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

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

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

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**Running title:** Population genetic structure of *Mastomys*

**Abstract**

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

## Introduction

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

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

provided and the habitat protected, that is where interspecific competition, predation and climatic pressures are strongly reduced (Boursot *et al.* 1993). Environmental stability and resource permanence may imply higher densities than in wild populations, such as in house mice (Pocock *et al.* 2005). High patch quality may reinforce the effects of habitat patchiness in reducing dispersal rates and increasing philopatry (Lin *et al.* 2006). Alternatively, human transports sometimes increase migration for commensal species between distant human settlements (Britton-Davidian 1990; McKinney 2006).

Only few studies have empirically investigated the effect of patchiness in synanthropic populations on population genetic structure (Pocock *et al.* 2004). Two alternative empirical approaches may be chosen to this end. One may be to work on commensal and wild populations of the same species, but in different locations in order to ensure that wild and commensal populations are not connected by gene flow. In this case, landscape contexts are not rigorously comparable. The other approach may be to work on two closely related species living in the same area, one having commensal and the other having wild populations. The effects of commensalism and of species identity are thus not formally disentangled, and the observed differences in genetic structure between both species may result from a complex interplay with population history or biogeography. Separating these effects is challenging but the comparative analysis of genetic structure may be a first step to carefully examine each alternative hypothesis (population history, geography, or habitat) that explain genetic patterns, and thus to provide demographic and ecological hypotheses that can be further tested (Matocq *et al.* 2000). Another challenge in species comparison is to have common genetic markers on both species, to avoid locus effects on genetic structure. This implies cross-priming which can lead to null alleles in one or both species when using microsatellites. Nevertheless, recent methods have been developed to account for the effects of null alleles in genetic analyses (Chapuis 2006; Chapuis & Estoup 2006; Wagner *et al.* 2006).

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

were obtained using an adapted (Leblois *et al.* 2003) nonparametric ABC bootstrap procedure from DiCiccio & Efron (1996).

*Assignment tests*

The effect of null alleles on assignment tests has never been investigated. We have thus decided to perform assignment tests on both the original datasets and the datasets that had been corrected for null alleles using the so-called INA (for including null alleles) traditional method described in Chapuis & Estoup (2006) and implemented in FREENA. Whereas null alleles can involve several alleles, the INA method attributes them a single allelic state (the same for all the loci and all the populations).

Individual assignment tests using the frequency method of Paetkau *et al.* (1995) were performed using the software GENECLASS2 (Piry *et al.* 2004). The frequency method is the most frequently employed in empirical studies against other assignment criterions (Guinand *et al.* 2002). GENECLASS2 uses multilocus genotypes to identify putative first-generation immigrants within each sampled population and the most likely source of these immigrants, on the basis of the likelihood that the individual's genotype originated in the population from which it was sampled. The statistical criterion computed was the likelihood of the individual genotype within the population where the individual has been sampled (L_home), as recommended when all putative source populations for immigrants have not been sampled (Piry *et al.* 2004). A probability of belonging to each of the potential population was calculated for every individual sampled (10 000 simulated individuals) following the simulation algorithm of Paetkau *et al.* (2004), and using the critical probability value $\alpha = 0.01$. This resampling method was found to perform better than other ones that generally result in an excess of resident individuals being excluded (Piry *et al.* 2004). Relative migrant rates were compared between both 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

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

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

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

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

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

For the commensal species *M. natalensis*, there was a clear pattern of isolation by distance between populations, suggesting first that savannas and fields are partial barriers to gene flow for this species, as already shown by genetic differentiation levels. Dispersal of *M. natalensis* through non-commensal areas may be limited by physical properties of the surrounding environment, but also by inter-specific competition or predation pressures that may be higher in outdoor environments (Boursot *et al.* 1993). It is not clear whether dispersal was limited in this species by patchiness, by the effects of resource permanence and stability on social structure (Lin *et al.* 2006), or by both factors. Evaluating the effects of population density on dispersal rates would help to evaluate the mechanisms that explain population structure in this species. Secondly, the isolation by distance pattern showed that dispersal occur primarily between neighbouring villages, and not at random or towards the town of Kedougou, as it could be expected in the case of a major human-mediated dispersal. In the eastern Senegal, human transport that often explain the homogenisation of commensal faunas (McKinney 2006) was not sufficiently implicated for *M. natalensis* to counteract the effects of patchiness and of geographic proximity. Whereas historical factors related to man may explain colonization patterns in commensal rodents, Britton-Davidian (1990) had also shown that dispersal by man would not be a prominent feature moulding microgeographic population structure in house mice.

## Conclusion

Genetic structure was clearly different between the commensal populations of *M. natalensis* and the wild populations of *M. erythroleucus* in south-eastern Senegal, with a higher genetic differentiation between populations in *M. natalensis* and a higher genetic diversity within populations in *M. 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
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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 |
| ***ā*** | **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 |

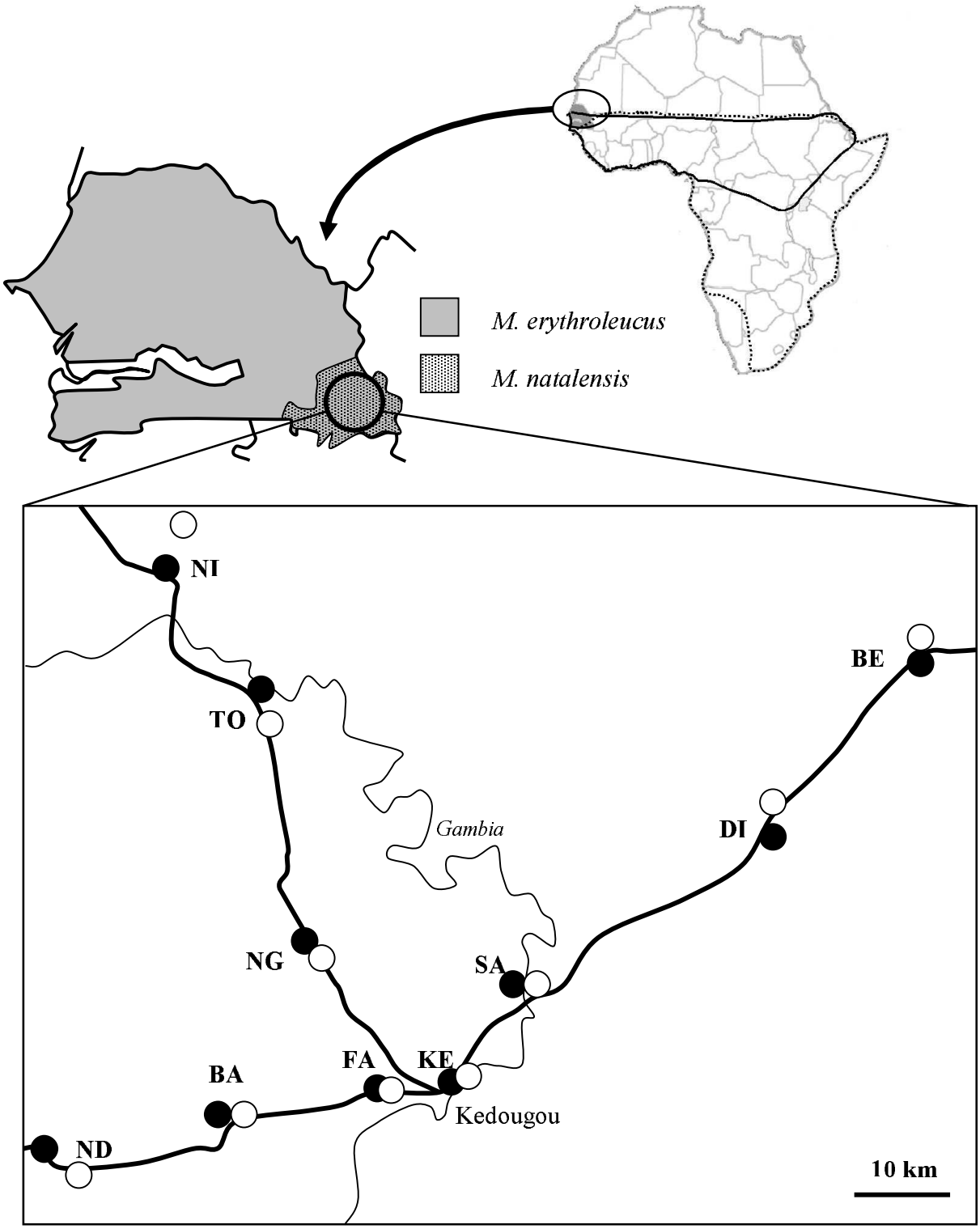
**Table 3.** Pairwise $F_{ST}^{ENA}$ values (below the diagonal) calculated for all loci, and counts of significant ($P < 0.05$) genotypic tests of allele frequency differences (above diagonal) between samples. A- *M. natalensis*; B- *M. erythroleucus*

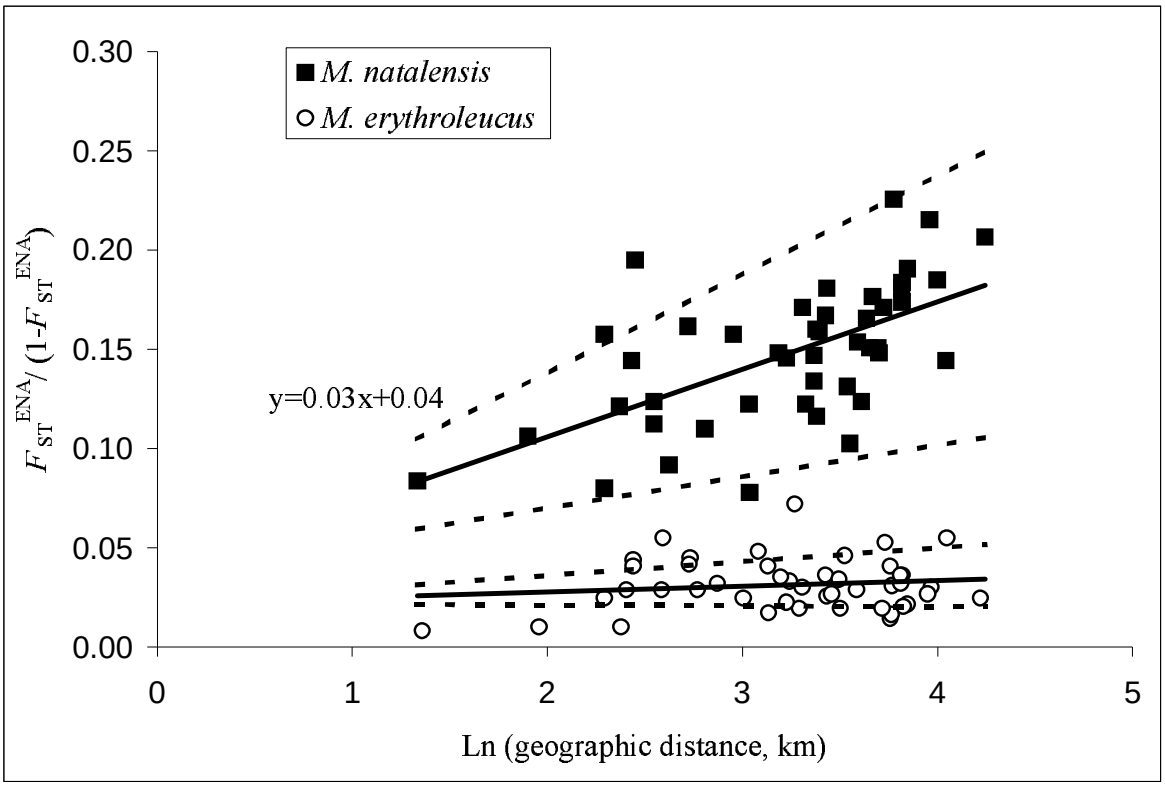
**A-**

| | 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
DI
Gambia
NG
SA
FA
KE
BA
ND
Kedougou
10 km


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