Reproductive characteristics of three sympatric species of *Mastomys* in Senegal, as observed in the field and in captivity

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Summary. – In Senegal, the occurrence of three sympatric species of the genus *Mastomys* is now well established. Reproductive studies were undertaken on field samples from different biotopes and by laboratory breeding experiments. For the three species the litter size at birth in captivity is lower than the number of embryos recorded from pregnant females in the field. The sex-ratio at birth and weaning is not different from 1/1. The other reproductive characteristics can be summarized for each species as follows :

- *M. erythroleucus* females, after a 21-day gestation period, give birth to 7.1 individuals, 80 % of which survive to weaning. The mean interval between two successive litters is about 61 days.
- For *M. huberti* females, the lengh of the gestation period is about 22 days. The mean litter size is about 6.4 and 72 % of newborn survive to weaning. Sixty eight days separate two successive litters.
- *M. natalensis* females, after a 21-day gestation period, produce about 6.5 young individuals every 53 days and only 50 % of them survive to weaning.

It seems that the larger distribution of *M. erythroleucus*, compared to the restricted distribution of the other species could be explained by its greater reproductive performances that allow this species to colonize new habitats faster than the other ones.

Résumé. – Au Sénégal, l'existence de trois espèces sympatriques du genre *Mastomys* est maintenant bien établie. Des études sur leur reproduction ont été entreprises à partir de données de terrain dans différents biotopes et à partir d'élevages. Pour les trois espèces, la taille des portées à la naissance en captivité est inférieure au nombre moyen d'embryons observés chez les femelles dans la nature. Le sex-ratio à la naissance et au sevrage est équilibré. Les autres caractéristiques de la reproduction peuvent être résumées comme suit pour chaque espèce :

- Les femelles de *M. erythroleucus,* après une gestation de 21 jours, donnent naissance à 7,5 jeunes, dont 66 % survivent au sevrage. L'intervalle moyen entre deux portées successives est de 61 jours.
- Pour les femelles de *M. huberti,* la gestation est d'environ 22 jours. La taille des portées est de 6,6 jeunes et 60 % d'entre eux survivent au sevrage. Soixante-huit jours en moyenne séparent deux portées successives.
- Les femelles de *M. natalensis,* après une gestation de 21 jours produisent 6,5 jeunes tous les 53 jours et 50 % d'entre eux survivent au sevrage.

Il semble que la plus grande répartition de *M. erythroleucus,* comparée à celles plus réduites des autres espèces, puisse s'expliquer par ses meilleures performances reproductives lui permettant de coloniser plus vite de nouveaux milieux.

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INTRODUCTION

Rodents of the genus *Mastomys* are commonly called the multimammate rats, because the females present the largest number of mammae known among the Murinae subfamily : 8 to 12 pairs. As a consequence of this anatomical character, they present high reproductive performances and outbreaks have been described throughout their distribution area (see Fiedler 1988, and Leirs 1992 for review).

Mastomys rodents are present in almost all the African continent south of the Sahara desert. Different karyological forms have been described (see Hubert *et al.* 1983 and Britton-Davidian *et al.* 1995 for review). But until the beginning of the eighties, with the work of Green *et al.* (1980), in Southern Africa, the taxonomic position of sympatric forms was not well established. For that reason many studies concerning *Mastomys* reproduction cannot be used today as we don't know what species is concerned, or sometimes because it can be suspected that sibling species have not been identified.

Some years ago we have demonstrated the occurrence of three different species of *Mastomys* in Senegal by the means of karyological analysis and crossing experiments (Duplantier 1988, Duplantier *et al.* 1990 a). Their geographic and ecological distributions are now well known (Duplantier et Granjon 1988, Duplantier *et al.* in press). The most common species, *M. erythroleucus,* occurs everywhere in the country and is characterized by a diploid number (2 N) of 38 and a autosomal fundamental number (aFN) of 52. The two other species share the same diploid number (2 N = 32) but have different aFN : *M. huberti* (*sensu* Petter 1977 = *M. hildebrandtii, sensu* Wilson and Reeder 1993) with aFN of 44, lives only in the south of the country, along the Atlantic seaside and in the north along the Senegal river. *M. natalensis* presents an aFN of 54 and is restricted to the south-eastern part of the country. As far as the habitat preferences of the three species are concerned, we have observed that *M. erythroleucus* is a generalist living in all kinds of biotops whereas the two other species are specialist : *M. huberti* is restricted to humid areas either natural or cultivated, like ricefields and marshes, and *M. natalensis* lives only inside the villages.

These ecological differences between three congeneric species showing very little morphological, biometrical (Duplantier 1988), genetical (Duplantier *et al.* 1990 b) and molecular (Chevret *et al.* 1994) differences, prompted us to compare their reproductive characteristics. Do these characteristics show any species-specific trend ? How could they be related to what is known about habitat preferences and natural history of these species ?

METHODS

This study was conducted during two periods : 1983 to 1986 and 1990 to 1994, but as no significant differences appear between these two periods, the results are pooled hereafter.

The first set of data was recorded in the field. Just after being trapped, females were autopsied and the following parameters recorded : body weight and measurements of females, number and size of embryos. Twenty *M. erythroleucus* females were trapped pregnant in the field but not autopsied. They were housed in individual cages and gave birth to a litter a few days later.

For the breeding experiments, only pairs composed of adult wild-caught animals have been used. They were housed in plastic cages with a metallic grid cover. Cages of two different sizes were used : 40 × 40 × 18 cm and 40 × 20 × 18 cm. The cage floor was covered with shavings. A tin and straw were put in each cage in order to allow rodents to build a nest. Rabbit pellets and water were provided *ad libitum* and germinated millet and insects from time to time. As there was no artificial light, day length was the same as outside : from 11 to 13 hours according to the season. The animal room was heated for the night during the coldest months (December to February). The newborn were removed from the parental cage after weaning, between one and two months of age generally, but anyway as soon as a new litter appears. The captivity conditions remained the same all along the study. Only pairs that have spent at least one month together have been considered in the results presented hereafter. Sex determination at birth was realized only on a few litters at the end of the experiments as we prefered to avoid handling of newborn.

The first parameter recorded in captivity was the litter size at birth. For *Mastomys* like for most Murids, weaning occurs at about three weeks of age : to know how many newborn survive to this critical period, survival at 30 days was estimated on a small number of litters. We also recorded the percentage of fertile pairs : we called fertile pair, a pair that give birth to a litter at least once during their captivity. In order to know the potentialities of reproduction it is not sufficient to know the total production of offspring per female, but it is also necessary to know the time needed to reach this number. First we have calculated the mean time between pairing and the birth of the first litter and then we have recorded the interval between two consecutive litters.

RESULTS

Field data

The mean number of embryos (Table 1) was about 12 for *M. erythroleucus* and *M. huberti :* (difference between species not significant, t = 0.816). For *M. natalensis* this mean (8.6) is significantly lower than for the two other species (t = 5.69, p < 0.001, for M.n./M.e. ; t = 5.886, p < 0.001, for M.n./M.h.) and the maximum number of embryos for this species is about twice lower than that of *M. huberti* (13 vs 27).

TABLE 1. – Number of embryos, observed in the field for the genus *Mastomys* in Senegal, according to autopsies of wild females.

	Mean	SD	min - Max
M. erythroleucus (n = 150)	11.8	3.7	1 - 21
M. huberti (n = 136)	12.2	4.5	1 - 27
M. natalensis (n = 30)	8.6	2.6	3 - 13

There were significant correlations between the number of embryos and the weight of the mother : n = 150, r = 0.396, $p < 0.001$ for *M. erythroleucus ;* n = 134, r = 0.369, $p < 0.01$ for *M. huberti ;* n = 32, r = 0.456, $p < 0.01$ for *M. natalensis.* The number and the size of embryos were not correlated : n = 150, r = 0.17, for *M.e. ;* n = 134, r = – 0.037 for *M.h. ;* n = 32, r = 0.102 for *M.n.* We compared in *M. erythroleucus,* the mean number of embryos between indoor and outdoor populations : the difference is not significant (n = 54, $\bar{X}$ = 10.9, sd = 3.4, for indoor populations ; n = 78, X = 12.0, sd = 3.8, for outdoor populations ; t = 1.74, p = 0.09).

For the *M. erythroleucus* females trapped pregnant in the field that gave birth to a litter in captivity, the mean litter size at birth was 10.1 (sd = 3.8). This was significantly higher (t = 3.60, $p < 0.001$) than the litter size at birth observed for captive females of the same species ($\bar{X}$ = 7.1), but significantly lower (t = 2.08, $p < 0.05$) than the mean number of embryos recorded in wild females ($\bar{X}$ = 11.8).

Breeding experiments

M. erythroleucus presents a significantly higher litter size than *M. huberti* (t = 2.15, p = 0.03) and *M. natalensis* (t = 2.42, p = 0.02) (Table 2). The difference between *M. natalensis* and *M. huberti* is not significant (t = 0.91, p = 0.36). Sex-ratio at birth was not significantly different from 1/1 for each species.

Survival at 30 days (Table 2) is about 80 % for *M. huberti* and *M. erythroleucus* (no significant difference between these species : χ^2 = 1.67, p = 0.2) and significantly lower for *M. natalensis* (M.n./M.e. : χ^2 = 12.67, $p < 0.001$; M.n./M.h. : χ^2 = 4.83, $p < 0.05$).

Concerning the percentage of fertile pairs (Table 2), *M. erythroleucus* and *M. huberti,* present once more very similar results : about 80 % (no significant difference : χ^2 = 2.26, $p < 0.2$). For *M. natalensis,* only one of two pairs gives birth to a litter, this proportion is significantly lower than for *M. erythroleucus* (χ^2 = 15.96, $p < 0.001$) and *M. huberti* (χ^2 = 5.79, $p < 0.02$).

The mean number of litters per female (Table 2) is very similar for the three species : about 2.8.

TABLE 2. – Reproduction in captivity for the three species of *Mastomys* living in Senegal : 1. Fertility, litter size and survival.

	% of fertile pairs			Number of litter per female				Litter size at birth				Survival at 30 days			
	Fertile pairs	Total pairs	%	Nb. of pairs	Mean	SD	min - Max	Nb. of litters	Mean	SD	min - Max	Nb. of litters	Nb. of live young at birth	Nb. of live young at 30 days	Survival
M. erythroleucus	69	82	84%	69	2.8	2.4	1 - 13	202	7.1	3.0	1 - 16	14	126	101	80%
M. huberti	42	57	74%	42	2.7	2.2	1 - 9	105	6.4	2.5	1 - 11	9	68	49	72%
M. natalensis	20	40	50%	20	2.7	2.2	1 - 7	58	6.0	2.1	1 - 10	4	34	17	50%

The mean time between pairing and the birth of the first litter (Table 3) is the same for the three species : about 65 days. The maximum intervals observed are over six months. The interval between two consecutive litters (Table 3) is about 60 days (range : 53-68) and presents no significant difference between species. The minimum interval between consecutive litters is an indicator of the length of the gestation period, as we know that there is a post-partum oestrus in *Mastomys* (Johnston and Oliff 1954).

From these data we can conclude that this gestation period is about 21-22 days for the three species, even for *M. huberti,* for which the minimum interval between consecutive litters is 26 days, but the minimum interval between pairing and birth of the first litter is 22 days.

TABLE 3. – Reproduction in captivity for the three species of *Mastomys* living in Senegal : 2. Intervals between pairing and first litter, and between consecutive litters.

Species	Interval between pairing and birth of first litter				Interval between two consecutive litters			
	Nb of intervals	Mean	SD	min - Max	Nb of intervals	Mean	SD	min - Max
M. erythroleucus	68	66 days	54	26 - 278	120	61 days	44	22 - 229
M. huberti	36	65 days	48	22 - 200	72	68 days	37	26 - 245
M. natalensis	19	66 days	44	21 - 204	36	53 days	41	21 - 257

DISCUSSION

The mean number of embryos recorded for the studies previously published ranged between 4.5 and 14.7 with a mode at 11-12 (Table 4) which is similar to the values for *M. erythroleucus* and *M. huberti* in our study. Only a few studies present lower results than those of *M. natalensis* here. The most surprising are probably those recorded by Rahm (1970) in eastern Zaire with only 4.5 embryos. According to Brambell and Davis (1940) and Hanney (1965) the number of embryos is positively correlated to the weight of the mother. We found the same correlation here : but we had only information on the total mass of females before autopsies and it would have been more correct to use the weight of the mother without the mass of the embryos. As Delany and Happold (1979), Dieterlen *(in litt),* Field (1975), Leirs (1992), Neal (1977) and Telford (1989) we have observed embryo resorption for the three species but we have not quantified its importance. For *M. erythroleucus,* evidence for embryo resorption could also be deduced from the significant difference between the mean number of embryos (11.8) and the litter size at birth in wild females (10.8). In contrast to our study, Chidumayo (1984) found a significant difference between indoor and outdoor populations in Zambia : it is possible that the situation is different between East and West Africa, but it is also possible that sibling species have not been identified in Chidumayo's study. This remark is also valid for Sheppe (1973) who observed important differences according to different biotops.

Average data for breeding colonies (*M. natalensis* or *M. coucha* ?) in South Africa range from 6.6 individuals per litter (Davis 1963) to 8.5 (Meester 1960). Oliff's study (1953) based upon more than one thousand litters led to an intermediate value : 7.3. This number is quite similar to this of *M. erythroleucus,* but higher than those of the Senegalese *M. natalensis.* Oliff (1953) found a significant higher number of females at birth but with a very large sample : more than 8000 newborn.

TABLE 4. – Numbers of embryos *in utero* previously recorded for the genus *Mastomys.*

REFERENCES	COUNTRY	N	Mean	SD	Min.	Max.
Hatt, 1940	Zaire	5	9.2	4.8	3	16
Brambell & Davis, 1941	Sierra Leone	17	11.8	2.7	7	17
Chapman et al., 1959	Tanzania	10	11.2		4	11
Goormans & Christiansen, 1960	Zaire	23	9.6			
Hanney, 1965	Malawi	27	11		7	17
Coetzee, 1965	South Africa	114	9.5	3.2	1	19
Verehyen & Verschuren, 1966	Zaire (Garemba)	3	11		11	11
Dieterlen, 1967 and in litt.	Zaire	13	9.8		6	13
Reichsten, 1967	Tanzania	34	13.4		7	17
Delany & Neal, 1969	Uganda	41	12.6	2.9	7	19
Rahm, 1970	Zaire	33	4.5		1	12
Smithers, 1971	Botswana		11			
Hubbard, 1973	Tanzania	40	6.6	3.7	2	16
Sheppe, 1973	Zambia		11			
Taylor & Green, 1976	Kenya	76	12		5	24
Baker & Meester, 1977	South Africa		11.3			
Cross, 1977	Sierra Leone	2	9		9	9
Cheeseman & Delany, 1979	Uganda		12.1			
Smithers & Wilson, 1979	Zimbabwe	17	10.9		6	20
Chidumayo, 1980	Zambia		12			
Hubert, 1982	Senegal				7	19
Verschuren et al., 1983	Zaire (Virunga)	13	8.4	3.1	1	12
Chidumayo, 1984	Zambia (outdoors)	95	12.4		1	20
Chidumayo, 1984	Zambia (indoors)	10	7.4		4	11
Gautun & Sicard, 1985	Burkina-Faso	21	14.7			28
Gliwicz, 1985	Mozambique	6	7.5	0.9	7	9
Happold, 1987	Nigeria		10		3	17
Telford, 1989	Tanzania (Morogoro)	427	11.7		3	23
Leirs, 1992	Tanzania (Morogoro)	234	11.3	2.96	1	23
Leirs, 1992	Tanzania (Dakawa)	19	11.7			

For *M. natalensis,* the survival at weaning is also lower than those observed in breeding colonies in South Africa by Oliff (1953) : 66 %, and Meester (1960) : 83 %. In contrast to Hubert and Adam (1975) for a *M. erythroleucus* population of Senegal, we have not observed a significant difference for survival at weaning between males and females.

As far as the percentages of fertile pairs is concerned, it seems that the lower rate presented by *M. natalensis* is a consequence of a high mortality of one of the two partners (male or female) between one and two months of cohabitation. In breeding experiments, for all rodents species, mortality is usually highest just after pairing. We have no explanations for the particular case of these *M. natalensis.* For the African murids it seems that the only available data about percentage of fertile pairs concerns three species of the genus *Lemniscomys* in Ivory Coast (Gautun 1972) and two species of the genus *Arvicanthis* (Ducroz *et al.* unpubl. data). The observed percentages for *Lemniscomys* species (33 % to 75 %) and *Arvicanthis* ones (25 % and 42 %) are lower than those observed for the *Mastomys* species (50 % to 84 %) : *Mastomys* seems more fertile than the two other genus or are better adapted to captivity conditions.

If we compare field data and captivity data, for the three species, it appears that the litter size at birth in captivity (table 2) is significantly lower than the mean number of embryos (table 1) recorded by autopsies of females trapped in the field (t = 11.89 for *M. erythroleucus ;* t = 12.15 for *M. huberti* and t = 4.72 for *M. natalensis*). This difference is quite low for *M. natalensis* and important for *M. huberti.* It seems that *M. natalensis* is less affected by captivity conditions than *M. huberti :* this could be related to the commensal way of life of these Senegalese *M. natalensis.* There are different reasons for this reduction of fertility. The first one is embryo resorption that occurs in captivity as well as in the field, but could be more important in captivity, because of stress and less diversified food ressources. This is well illustrated for *M. erythroleucus,* by the fact that litter size at birth in wild females is significantly higher than that of captive females (10.1 vs 7.1). Another problem is cannibalism by parents : as the cages are checked only once a day, there may be several hours between the birth and the observation of the litter. So the litter size recorded is sometimes lower than the true number of newborn. In Senegal, Hubert and Adam (1975) indicate a litter size at birth for *M. erythroleucus* between 7 and 13, whereas Hubert (1982) for the same species and population observed a number of embryos per pregnant female between 7 and 19. In South Africa also the values for litter size at birth (Davis 1963, Oliff 1953, Meester 1960) are lower than those for numbers of embryos (Coetzee 1965, Baker and Meester 1977).

The mean numbers of litter per female are about twice smaller than those published by Leirs (1992) : 2.8 vs 5.2 litters. But the two experiments are not really comparable. Our study was realised with adult wild-caught animals and the pairs survived for different periods whereas in Leirs's study : "... animals were paired at young age and kept together for up to one year."

In conclusion, we can summarize the results of reproduction in captivity as follows. If we take into account the mean litter size at birth, the survival at weaning, the mean number of litters per female and the proportion of fertile pairs (see data in table 2) : the mean number of young produced by one female during its captivity was 13 for *M. erythroleucus,* 9 for *M. huberti* and only 4 for *M. natalensis.* For the South African breeding colonies, Oliff (1953) indicated a mean of 21, but without taking into account the reductions due to survival at weaning and percentage of fertile pairs. If we consider now the maximum numbers for litter size and for the number of litters per female, the maximum number of young produced per female is then of 140 for *M. erythroleucus,* 53 for *M. huberti* and 18 for *M. natalensis.* With these numbers, it is possible to understand, at least for *M. erythroleucus,* how outbreaks can occur when the environmental conditions are appropriate. There is a gradient between the three species, for the mean number as well as for the maximum number. The most prolific species *(M. erythroleucus)* is a generalist, whereas the less prolific ones (*M. huberti* and *M. natalensis*) are specialist living in particular habitats. A first hypothesis to explain the restriction to humid zones of *M. huberti* was to suppose that this species had higher water requirements than *M. erythroleucus.* According to ecophysiological studies conducted in laboratory conditions and on a small sample (Maiga 1984), it seems that this is not true. So, according to our reprodutive data, another hypothesis appears to be more likely. We know that reproduction in African rodents is correlated to rainfall (Neal 1977, 1986) and that at the end of the dry season, in Sahelian countries at least, populations of *Mastomys* reach their lower annual densities. At this time also their distributions are restricted and the *Mastomys* survive only in refuge areas like villages and humid zones.

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If we compare field data and captivity data, for the three species, it appears that the litter size at birth in captivity (table 2) is significantly lower than the mean number of embryos (table 1) recorded by autopsies of females trapped in the field (t = 11.89 for *M. erythroleucus ;* t = 12.15 for *M. huberti* and t = 4.72 for *M. natalensis*). This difference is quite low for *M. natalensis* and important for *M. huberti.* It seems that *M. natalensis* is less affected by captivity conditions than *M. huberti :* this could be related to the commensal way of life of these Senegalese *M. natalensis.* There are different reasons for this reduction of fertility. The first one is embryo resorption that occurs in captivity as well as in the field, but could be more important in captivity, because of stress and less diversified food ressources. This is well illustrated for *M. erythroleucus,* by the fact that litter size at birth in wild females is significantly higher than that of captive females (10.1 vs 7.1). Another problem is cannibalism by parents : as the cages are checked only once a day, there may be several hours between the birth and the observation of the litter. So the litter size recorded is sometimes lower than the true number of newborn. In Senegal, Hubert and Adam (1975) indicate a litter size at birth for *M. erythroleucus* between 7 and 13, whereas Hubert (1982) for the same species and population observed a number of embryos per pregnant female between 7 and 19. In South Africa also the values for litter size at birth (Davis 1963, Oliff 1953, Meester 1960) are lower than those for numbers of embryos (Coetzee 1965, Baker and Meester 1977).

The mean numbers of litter per female are about twice smaller than those published by Leirs (1992) : 2.8 vs 5.2 litters. But the two experiments are not really comparable. Our study was realised with adult wild-caught animals and the pairs survived for different periods whereas in Leirs's study : "... animals were paired at young age and kept together for up to one year."

In conclusion, we can summarize the results of reproduction in captivity as follows. If we take into account the mean litter size at birth, the survival at weaning, the mean number of litters per female and the proportion of fertile pairs (see data in table 2) : the mean number of young produced by one female during its captivity was 13 for *M. erythroleucus,* 9 for *M. huberti* and only 4 for *M. natalensis.* For the South African breeding colonies, Oliff (1953) indicated a mean of 21, but without taking into account the reductions due to survival at weaning and percentage of fertile pairs. If we consider now the maximum numbers for litter size and for the number of litters per female, the maximum number of young produced per female is then of 140 for *M. erythroleucus,* 53 for *M. huberti* and 18 for *M. natalensis.* With these numbers, it is possible to understand, at least for *M. erythroleucus,* how outbreaks can occur when the environmental conditions are appropriate. There is a gradient between the three species, for the mean number as well as for the maximum number. The most prolific species *(M. erythroleucus)* is a generalist, whereas the less prolific ones (*M. huberti* and *M. natalensis*) are specialist living in particular habitats. A first hypothesis to explain the restriction to humid zones of *M. huberti* was to suppose that this species had higher water requirements than *M. erythroleucus.* According to ecophysiological studies conducted in laboratory conditions and on a small sample (Maiga 1984), it seems that this is not true. So, according to our reprodutive data, another hypothesis appears to be more likely. We know that reproduction in African rodents is correlated to rainfall (Neal 1977, 1986) and that at the end of the dry season, in Sahelian countries at least, populations of *Mastomys* reach their lower annual densities. At this time also their distributions are restricted and the *Mastomys* survive only in refuge areas like villages and humid zones.

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When the next breeding season begin, it is obvious that from this refuge areas, *M. erythroleucus* with its higher fertility can colonize new habitats faster than the two other species.

Concerning *M. natalensis* it is necessary to remember that in Senegal, this species reaches its north-western limit. There *M. natalensis* is only commensal, although indoor and outdoor populations are known in Eastern and Southern Africa. We have also demonstrated (Duplantier *et al.* 1990 b) that the Senegalese populations of *M. natalensis* present a low genetic variability. For these reasons, the lower fertility of these particular populations cannot be generalised to the whole distribution area and reproductive studies are needed from Eastern and Southern Africa.

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