POPULATION STRUCTURE AND REPRODUCTION OF *HEIMYSCUS FUMOSUS* (BROSSET *ET AL.*, 1965) IN SOUTH-WESTERN GABON

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RÉSUMÉ

La reproduction et la structure de population du Muridé africain Heimyscus fumosus ont été étudiées dans une population sauvage du sud-ouest du Gabon. Pour chaque animal, nous avons noté, lors de l'autopsie, s'il était sexuellement actif et, pour les femelles, si elles étaient prégnantes ou allaitantes. De plus, l'âge des animaux a été estimé en fonction de leur usure dentaire et de leur poids. Le sexe-ratio obtenu était équilibré quels que soient l'âge ou la saison. Bien que l'âge de la puberté diffère entre individus de même sexe, les femelles atteindraient leur maturité sexuelle plus tardivement que les mâles. La plupart des mois, de larges gammes de classes de poids et de classes d'âge dentaires étaient présentes. Bien que des individus sexuellement actifs aient été capturés tout au long de l'année, les femelles allaitantes et prégnantes ne l'ont été que d'août à mars, tandis que les très jeunes individus l'ont été d'octobre à mars. Ainsi, la reproduction de H. fumosus serait partiellement saisonnière, avec une interruption d'avril à juillet (fin de la petite saison des pluies et début de la grande saison sèche). Nous discutons du rôle potentiel de la disponibilité des ressources sur cette saisonnalité de la reproduction.

SUMMARY

Population structure and annual reproduction cycle of the De Balsac's mouse (Heimyscus fumosus) were studied in a wild population of south-western Gabon. The reproductive status of the mice was investigated at autopsy, and age of each animal was estimated by tooth wear patterns and body weight. Sex-ratio was equilibrated whatever the season and the ageclass. Females tended to reach sexual maturity more slowly than males. However, the average age at puberty differed between individuals of the same sex. A wide range of tooth-wear-classes and weight-classes were present in most months of the year, and sexually active individuals of both sexes were captured in most months. However pregnant or lactating females were only captured from August to March, while very young individuals were only captured from October to March. Thus, the reproduction of H. fumosus would be partly seasonal with an interruption from April to July (end of the short wet season, and beginning of the long dry season). We discussed the potential role of food availability on this seasonality.

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INTRODUCTION

Many researches dealt with the reproduction of African rodents; however, the number of species for which there is detailed knowledge is limited, and most of them are savannah species (review in Happold, 2001). Reproduction of some rainforest species (e.g. Praomys tullbergi, Hylomyscus stella, Malacomys longipes, Hybomys univitatus) was studied by Dubost (1968), Delany (1986), Happold (1977, 1978), Duplantier (1982) and Struhsaker (1997). Only one study deals with the reproduction of the De Balsac's mouse (Heimyscus fumosus): Duplantier (1982), after a six months study in Gabon, suggested a peak of reproduction between January and March. Because of their short gestation and lactation, rodents may be expected to be particularly responsive to seasonal changes in the environment and able to modify their reproductive activities accordingly. In rainforest, the reproductive activity of rodents would be strongly related to seasonal pattern of rainfall (Happold, 1996). Near the equator, reproduction may occur throughout the year (but with seasonal peaks of births; e.g. Happold, 1977; Duplantier, 1982); while in West Africa, reproduction is mostly at the end of the wet season and the early part of the dry season (Happold, 1978; Happold, 1996).

This paper presents data on the population structure and annual reproduction cycle of *H. fumosus* in a population of south-western Gabon.

MATERIAL AND METHODS

STUDY SITE

Created in January 1998, the "Aire d'Exploitation Rationnelle de Faune (AERF) des Monts Doudou" (south-western Gabon) comprises 332 000 hectares. Our study was conducted in its eastern part (02°09S-10°30E), in a lowland primary forest (110 m A.S.L.).

The seasonal distribution of rainfall is bimodal with a small rainy season from March to May, and a long one from October to December. Temperature is more or less uniform along the year, with monthly minima between 19° and 23°, and maxima between 24° and 29°C.

SAMPLING METHODS

Between April 2000 and March 2001, small mammals were trapped monthly with two types of devices: (i) six lines (one kilometre long each) of 200 traps, spaced at five meters, including one Sherman and one metal snap trap alternatively. Each line was functional for seven days; (ii) two pitfall lines with drift fences (each line 300 m long), comprising 30 buckets spaced at five meters interval. Trapping sessions lasted 21 consecutive days per pitfall line (see details in Nicolas & Barrière, 2001).

METHODS OF ANALYSIS

Body weight (in grams) was taken on freshly killed mice. To determine the reproductive status of each individual, we recorded for males, the position of testes (scrotal or not), and for females, the perforation of the vagina (indicating an oestrus status), the presence of embryos in the uteri (indicating pregnancy), and swollen teats and a naked ring around the nipple (indicating lactation). Males were considered to be sexually active when the testes were scrotal, and females when they were in oestrus, pregnant or lactating. Embryos were counted to estimate litter sizes.

Two methods were employed to estimate the relative age of the collected animals: tooth wear and body weight. Rodent molars have a fair number of cuspids that gradually eroded with aging. This process goes slower at the harder enamel sides of the cuspids, faster where the softer dentine is exposed. As a result, different patterns of dentine surfaces with enamel lining originate during the wearing process. These tooth wear patterns give an indication of age because the intensity of wearing is a function of the time that the rodent spent using its teeth (Leirs, 1995), and it is regularly employed to estimate age-classes (e.g. Gliwicz, 1985; Chou et al., 1998; Yu & Lin, 1999; Innes et al., 2001). All specimens were age-classified using the following stages of tooth eruption and tooth wear patterns of the maxillary toothrows: age-class 0: M³ not yet fully erupted; age-class 1: all cheekteeth fresh but fully erupted, the exposed dentine of the three cusps of the first row of M¹ are not yet fused; age-class 2: wear is light, dentine-bridge between the cusps of the first row of M¹ becomes progressively wider as the cusps wear down; age-class 3: wear is obvious, the bottom of the grove between row 2 and 3 is reached and the grove is interrupted on the lingual side of the molar; age-class 4; wear is extensive. the dentine of row 2 and 3 make contact with each other; age-class 5: wear is severe, M¹ is heavily eroded and all rows are communicating. Finally, specimens were grouped in weight classes of 2 grams each, that were used to provide some insight in the age structure of the population.

Chi-square tests were performed on contingency tables to study interactions among age, sex-ratio and maturity rate. Chi-square tests were also used to investigate seasonal variations in the proportion of young individuals, and the sex ratio.

RESULTS

POPULATION STRUCTURE

The whole population captured included 95 males and 79 females and the overall sex ratio did not differ significantly ($\chi^2 = 1.290$, df = 1, P > 0.05). Moreover, the sex ratio did not vary significantly among seasons ($\chi^2 = 3.542$, df = 3, P = 0.315) or between age-classes (for statistical analysis tooth wear classes 4 and 5 were combined; $\chi^2 = 5.072$, df = 4, P = 0.280).

Depending on the month, one to five tooth-wear classes and three to height weight classes were present in the captures (Figs. 1 and 2 respectively). The age class composition of the population differed significantly among seasons: young of tooth-wear class 0 and of light body weight (< 11 g) were only captured from October to March (Figs. 1 and 2), and only young of tooth-wear classes 0-1 were

captured from October to December (Fig. 1). An ageing of the population was observed from April to September, together with an increase of its mean body weight from June to September. In October, the population was getting younger as indicated by tooth wear pattern and the overall decrease in body weight.

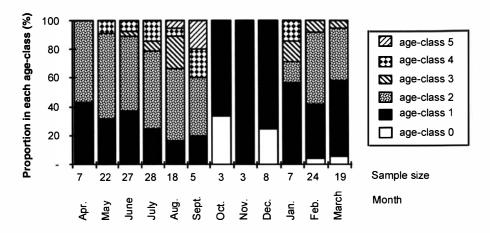


Figure 1. — Proportion of individuals in each tooth-wear class, captured monthly between April 2000 and March 2001 in Monts Doudou lowland forest.

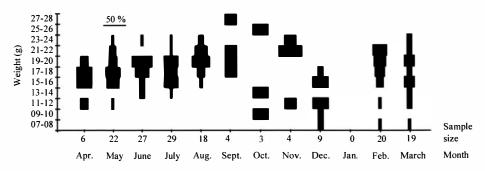


Figure 2. — Proportion of individuals, in each body weight category, captured monthly between April 2000 and March 2001 in Monts Doudou lowland forest (weights were not recorded, for technical reason, in January 2001).

REPRODUCTION

As expected, the percentage of sexually mature individuals of both sexes increased progressively with aging ($\chi^2 = 22.414$, df = 5, P = 0.000) from the age-class 0 to 3 (0-100 %). This increase differed between sexes ($\chi^2 = 5.732$, df = 1, P = 0.017), with females reaching sexual maturity later than males. As an example,

57 % of females of age-class 2 had a perforate vagina, when 87 % of males were scrotal. The youngest pregnant or lactating female was of age-class 1 and the oldest lactating female was classified in age-class 5.

Among the 95 males autopsied, 71 were scrotal. In all months, sexually active males were more abundant than sexually inactive ones, except in April and October were they were less abundant (however only one individual was captured in October) and in March were they were equally represented (Fig. 3). Out of the 79 females examined, 45 were sexually active (either in oestrus, pregnant or lactating). They were more abundant from August to March (67-100 %) than during the rest of the year (0-33 %), except in December (33 %). Moreover, pregnant and lactating females were only captured from August to March. Overall, we captured less pregnant than lactating females (9 % versus 24 %), and only 6 out of 79 females had embryos in the uteri. Litter size ranged from two to four with an average of 2.66.

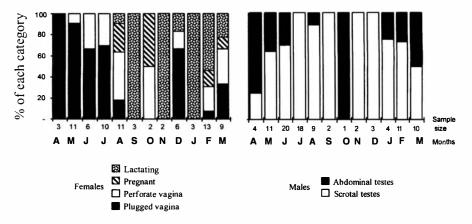


Figure 3. — Proportion of males and females, in each reproductive condition, captured monthly between April 2000 and March 2001 in Monts Doudou lowland forest.

DISCUSSION

In the studied population, the overall sex-ratio is equilibrated whatever the season and the age-class, indicating that differential mortality between sexes is absent or low. Contrastingly, Duplantier (1982) captured more females than males of *H. fumosus*, and seasonal differences in the sex-ratio is known to occur in some small rodents species (e.g. *Mastomys natalensis*, Leirs, 1995) as well as differential mortality rates related to sex (e.g. *Mus musculus castaneus*, Chou *et al.*, 1998). However, differences in trapping success according to age or sex-class may biased some results. In our study, the low trapping success of pregnant females compared to lactating ones may result from a reduced locomotory activity of the former and / or an increased activity of lactating females which have to ingest large quantity of energy in order to supply their offspring with milk (Speakman *et al.*, 2001).

Though sexually active individuals of both sexes were found most of the year, it seems to exist a period of reproduction extending from August to March, i.e. from the end of the long dry season, through the long wet season and the short dry season up to the beginning of the short wet season. For a population of north-eastern Gabon, Duplantier (1982) also found a peak of reproduction at least from January to March (no trapping occurred between September and December).

Rainfall has regularly been proposed as an important factor affecting the timing of reproduction in African tropical murids (Dubost, 1968; Happold, 1977; Duplantier, 1982; Delany, 1986; Happold, 1996; Struhsaker, 1997), and a decrease in reproductive activity at the beginning of the long dry season has been reported for several murid species in Nigeria (Happold, 1977; Happold, 1996), and Gabon (Dubost, 1968). In Gabon, seasonal variations in rainfall are known to induce variations in resource availability for both fruits (Gautier-Hion et al., 1985; Tutin & Fernandez, 1993) and insects (Charles-Dominique, 1977): minimum fruits and insects abundances both occur during the long dry season. In many mammals, seasonal breeding has often been correlated with resource availability and considered as primarily shaped by dietary factors: as long as energy demands are met, mammals usually breed continuously to maximize the life-time reproductive output (Bronsson, 1989). H. fumosus is mainly insectivore, but fruits and seeds also constitute a significant proportion of its diet (V.N. pers. obs.) and its breeding occurs when food is abundant. In north-eastern Gabon, births of some insectivorous species such as galagos (e.g. Galago demidovii) are maximal in January-April, the period of greatest abundance of insects, and minimum in June-July, when insects are scarce (Charles-Dominique, 1977). Finally, birth season of many frugivorous mammals such as monkeys is maximal during the peak of fruit production (Butynski, 1988). This similitude between different trophic guilds may support the relation between resource and reproduction; however, it does not allow to exclude another single driving factor.

In the studied population, the age at sexual maturity varied from age-class 0 to age-class 3, and between sexes. Such intrapopulational and inter-sex variability has been described for several mammal species (Bronsson, 1989). Intra-sexual variability within a population could result from both genetic and environmental factors. Thus maturation of mice can be influenced by population densities and food quantity and/or quality; however not all individuals within a population respond the same way to the same conditions (Mac Adam & Millar, 1999; Eccard & Ylönen, 2001; Singleton et al., 2001). While mammal females often compete with each other for food and nesting resources necessary to sustain energy demands of pregnancy and lactation, males compete for breeding territories and mates; therefore we expect pubertal strategies to differ between sexes. On the whole, H. fumosus females reach their sexual maturity later than males. If, as it was found in house mice, the litter size is positively correlated with body size (Singleton et al., 2001), it could be an interesting strategy for females to delay the age at maturity.

In mean, the litter size of females is 2.66, and females are able to reproduce at a few months and during all their life span indicating a good potential contribution to the population. The only comparative data available for *H. fumosus* is those of Duplantier (1982) who found three embryos in the three pregnant females he trapped. The mean litter size of *H. fumosus* is comparable to those of others African rainforest mice species, which often vary from 2.0 to 3.5 (Dubost, 1968; Happold, 1977; Happold, 1978; Duplantier, 1982; Dudu, 1991). In the African forest murid species, *Praomys tullbergi*, Happold (1977, 1978) also showed that females may

reproduce when they are about four months-old and may continue to breed until at least 12 months of age; their litter size ranges from 1 to 6, and the minimum litter interval is usually 24-26 days. Consequently the reproductive potential of some females may be high; however the fecundity of some females may be off-set by reduces fecundity in other females.

In conclusion, despite new insights on the population structure and reproduction in *H. fumosus*, some critical points are missing such as the gestation length and the relation between age-classes and actual age.

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