 Amazonian spiny rats: Separating history and current ecology. *Evolution*, **54**, 1423-1432.
577 McKinney ML (2006) Urbanization as a major cause of biotic homogenization. *Biological*
578 *Conservation*, **127**, 247-260.
579 Meirmans PG (2006) Using the AMOVA framework to estimate a standardized genetic differentiation
580 measure. *Evolution*, in press.
581 Nei M (1987). *Molecular Evolutionary Genetics.* Columbia University Press, New-York.
582 Nevo E (1985) Ecological and populational correlates of allozyme polymorphisms in mammals. *Acta*
583 *Zoologica Fennica*, **170**, 25-29.
584 Paetkau D, Strobeck C (1995) The molecular basis and evolutionary history of a microsatellite null
585 allele in bears. *Molecular Ecology*, *4*, 519-520.
586 Paetkau D, Calvert W, Stirling I, Strobeck C (1995) Microsatellite analysis of population structure in
587 Canadian polar bears. *Molecular Ecology*, **4**, 347–354.
588 Paetkau D, Slade R, Burden M, Estoup A (2004) Genetic assignment methods for the direct, real-time
589 estimation of migration rate: a simulation-based exploration of accuracy and power. *Molecular*
590 *Ecology*, **13**, 55–65.
591 Paetkau D, Waits LP, Clarkson PL, Craighead L, Strobe C (1997) An empirical evaluation of genetic
592 distance statistics using microsatellite data from bear (Ursidae) populations. *Genetics*, **147**, 1943-
593 1957.

594 Peakall R, Ruibal M, Lindenmayer DB (2003) Spatial autocorrelation analysis offers new insights into
595 gene flow in the Australian Bush Rat, *Rattus fuscipes*. *Evolution* **57**, 1182-1195.
596 Piry S, Alapetite A, Cornuet, J-M *et al.* (2004) GeneClass2: A Software for Genetic Assignment and
597 First-Generation Migrant Detection. *Journal of Heredity*, **95**, 536-539.
598 Pocock MJO, Hauffe HC, Searle JB (2005) Dispersal in house mice. *Biological Journal of the Linnean*
599 *Society*, **84**, 565-583.
600 Pocock MJO, Searle JB, White PCL (2004) Adaptations of animals to commensal habitats: population
601 dynamics of house mice *Mus musculus domesticus* on farms. *Journal of Animal Ecology*, **73**, 878–
602 888.
603 Queller DC, Goodnight KF (1989) Estimating relatedness using genetic markers. *Evolution*, **43**, 258-
604 275.
605 Raymond M, Rousset F (1995) GENEPOP Version 1.2.: population genetics software for exact tests
606 and ecumenicism. *Journal of Heredity*, **86**, 248–249.
607 Rousset F (1997). Genetic differentiation and estimation of gene flow from *F*-statistics under isolation
608 by distance. *Genetics*, **145**, 1219–1228.
609 SAS (2002). *SAS for Windows 9.1.* SAS Institute, Cary, NC, USA.
610 Schmuki C, Vorburger C, Runciman D, Maceachern S, Sunnucks P (2006) When log-dwellers meet
611 loggers: impacts of forest fragmentation on two endemic log-dwelling beetles in southeastern
612 Australia. *Molecular Ecology*, **15**, 1481–1492.
613 Slatkin M (1993) Isolation by distance in equilibrium and nonequilibrium populations. *Evolution*, **47**,
614 264–279.

615 Smit A, van der Bank H, Falk T, de Castro A (2001) Biochemical genetic markers to identify two
616 morphologically similar South African *Mastomys* species (Rodentia: Muridae). *Biochemical*
617 *Systematics and Ecology*, **29**, 21-30.
618 Storz JF, Bhat HR, Kunz TH (2001) Genetic consequences of polygyny and social structure in an
619 indian fruit bat, *Cynopterus sphinx*. I. Inbreeding, outbreeding and population subdivision. *Evolution*,
620 **55**, 1215–1223.
621 Stow AJ, Sunnucks P, Briscoe DA, Gardner MG (2001) The impact of habitat fragmentation on
622 dispersal of Cunningham's skink (*Egernia cunninghami*): evidence from allelic and genotypic
623 analyses of microsatellites. *Molecular Ecology*, **10**, 867-878.
624 Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004). Micro-Checker: software for
625 identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes,* **4**, 535-
626 538.
627 Vucetich JA, Waite TA (2003) Spatial patterns of demography and genetic processes across the species
628 range: Null hypotheses for landscape conservation genetics. *Conservation Genetics*, **4**, 639-645.
629 Wagner AP, Creel S, Kalinowski ST (2006) Estimating relatedness and relationships using
630 microsatellite loci with null alleles. *Heredity*, 1-10.
631 Waples RS (2006) A bias correction for estimates of effective population size based on linkage
632 disequilibrium at unlinked gene loci. *Conservation Genetics*, 7, 167–184.
633 Weir, BS (1996) *Genetic Data Analysis II.* Sinauer Associates, Sunderland, Massachussets, USA
634 Whitlock MC, Barton NH (1997) The Effective Size of a Subdivided Population. *Genetics*, **146**, 427-
635 441.
636 Wilson GA, Rannala B (2003) Bayesian Inference of Recent Migration Rates Using Multilocus
637 Genotypes. *Genetics*, **163**, 1177–1191.

638 Wright S (1931) Evolution in Mendelian populations. *Genetics*, **16**, 97-159.

639

640 **Acknowledgements**

641 The authors gratefully acknowledge the assistance of C. Bâ during field sampling. F. Rousset, P.
642 Meirmans, and S. Piry provided help for some analyses. The manuscript benefited from the helpful
643 comments of M.-P. Chapuis, J.-F. Cosson, G. Dobigny, A. Estoup, G. Ganem, L. Granjon, and L.
644 Crespin.

645 **Figure legends**

646

647 **Fig. 1**. Distribution area of *M. erythroleucus* (continuous line) and *M. natalensis* (dotted line) in Africa,
648 in Senegal, and location of the 20 trapping sites in south-eastern Senegal, along the two main roads of
649 the region. Black circles: villages, *M. natalensis* sampling sites; White circle: wild habitat, *M.*
650 *erythroleucus* sampling sites. BA: Bandafassi; BE: Bembou; DI: Diakhaba; FA: Fadiga; KE:
651 Kedougou; ND: Ndebou; NG: Ngari; NI: Niemenike; SA: Samekouta; TO: Tomboronkoto.

652

653 **Fig. 2.** Relationship between logarithms of geographical distances and genetic dissimilarities
654 [estimated as F_{ST}^{ENA} /(1 - F_{ST}^{ENA})] for each *Mastomys* species. The equation was reported only for the
655 significant relationship. Dotted lines indicated 95% CI for slopes of each relationship, calculated using
656 ABC bootstrap procedures.

Table 1. Population polymorphism at 15 microsatellite loci over the ten populations sampled for *M. natalensis* and *M. erythroleucus*. N is the number of individuals analysed per population, *n* the number of alleles, *r* the allelic richness and H_O and H_E the observed and expected heterozygosities. † and ‡ indicates loci deviating from Hardy-Weinberg expectations (after fdr correction for multiple comparisons) for *M. natalensis* (†) and *M. erythroleucus* (‡) (P < 0.05).

		M. natalensis										*M. erythroleucus*									
		BA	BE	DI	FA	KE	ND	NG	NI	SA	TO	BA	BE	DI	FA	KE	ND	NG	NI	SA	TO
N		21	21	23	23	16	23	24	26	26	22	23	19	24	79	39	27	34	20	24	21
MH1 †, ‡	*n*	7	7	5	5	6	6	4	5	7	5	11	13	8	17	13	13	14	13	14	13
	r	6.4	6.5	5.6	5.0	6.0	5.6	4.0	4.9	6.8	6.0	10.2	12.3	7.9	12.4	11.0	11.6	11.6	12.3	12.4	11.9
	H_O	0.67	0.62	0.22	0.65	0.56	0.48	0.75	0.69	0.65	0.47	0.96	0.84	0.88	0.85	0.82	0.96	0.88	0.90	0.88	0.86
	H_E	0.75	0.72	0.72	0.73	0.75	0.76	0.72	0.69	0.81	0.80	0.89	0.92	0.88	0.91	0.90	0.90	0.91	0.92	0.90	0.90
MH10 †, ‡	*n*	5	7	7	6	5	6	6	6	7	5	4	5	5	7	6	5	7	7	7	6
	r	4.8	6.5	7.5	5.7	5.0	5.7	6.6	7.0	7.4	5.7	3.7	5.0	4.9	5.7	4.7	4.6	6.0	6.6	6.5	5.7
	H_O	0.57	0.52	0.18	0.52	0.25	0.57	0.29	0.14	0.40	0.11	0.30	0.58	0.71	0.71	0.62	0.74	0.65	0.65	0.54	0.71
	H_E	0.74	0.83	0.65	0.76	0.74	0.77	0.78	0.81	0.79	0.69	0.69	0.74	0.77	0.75	0.71	0.76	0.69	0.77	0.77	0.68
MH188	*n*	5	4	3	3	4	4	4	4	4	3	6	7	6	10	10	7	11	10	10	8
	r	5.7	3.8	3.0	3.0	4.0	4.0	4.7	4.0	3.6	3.0	5.5	6.5	5.8	8.0	7.1	6.8	8.8	8.8	8.8	7.5
	H_O	0.75	0.52	0.65	0.74	0.56	0.83	0.64	0.69	0.62	0.59	0.65	0.58	0.83	0.63	0.74	0.74	0.77	0.80	0.63	0.67
	H_E	0.69	0.61	0.59	0.61	0.69	0.76	0.68	0.71	0.62	0.52	0.66	0.68	0.67	0.71	0.73	0.84	0.75	0.77	0.78	0.74
MH3 ‡	*n*	2	2	2	2	1	2	2	2	2	4	2	3	2	5	4	3	4	4	3	4
	r	2.0	2.0	1.7	2.0	1.0	2.0	2.0	2.0	2.0	3.5	2.0	3.0	2.0	3.8	3.8	2.6	3.5	3.8	2.7	3.8
	H_O	0.57	0.33	0.04	0.13	0.00	0.39	0.38	0.23	0.19	0.32	0.17	0.26	0.33	0.37	0.31	0.11	0.12	0.35	0.21	0.38
	H_E	0.46	0.49	0.04	0.13	0.00	0.41	0.40	0.21	0.24	0.40	0.16	0.40	0.34	0.51	0.41	0.17	0.41	0.38	0.26	0.64
MH39	*n*	5	5	5	5	2	5	4	4	3	5	12	12	14	18	15	16	18	13	17	11
	r	5.0	4.9	4.8	4.3	2.0	4.6	4.0	3.5	3.0	4.6	10.9	11.6	12.5	13.7	12.5	14.0	13.7	11.9	14.6	10.0
	H_O	0.91	0.57	0.52	0.44	0.06	0.74	0.67	0.52	0.31	0.64	1.00	0.90	0.96	0.91	0.95	0.96	1.00	0.95	0.96	0.95
	H_E	0.78	0.74	0.61	0.48	0.06	0.61	0.70	0.43	0.41	0.54	0.91	0.91	0.92	0.91	0.92	0.93	0.92	0.90	0.94	0.90
MH80 †, ‡	*n*	8	6	6	8	8	8	5	7	11	12	13	20	16	38	25	22	22	21	25	20
	r	7.5	5.9	5.6	7.3	8.0	7.3	4.9	6.3	10.3	10.5	12.5	18.2	13.7	19.2	16.6	17.2	15.5	18.4	20.6	17.3
	H_O	0.71	0.81	0.52	0.83	0.75	0.78	0.88	0.65	0.73	0.41	0.91	1.00	0.96	0.95	0.92	0.89	0.97	1.00	1.00	0.91
	H_E	0.77	0.83	0.77	0.77	0.78	0.76	0.73	0.74	0.88	0.87	0.90	0.96	0.92	0.96	0.94	0.95	0.93	0.95	0.97	0.94

MH105[†, ‡]	n	6	5	2	5	3	5	5	4	3	9	12	13	11	20	14	15	15	15	14	12
	r	5.5	4.7	2.0	4.3	3.0	4.4	4.8	3.9	2.6	7.9	10.6	12.1	10.7	13.4	10.9	13.6	12.2	13.3	11.7	11.2
	H_O	0.67	0.62	0.48	0.48	0.38	0.17	0.46	0.08	0.62	0.32	1.00	0.84	0.96	0.85	0.85	0.96	0.97	0.95	0.88	0.95
	H_E	0.74	0.62	0.50	0.57	0.51	0.50	0.62	0.45	0.47	0.82	0.86	0.91	0.89	0.91	0.89	0.94	0.92	0.91	0.87	0.89
MH133[‡]	n	9	7	7	7	6	11	7	7	11	6	12	9	15	19	15	15	10	12	16	12
	r	8.7	6.5	7.5	6.3	6.0	9.8	6.3	5.9	10.3	5.7	10.3	8.5	12.8	12.4	10.8	12.8	9.5	10.8	13.3	10.9
	H_O	0.81	0.76	0.64	0.61	0.81	1.00	0.79	0.58	0.89	0.91	0.70	0.79	0.88	0.72	0.64	0.59	0.94	0.70	0.79	0.81
	H_E	0.88	0.74	0.78	0.72	0.81	0.86	0.80	0.57	0.90	0.80	0.86	0.83	0.91	0.90	0.87	0.91	0.88	0.86	0.90	0.90
MH146[†, ‡]	n	9	6	9	9	5	7	8	7	9	9	9	9	10	19	16	13	11	11	13	11
	r	8.7	5.8	7.9	8.2	5.0	6.7	6.7	6.5	8.3	7.9	8.3	8.8	9.2	11.1	11.9	12.7	9.3	10.0	11.6	10.4
	H_O	0.86	0.91	0.78	0.96	0.69	0.87	0.88	0.69	0.89	0.82	0.74	0.74	0.58	0.63	0.72	0.65	0.71	0.70	0.79	0.52
	H_E	0.88	0.82	0.75	0.82	0.74	0.82	0.78	0.82	0.85	0.75	0.86	0.88	0.85	0.86	0.91	0.93	0.85	0.86	0.89	0.89
MH174	n	8	8	5	8	9	8	5	6	9	10	10	12	9	17	16	16	11	11	11	14
	r	7.9	8.0	5.7	7.3	9.0	7.2	4.7	4.7	7.6	9.0	9.4	11.6	9.5	11.6	12.1	14.4	8.8	10.3	10.6	13.8
	H_O	0.80	0.68	0.64	0.74	0.81	0.83	0.75	0.42	0.65	0.77	0.83	0.84	0.91	0.81	0.90	0.93	0.68	0.75	0.83	1.00
	H_E	0.75	0.80	0.68	0.73	0.83	0.75	0.72	0.57	0.73	0.78	0.87	0.91	0.87	0.91	0.89	0.94	0.83	0.88	0.90	0.93
MH206[†]	n	5	7	5	5	4	5	4	5	6	5	7	9	9	11	12	11	9	9	11	9
	r	4.8	6.4	4.9	4.7	4.0	4.6	4.0	4.6	6.3	5.0	7.8	8.5	9.7	9.8	10.2	9.7	8.3	8.5	9.9	8.2
	H_O	0.38	0.81	0.61	0.78	0.56	0.52	0.63	0.65	0.64	0.82	1.00	0.90	0.87	0.83	0.90	0.85	0.70	0.70	0.92	0.81
	H_E	0.65	0.74	0.68	0.64	0.70	0.58	0.61	0.64	0.73	0.77	0.83	0.82	0.89	0.84	0.86	0.74	0.82	0.76	0.90	0.70
MH216	n	6	4	5	4	4	8	5	4	6	6	8	9	9	14	12	12	10	12	11	13
	r	6.9	4.0	4.7	4.0	4.0	7.8	4.9	3.9	5.5	5.7	7.0	8.3	8.8	9.5	9.7	10.5	8.8	11.1	10.2	12.1
	H_O	0.90	0.67	0.70	0.87	0.88	0.78	0.54	0.58	0.62	0.77	0.78	0.95	0.92	0.85	0.77	0.74	0.94	0.90	0.88	0.91
	H_E	0.81	0.72	0.75	0.64	0.64	0.86	0.60	0.61	0.75	0.76	0.77	0.82	0.88	0.87	0.88	0.89	0.86	0.87	0.91	0.91
MH30[†, ‡]	n	8	4	4	6	6	7	6	7	6	6	9	9	11	17	15	16	11	11	15	12
	r	7.2	3.9	4.0	5.9	6.0	6.6	5.6	6.3	5.6	5.3	8.4	8.8	10.5	12.3	11.8	13.2	9.2	10.7	13.6	10.9
	H_O	0.62	0.38	0.48	0.74	0.69	0.83	0.75	0.54	0.89	0.50	0.65	1.00	1.00	0.85	0.92	0.78	0.85	0.90	0.88	0.67
	H_E	0.60	0.47	0.61	0.79	0.80	0.79	0.74	0.77	0.77	0.55	0.87	0.86	0.91	0.90	0.91	0.90	0.85	0.91	0.92	0.90
MH52[‡]	n	6	4	5	5	4	7	5	5	6	5	9	11	8	16	13	14	11	7	10	11
	r	5.5	3.9	4.7	5.0	4.0	6.4	5.8	5.0	5.8	4.7	8.0	10.5	7.9	13.0	11.7	12.6	9.3	7.0	9.2	11.1
	H_O	0.52	0.38	0.57	0.70	0.81	0.74	0.52	0.77	0.77	0.82	0.87	0.68	0.54	0.68	0.82	0.84	0.56	0.90	0.63	0.90
	H_E	0.51	0.34	0.72	0.77	0.61	0.76	0.72	0.68	0.75	0.69	0.81	0.87	0.87	0.92	0.92	0.90	0.80	0.86	0.87	0.88
MH60[‡]	n	7	5	7	12	7	9	7	10	11	7	15	17	17	36	19	25	20	20	25	18
	r	6.7	4.7	6.5	10.5	7.0	8.0	6.8	8.3	9.1	6.7	12.8	15.6	14.5	19.1	14.9	19.4	14.3	17.8	20.3	16.4

H_O	0.71	0.33	0.48	0.91	0.88	0.74	0.79	0.89	0.89	0.91	1.00	0.95	0.96	0.86	0.90	0.93	1.00	1.00	0.92	0.95
H_E	0.81	0.41	0.61	0.89	0.86	0.78	0.82	0.81	0.83	0.81	0.90	0.94	0.93	0.96	0.94	0.96	0.92	0.95	0.97	0.95
Across all loci																				
n	96	81	77	90	74	98	77	83	101	97	139	158	150	264	205	203	184	176	202	174
r	6.2	5.2	5.1	5.6	4.9	6.0	5.0	5.1	6.3	6.1	8.5	10.0	9.4	11.6	10.6	11.7	9.9	10.7	11.7	10.8
H_O	0.70	0.60	0.50	0.67	0.58	0.68	0.65	0.54	0.65	0.61	0.77	0.79	0.82	0.77	0.79	0.78	0.78	0.81	0.78	0.80
H_E	0.72	0.66	0.63	0.67	0.64	0.72	0.70	0.63	0.70	0.70	0.79	0.83	0.83	0.86	0.85	0.84	0.82	0.84	0.85	0.85

Table 2. Estimates of null allele frequencies for loci having heterozygote deficiencies, and mean null allele frequency ($\bar{a}$) per locus. A- *M. natalensis*; B- *M. erythroleucus*.

A-

	MH1	MH10	MH80	MH105	MH146	MH206	MH30
BA	0.06	0.10	0	0.02	0.01	0.16	0
BE	0.05	0.16	0	0	0	0	0.08
DI	0.48	0.34	0.14	0	0.01	0	0.08
FA	0.02	0.12	0	0.03	0	0	0
KE	0.13	0.27	0.02	0.04	0	0.07	0
ND	0.15	0.12	0	0.21	0	0	0
NG	0	0.39	0.00	0.10	0	0	0.00
NI	0	0.48	0.06	0.26	0.06	0	0.12
SA	0.07	0.25	0.06	0	0.02	0.11	0
TO	0.48	0.49	0.24	0.26	0	0	0.06
$\bar{a}$	**0.14**	**0.27**	**0.05**	**0.09**	**0.01**	**0.03**	**0.03**

B-

	MH1	MH10	MH3	MH80	MH105	MH133	MH146	MH30	MH52	MH60
BA	0	0.22	0	0	0	0.08	0.04	0.11	0	0
BE	0.03	0.10	0.11	0	0.01	0.01	0.07	0	0.08	0
DI	0.02	0.03	0	0	0.05	0	0.14	0	0.17	0
FA	0.03	0.02	0.11	0	0.02	0.09	0.14	0.02	0.19	0.05
KE	0.03	0.04	0.09	0.03	0.02	0.12	0.09	0	0.05	0.02
ND	0	0	0.09	0.03	0	0.16	0.18	0.05	0.12	0
NG	0	0	0.23	0	0	0	0.08	0	0.12	0
NI	0.02	0.07	0.03	0	0	0.07	0.08	0	0	0
SA	0	0.12	0.06	0	0	0.07	0.04	0.01	0.13	0.01
TO	0	0	0.16	0	0	0.04	0.19	0.12	0.07	0

$\bar{a}$	0.01	0.06	0.09	0.01	0.01	0.06	0.10	0.03	0.09	0.01

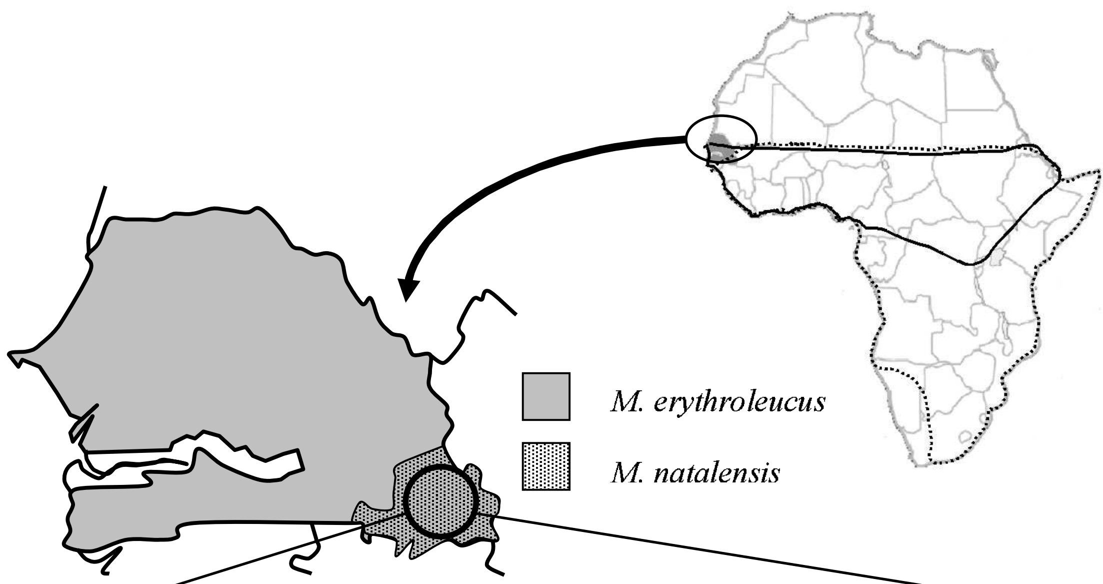
Table 3. Pairwise F_{ST}^{ENA} values (below the diagonal) calculated for all loci, and counts of significant ($P < 0.05$) genotypic tests of allele frequency differences (above diagonal) between samples. A- *M. natalensis*; B- *M. erythroleucus*

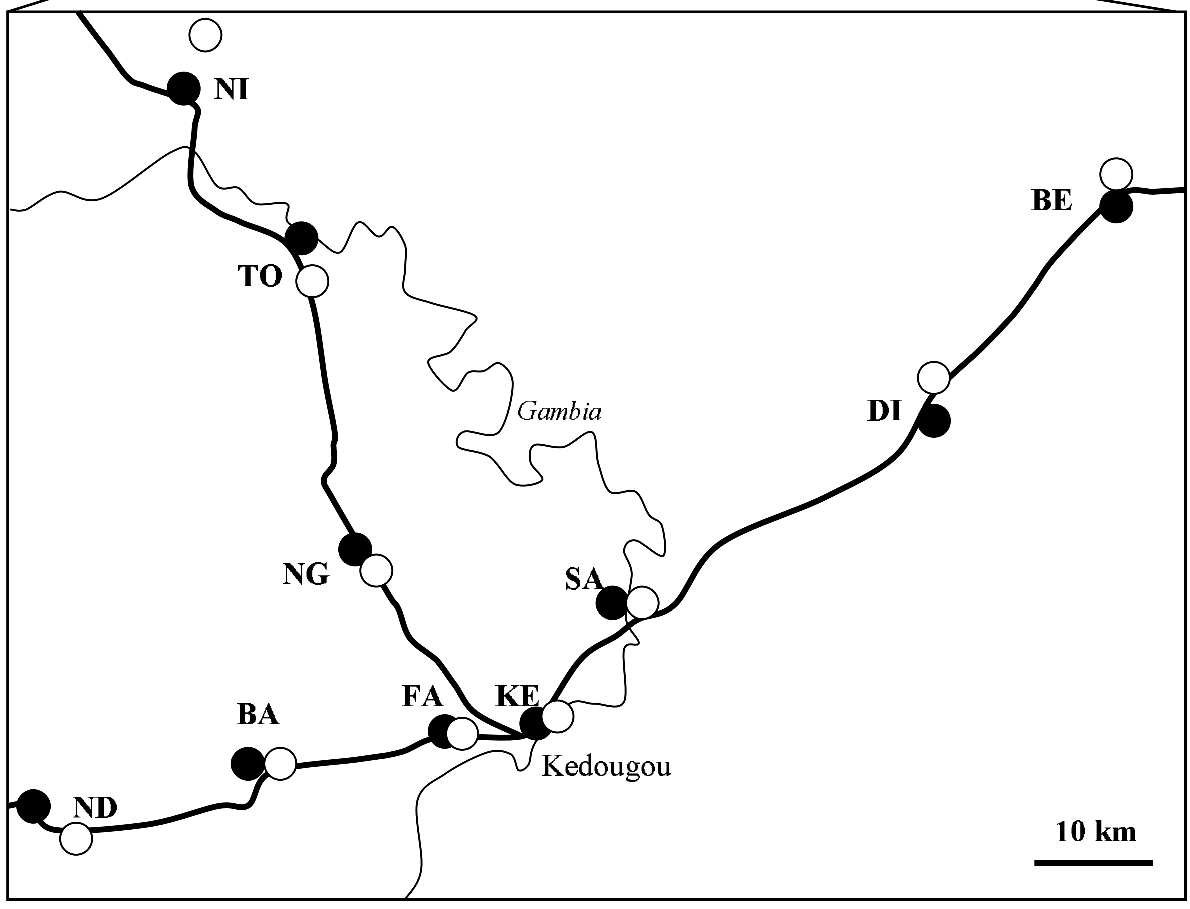
A-

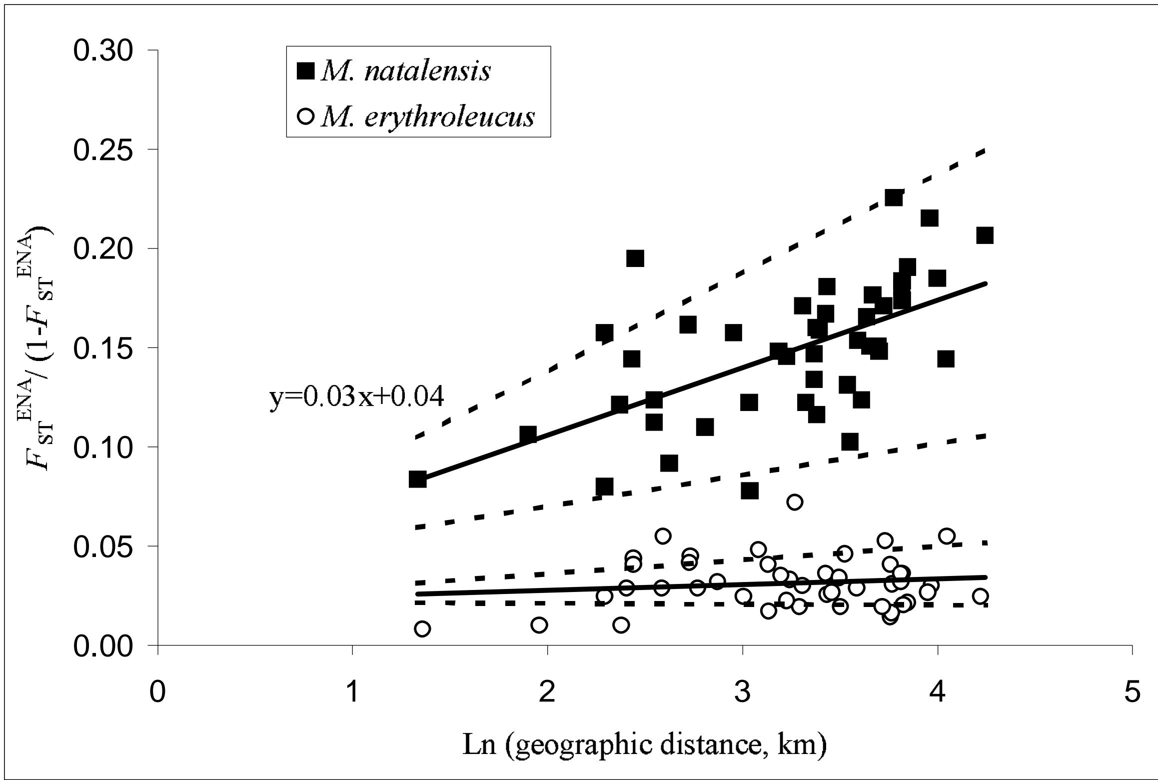
	BAi	BEi	DIi	FAi	KEi	NDi	NGi	NIi	SAi	TOi
BAi		14	15	15	13	10	14	15	15	13
BEi	0.13		12	13	14	14	13	15	12	14
DIi	0.15	0.10		12	13	15	15	13	11	14
FAi	0.13	0.16	0.14		12	15	14	15	10	15
KEi	0.14	0.18	0.15	0.08		14	14	14	13	15
NDi	0.08	0.17	0.16	0.13	0.12		13	14	14	12
NGi	0.11	0.15	0.15	0.14	0.16	0.13		13	14	14
NIi	0.14	0.18	0.16	0.15	0.13	0.13	0.14		13	14
SAi	0.11	0.11	0.07	0.07	0.10	0.12	0.10	0.13		14
TOi	0.10	0.15	0.13	0.13	0.14	0.09	0.14	0.11	0.11	

B-

	BAe	BEe	DEe	FAe	KEe	NDe	NGe	NEe	SAe	TOe
BAe		13	14	14	12	11	13	10	11	15
BEe	0.05		10	10	10	7	9	8	8	10
DEe	0.05	0.03		12	13	12	12	11	9	13
FAe	0.04	0.02	0.03		6	11	11	7	3	8
KEe	0.04	0.03	0.03	0.01		6	11	5	5	12
NDe	0.04	0.02	0.03	0.02	0.02		13	7	6	10
NGe	0.05	0.04	0.03	0.02	0.03	0.04		9	10	12
NIe	0.04	0.03	0.03	0.01	0.02	0.02	0.03		5	9
SAe	0.05	0.03	0.02	0.01	0.01	0.02	0.03	0.02		7
TOe	0.07	0.04	0.04	0.02	0.03	0.03	0.04	0.03	0.03	


M. erythroleucus
M. natalensis


NI
TO
BE
Gambia
DI
NG
SA
FA
KE
BA
Kedougou
ND
10 km



M. natalensis
M. erythroleucus
y=0.03x+0.04
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
1
2
3
4
5
Ln (geographic distance, km)
$F_{ST}^{ENA}/(1-F_{ST}^{ENA})$