

## Water redistribution and the life cycle of sahelian rodents

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**Summary.** – In the North of Burkina Faso (Oursi : 14°20'-14°50'N/0°10'-0°40'W), in *Mastomys huberti* and *Arvicanthis niloticus* which experience a rich diet all year round in unrestricted habitats, water metabolism is constantly high, reproduction is continuous and animals are sedentary throughout the year (only *A. niloticus* shows a short sexual rest period induced by some non-trophic factors : daylength and temperature). In *A. niloticus* which experience a constantly rich diet, but face an annual flooding period (in flooding habitats), annual dispersion and sexual rest phases are induced by some non-trophic factors : daylength, temperature and air humidity. In *Taterillus gracilis* and *Mastomys erythroleucus* which experience an annual rich-food period twice as long as the annual poor-food period (in semi-arid habitats), the annual dispersion and sexual rest phases are both related to a reduction in water metabolism, while the annual sedentarization and breeding phases are both related to an increase in water metabolism. In *Gerbillus nigeriae* which experience an annual poor-food period twice as long as the annual rich-food period (in arid habitats), the annual dispersion and sexual rest phases are both related to a reduction of water metabolism, but the annual sedentarisation and breeding phases are both induced by non-trophic factors (mainly daylength).

**Résumé.** – Au Burkina Faso (Oursi), outre une phase de repos sexuel induite par des facteurs non-trophiques (photopériode et température) chez *Arvicanthis niloticus*, le métabolisme hydrique est constamment élevé, la reproduction permanente et les individus sédentaires chez les *A. niloticus* et *Mastomys huberti* qui ont une alimentation riche tout au long de l'année (milieux non-restreints). Chez les *A. niloticus* qui bénéficient d'une alimentation toujours riche mais affrontent une période d'inondation (milieux inondables), des phases annuelles de dispersion et de repos sexuel apparaissent, induites par des facteurs non-trophiques (photopériode, température et humidité atmosphérique). Chez les *Taterillus gracilis* et *Mastomys erythroleucus* qui bénéficient d'une période trophique annuelle favorable deux fois plus longue que la période trophique annuelle défavorable (milieux semi-arides), les phases annuelles de dispersion et de repos sexuel sont induites par une réduction du métabolisme hydrique, alors que les phases annuelles de sédentarisation et d'activité sexuelle sont induites par une augmentation du métabolisme hydrique. Chez les *Gerbillus nigeriae* qui affrontent une période trophique défavorable deux fois plus longue que la période trophique favorable (milieux arides), les phases annuelles de dispersion et de repos sexuel sont liées à une réduction du métabolisme hydrique, mais les phases annuelles de sédentarisation et de reproduction dépendent de facteurs non-trophiques (principalement la photopériode).

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## INTRODUCTION

Rodent population outbreaks have dramatic consequences for human health and agriculture in the developing countries of the soudano-sahelian zone. Because of the unpredictability of this demographic phenomenon, it has only been studied by a few teams of researchs who have been working in the field over several years. Works carried out in both North (Poulet 1982) and South (Hubert 1982) of Senegal, as well as that of Sissou (1987) in the North of Burkina Faso demonstrate that the population

tats ; our laboratory experiments were performed on specimens originating from these wild populations.

### ECOPHYSIOLOGICAL INDICATORS

Seasonal variations in rodent diet were determined from regular analysis of stomach contents (Sicard 1987, 1992). Seasonal variations in water metabolism were monitored at the peripheral level using the tritiated water method in order to determine monthly means of total body water turnover (TBWT) and total body water balance (BWB) ; see Nagy and Costa (1980) for details on the application of this technique in the field. Seasonal variations in water metabolism were also determined at the control level of the antidiuretic hormone which is situated in the central nervous system, from monthly quantification of the vasopressinergic activity in the paraventricular, supraoptic and suprachiasmatic nuclei (PVN, SON and SCN) ; see Fuminier *et al.* (1993) and Sicard and Fuminier (1994) for details of immunohistochemical procedures and immunostaining analysis. Seasonal variations in rodent mobility were determined from monthly means of size and movement of rodent home ranges (HRS, HRM) using the elliptical method of Mazurkiewicz (1970) which is based on the Catch-Mark-Release method (CMR) ; see Sicard (1987) and Sicard *et al.* (1994) for details on CMR programs carried out in studied rodent habitats.

Seasonal changes in reproduction were determined at the population level from various indicators (percentages of sexually active adults and young, existence and duration of oestrous cycles and plasma testosterone levels). In order to detect reproductive starting and stopping, we regularly recorded the activity of neurons producing the Gonadotrophic Releasing Hormone implicated in seasonal changes of the pulsatile production of luteotrophic hormone and follicule stimulating hormone by the LH- and FSH-neurons of the adeno-hypophysis ; see Sicard *et al.* (1994), Kyelem and Sicard (1994) and Fuminier (1993) for details on determination of sexual state in living animals, analysis of vaginal smears in the field, radioimmunoassay of plasma testosterone, immunocytochemical procedures and quantification of GnRH labelling.

### RODENTS' LIFE CYCLE

#### *Unrestricted habitats*

Populations of *Mastomys huberti* and *Arvicanthis niloticus* living in vegetable gardens and permanent cultivations in the North-East edges of the Oursi pond (unrestricted habitats : UH) have abundant foodstuffs all year round. The two populations have a rich diet throughout the year (natural or cultivated green plants, seeds, arthropods, the barks of certain woody plants and any accessible stockpiles of cultivated produce). The total body water turnover remains high, the water balance equilibrated, and vasopressinergic activity in PVN and SON low, all year round in the two populations (see examples given in Tables 1 and 2). Size and movement of home ranges indicate that the two populations are sedentarised throughout the year (Table 3). Gonadotrophic activity (GA) is marked all year round in *M. erythroleucus*, while GA strongly decreases in August-September in *A. niloticus* (Table 4). Laboratory results indicate that the sexual rest period of *A. niloticus* results from gonado-inhibitory effects of long days and high temperature (non-trophic factors : NTF ; Fig. 1).

TABLE 1. — Seasonal changes in total body water turnover (TBWT) and body water balance (BWB) in some rodent species monitored from 1984 to 1991 in the Oursi region. TBWT and BWB are expressed as percent of the total body water (TBW). Values are means  $\pm$  sem, with (n) = number of data in statistical groups (groups with high values of TBWT and BWB have been colored). All possible pairwise comparisons of monthly means of TBWT and BWB were performed (using the Wilcoxon 2-Sample test and the SAS com-

TABLE 3. – Seasonal changes in the size and the movement of home range (HRS and HRM) in some rodent species monitored from 1984 to 1991 in the Oursi region. HRS and HRM are expressed in m<sup>2</sup> and m, respectively. Values are means ± sem, with (n) = number of data in statistical groups (groups with high values of HRS and HRM have been colored). All possible pairwise comparisons of monthly means of HRS and HRM were performed (Wilcoxon 2-Sample test of the SAS computer statistic package) to determine statistical groups; then the yielding Hochberg's method (which allows *a posteriori* comparisons; see Freund *et al.* 1986) was used to verify the significance of the differences between groups (0.001 ≤ p < 0.05). UH = unrestricted habitats, FH = flooding habitats, SH = semi-arid habitats and AH = arid habitats. Mh = *Mastomys huberti*, An = *Arvicanthis niloticus*, Tg = *Taterillus gracilis*, Me = *Mastomys erythroleucus* and Gn = *Gerbillus nigeriae*.

			J	F	M	A	M	J	J	A	S	O	N	D
UH	Mh	HRS	388 ± 39 (30)											
		HRM	34 ± 3 (13)											
	An	HRS	405 ± 30 (43)											
		HRM	32 ± 2 (21)											
FH	An	HRS	392 ± 41 (26)			1156 ± 75 (13)								
		HRM	31 ± 3 (16)			60 ± 7 (8)								
SH	Tg	HRS	1254 ± 77 (18)					595 ± 47 (22)						
		HRM	78 ± 7 (11)					29 ± 3 (10)						
	Me	HRS	1180 ± 81 (16)					531 ± 42 (17)						
		HRM	71 ± 9 (8)					26 ± 3 (8)						
AH	Gn	HRS	2106 ± 161 (9)		≈ 0		982 ± 53 (18)			1581 ± 101 (10)				
		HRM			≈ 0		18 ± 2 (10)			68 ± 5 (7)				

TABLE 4. – Seasonal changes in GnRH immunostaining of median eminence fibers in some rodent species. Animals were perfused at the site of capture in the field (trapping, sessions, carried out from 1989 until 1991, are indicated by black shaded areas under the letterhead of months). Values are means ± sem, with (n) = number of data in statistical groups (groups with high values of OD and IA have been colored). The yielding Hochberg's method (which allows *a posteriori* comparisons) indicates that the differences between groups are significant (0.001 ≤ p < 0.05). OD = optical density and IA = percent of immunolabelled area. UH = unrestricted habitats, FH = flooding habitats, SH = semi-arid habitats and AH = arid habitats. An = *Arvicanthis niloticus*, Tg = *Taterillus gracilis* and Gn = *Gerbillus nigeriae*.

			D	J	F	M	A	M	J	J	A	S	O	N
(n)			5		5		2		3		5			
UH	An	OD	292 ± 40					62 ± 8		195 ± 47				
		IA	4,8 ± 0,7					1,1 ± 0,3		2,9 ± 0,7				
FH	An	OD	314 ± 46					67 ± 9		187 ± 44				
		IA	5,3 ± 0,8					0,7 ± 0,1		2,8 ± 0,7				
SH	Tg	OD	125 ± 18		70 ± 14		333 ± 49							
		IA	2,3 ± 0,2		1 ± 0,2		5,6 ± 0,8							

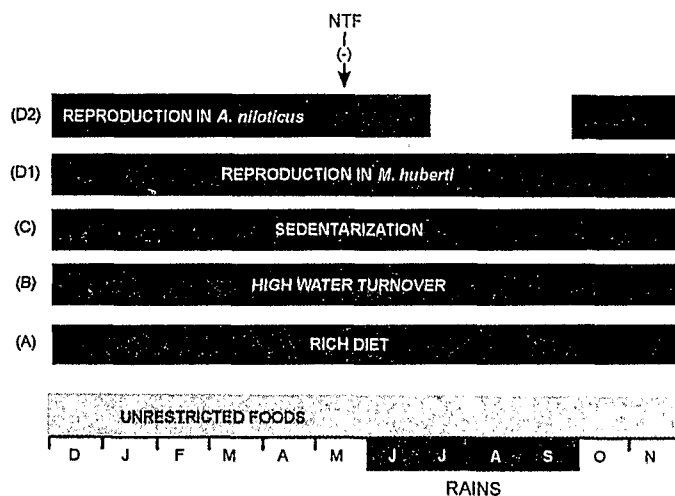


Fig. 1. – Annual Life cycles of *Mastomys huberti* and *Arvicanthis niloticus* in unrestricted habitats (vegetable gardens and permanent cultivations) in the Oursi region (Burkina Faso: 14°20'–14°50'N/0°10'–0°40'W). Seasonal variations in diet (A), water metabolism (B), mobility (C) and reproduction (*M. huberti*: D1; *A. niloticus*: D2). Gonado-inhibiting effects of non-trophic factors (NTF). Reproduced from Sicard (1987, 1992), Sicard and Gautun (1991), Fuminier (1993) and Sicard *et al.* (1988, 1992, 1993, 1994).

#### *Flooding habitats*

Populations of *A. niloticus* living in low lying areas of clay situated in the South-West part of the Oursi region (flooding habitats: FH) have abundant foodstuffs all year round, but face a period of flooding during the rainy season. Field results indicate that rodents have a constantly rich diet, a constantly high and equilibrated water metabolism and a constantly low vasopressinergic activity in PVN and SON (see examples given in Tables 1 and 2). By contrast, the size and movement of rodent home ranges show marked seasonal variations, which enable us to distinguish a sedentarisation period from mid-September to March and a dispersion period from March to mid-September (Table 3). GA shows important seasonal variations indicating that animals are sexually inactive from mid-April until the end of September (Table 4). Laboratory results indicate that the sexual rest period is related to combined gonado-inhibitory effects of long days, high temperature and dry air, and we are currently trying to find out if air humidity is involved in the induction of the dispersion period (non-trophic factors: NTF; Fig. 2).

#### *Semi-arid habitats*

Populations of *Mastomys erythroleucus* and *Taterillus gracilis* living in enclosed cultivations situated at the edge of low lying areas (semi-arid habitats: SH) have water-restricted foodstuffs from February to May. The total body water balance remains equilibrated throughout the year, but seasonal changes in water metabolism, mobility and reproduction, which are correlated with seasonal changes in the diet, appear in the two populations. During the rich-diet period (June–January), the total

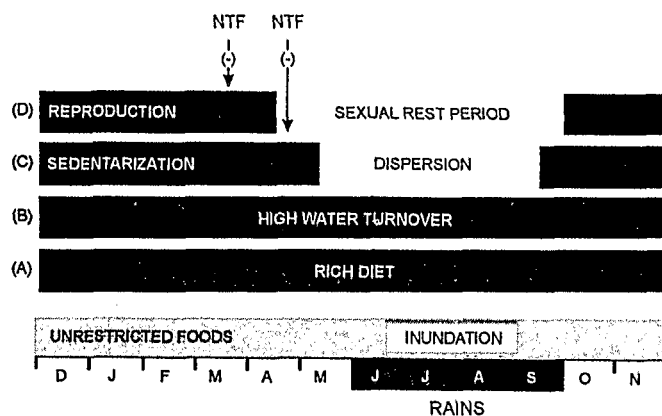


Fig. 2. – Annual Life cycles of *Arvicanthis niloticus* in flooding habitats (low lying areas) in the Oursi region (Burkina Faso : 14°20'-14°50'N/0°10'-0°40'W). Seasonal variations in diet (A), water metabolism (B), mobility (C) and reproduction (D). Inhibiting effects of non-trophic factors (NTF) on reproduction and sedentarisation. Reproduced from Sicard (1987, 1992), Sicard and Gautun (1991), Fuminier (1993) and Sicard *et al.* (1988, 1992, 1993, 1994).

body water turnover is important, the vasopressinergic activity in PVN and SON is low, the size and movement of rodent home ranges indicate that animals are sedentarised and GA is very marked (see examples given in Tables 1 to 4). By contrast, during period of water-restricted diet, the total body water turnover is low, the vasopressinergic activity in PVN and SON is marked, the size and movement of rodent home ranges indicate that animals experience a dispersion period and GA indicates that animals are sexually inactive) (Tables 1 to 4). Laboratory results indicate that a water-restricted diet strongly inhibits GA, while a rich diet is sufficient to stimulate GA in the two populations. In addition, combined gonado-stimulating effects of daylength and humid air strengthen the gonado-stimulating effects of a rich diet in *T. gracilis* (non-trophic factors : NTF ; Fig. 3).

#### Arid habitats

Populations of *Gerbillus nigeriae* and *Taterillus petteri* which live on the sand dune belt in the North of the study region, populations of *M. erythroleucus* which live in dried cracks situated in the upper part of the hydrographic system, and populations of *Acomys sp.* which live in granitic inselbergs (arid habitats : AH) have water- and protein-restricted foodstuffs from October to May. In this paper we present only the field and laboratory results obtained about *G. nigeriae*, the most studied species. During the annual period of unrestricted diet, the total body water turnover is important and the vasopressinergic activity in PVN and SON is low, while during the period of water- and protein restricted diet, the water metabolism decreases near by 10 % TBW per day and the vasopressinergic activity in PVN and SON increases widely (see examples in Tables 1 and 2). The movement of home-ranges indicate that animals experience a dispersion phase from October to January and a sedentarisation phase during the rest of the year, while the size of home ranges indicates that the sedentarisation period comprises three phases (Table 3) : during pre-estivation (PE ; Fig. 4) which

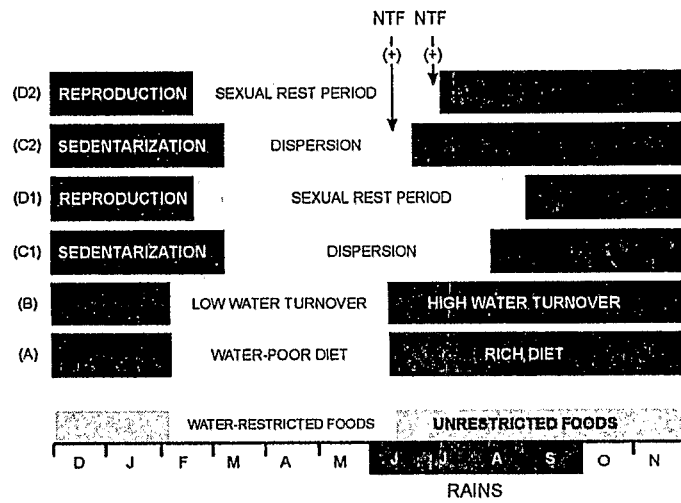


Fig. 3. — Annual Life cycles of *Mastomys erythroleucus* and *Taterillus gracilis* in semi-arid habitats (edges of low lying areas and enclosed cultivation) in the Oursi region (Burkina Faso : 14°20'-14°50'N/0°10'-0°40'W). Patterns of seasonal variations in diet (A), water metabolism (B), mobility and reproduction (*M. erythroleucus* : C1, D1 ; *T. gracilis* : C2, D2). Stimula-



occurs in January-February, animals build a deep burrow while increasing the size of their home range in order to stock up their burrow ; during estivation (March to May) animals estivate in their burrow ; during sedentarisation (June to September) animals breed on herbaceous covered areas. Probably because PE occurs at the time when resources are most restricted, animals experience a water imbalance of about 4 % TBW per day during PE (Table 2 ; WIB in Fig. 4). Once estivation starts, the water balance is re-established because of steep reduction in water expenditure. The gonadotrophic activity (GA) starts in April during estivation and remains important until September (Table 4). Laboratory results indicate that restricted diet, when associated with dry air, exerts a gonado-inhibiting effects in *G. nigeriae*, while daylength when associated with humid air (in burrow of estivation animals live in a water-saturated atmosphere) exerts a gonado-stimulating effect in April. We have put forward the hypothesis that WIB is the « physiological trigger » for going into estivation, and we have unpublished indications that the pre-estivation is induced by the decrease in temperature in December-January (non-trophic factors : NTF ; Fig. 4).

#### LIFE CYCLE OF SAHELIAN RODENTS

Although, reproduction and mobility are generally considered to be related to trophic factors in mammals with short life-spans living in low latitudes (review in Bronson 1989), our results support some suggestions that non-trophic factors play a role in regulating these functions in *Gerbillus gerbillus* (Khammar and Brudieux 1987), *Psammomys obesus* (Kammar and Brudieux 1986) and others (Happold 1983). To summarize our results : (1) except for *A. niloticus* which presents a short sexual rest period induced by non-trophic factors during the second half of the rainy season, water metabolism, mobility and reproduction are not seasonal in rodents (*A. niloticus* and *M. huberti*) which experience a constantly rich diet (UH) ; (2) when rodents (*A. niloticus*) experience a constantly rich diet but face a flooding period (FH), water metabolism remains related to food intake, but mobility and reproduction become seasonal : a dispersion period and a sexual rest period, both induced by non-trophic factors, appear before and remain until the end of the flooding period ; (3) when rodents (*T. gracilis* and *M. erythroleucus* in SH) experience marked seasonal changes in their diet with a rich-food period twice as long as the poor-food period, water metabolism, mobility and reproduction become seasonal : the dispersion period and the sexual rest period, are both related to a decrease of water metabolism, while the reproduction period and the sedentarisation period are both related to an increase in water metabolism ; non-trophic factors exert a stimulating effect on reproduction and sedentarization only in *T. gracilis* (which may explain why sedentarisation and reproduction appear two months earlier than in *M. erythroleucus*) ; (4) when rodents (*G. nigeriae* in AH) experience very marked seasonal changes in their diet with a poor-food period twice as long as the rich-food period, water metabolism, mobility and reproduction become seasonal : if the dispersion period and the sexual rest period are both related to a reduction in water metabolism, the reproduction period and the complex sedentarisation period (PE, estivation, sedentarisation) are both related to non-trophic factors.

Results show that the preservation of rodent populations in Sahelian zone results from adaptations of reproduction and mobility. When rodents face a trophic (poor foods in SH and AH) or non-trophic (inundations in FH) unfavourable period, a dispersion phase and sexual rest phase occur during the unfavourable period, while a sedentarisation phase and a sexual rest phase occur during the favourable period. When the

unfavourable period is short (e.g. four months in SH) seasonal changes in water metabolism are sufficient to induce the dispersion and the sexual rest phases. When the unfavourable period cannot be perceived through a change in the diet (inundations in FH) non-trophic factors are involved in the onset of the dispersion and the sexual rest phases, which anticipate the arrival of the unfavourable period. When the unfavourable period is long (e.g. eight months in AH), non-trophic factors are involved in the onset of the sedentarisation and of the breeding phases, which anticipate the arrival of the favourable period. The common feature of these adaptive mechanisms is that reproduction is linked with a sedentarisation period, while breeding cessation is linked with a dispersal phase. Indeed, results indicate that the dispersion always occurs after the cessation of reproduction, while breeding onset always occurs after the beginning of the sedentarization phase. We are currently trying to study the linkage between mobility and reproduction at the level of the central nervous system. Our unpublished preliminary results obtained in the laboratory indicate that the nervous central areas which could be involved in the determination of seasonal changes in mobility are sensitive to plasma sexual steroids.

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