

Environmental cues and seasonal breeding patterns in Sahelian rodents

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Summary. – In the Oursi region (North of Burkina Faso) rodent populations live in four types of habitats. In habitats where food is available all year round (unrestricted habitats) reproduction of *Mastomys huberti* is continuous. In habitats where food is available throughout the year, but in which *Arvicanthis niloticus* face a period of flooding (flooding habitats), non-trophic factors (daylength, temperature, air humidity) induce a sexual rest period before the arrival of the flooding period. In habitats where food is seasonally available with an annual rich-food period lasting twice as long as the annual restricted-food period (semi arid habitats), reproduction of *Mastomys erythroleucus* and *Taterillus gracilis* is mainly related to seasonal variations in the diet. When available food is widely seasonal, with an annual restricted-food period twice as long as the rich-food period (arid habitats), reproductive cessation is mainly related to the appearance of a restricted-diet in *M. erythroleucus*, *Gerbillus nigeriae*, *Taterillus petteri* and *Acomys sp.*, while the reproductive onset is related to non-trophic factors, which permit it to anticipate the arrival of the rich-food period. The ecological significance of these regulatory mechanisms is discussed.

Résumé. – Les populations de rongeurs d'Oursi (Nord du Burkina Faso) occupent quatre types d'habitats. Dans les habitats non-restreints qui offrent des ressources trophiques permanentes, *Mastomys huberti* a une reproduction continue. Dans les habitats inondables qui offrent des ressources trophiques permanentes, mais dans lesquels *Arvicanthis niloticus* doit affronter une période d'inondation, les facteurs non-trophiques (photopériode, température, humidité atmosphérique) induisent un arrêt de la reproduction avant l'arrivée des inondations. Dans les habitats fluctuants qui offrent des ressources saisonnières, avec une période trophique favorable deux fois plus longue que la période trophique défavorable, la reproduction est étroitement liée aux variations du régime alimentaire chez *Mastomys erythroleucus* et *Taterillus gracilis*. Dans les habitats semi-arides qui offrent des ressources très saisonnières, avec une période trophique défavorable deux fois plus longue que la période trophique favorable, l'arrêt de la reproduction reste sous dépendance d'une restriction alimentaire chez *M. erythroleucus*, *Gerbillus nigeriae*, *Taterillus petteri* et *Acomys sp.* ; mais le démarrage de cette activité dépend de facteurs non-trophiques, ce qui lui permet d'anticiper l'arrivée de la période favorable. La signification écologique de ces résultats est discutée.

INTRODUCTION

Rodent population outbreaks have dramatic consequences for human health and agriculture in the developing countries of the soudano-sahelian zone. Reproduction-

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dependant outbreaks occur due to the impact of temporary climatic disturbances on the annual reproductive cycle of certain species (Sicard *et al.* 1995). To understand how a climatic disturbance can lead to a reproduction-dependant outbreak, it is necessary to understand the mechanisms involved in the regulation of the annual reproductive cycle during years of normal climate. To this end, we have investigated (from 1984 to 1992) amongst a large number of rodent populations of the Oursi region (Burkina Faso : 14°20'-14°50'N / 0°10'-0°40'W), correlations between annual breeding patterns and seasonal appearance of trophic (available foodstuffs and chemical substances in germinating plants) and non-trophic (daylength, temperature, air humidity) factors. Experimental studies, started in 1988, indicate that some of these correlations are linked to causal relations. Here, we present a short review of these complementary field and laboratory results (Sicard 1987, 1992, Sicard and Fuminier 1994, Sicard and Gautun 1991, Sicard *et al.* 1988, 1992, 1993, 1994, Fuminier 1993, Kyelem and Sicard 1994).

ENVIRONMENTAL CUES UNDER SAHELIAN CLIMATE

The Sahelian climate is characterized by the appearance with chronological precision of various non-trophic factors : an increase in temperature (March), an increase in daylength (which is maximal at the spring equinox), an increase in air humidity (May), appearance of rains (June-September), a simultaneous decrease in daylength and air humidity (September), a decrease in temperature (December). According to these climatological data, the Sahelian climate is characterised by three well-defined seasons : the rainy season (June-September), the cold dry season (December-January) and the hot dry season (March- May) which are separated by periods of transition which are themselves less well-defined (Fig. 1A). In spite of the fact that the Sahelian climate has a single rainy season, numerous factors condition the redistribution of rainfall and, thus, the seasonal appearance of various trophic factors (chemical triggers in germinating plants, arthropod populations and seasonal variations in water content of the barks of certain trees such as *Acacia seyal*). As confirmed from our analysis of stomach contents (Sicard 1987, 1992), Sahelian rodents occupy a great range of habitats in which seasonal variations in foodstuffs are very different (Papillon and Sicard 1995). In unrestricted habitats (UH) rodents find abundant foodstuffs throughout the year ; in flooding habitats (FH) the available resources are abundant all year round, but rodents face a period of flooding during the rainy season ; in semi-arid habitats (SH) foodstuffs have a low water content from March to May ; in arid habitats (AH) foodstuffs are low in water and protein content from October until May (Fig. 1B). Our field monitoring was carried out among a large number of rodent populations living in the four types of habitats ; our laboratory experiments were performed on specimens originating from these wild populations.

INDICATORS OF REPRODUCTIVE ACTIVITY

In order to determine seasonal variations of reproduction at the population level, we regularly monitored various reproductive indicators (percentages of sexually active adults and of young, the existence and the duration of estrous cycles and plasma testos-

terone levels). In order to determine breeding patterns with well-defined reproductive beginnings and ends, we regularly recorded the activity of neurons which produce the Gonadotropin 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. Details on determination of sexual state in living animals, analysis of vaginal smears in the field, radioimmuno assay of plasma testosterone, immunocytochemical procedures and quantification of GnRH labeling, are given in Fuminier (1993), Kyelem and Sicard (1994) and Sicard *et al.* (1994).

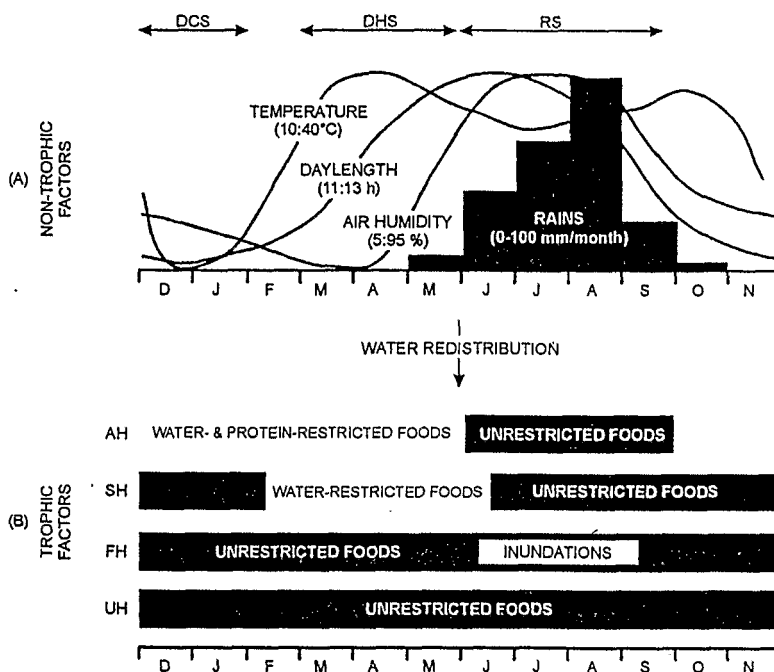


Fig. 1. – Sahelian climate and water redistribution in the Oursi region (Burkina Faso: 14°20'-14°50'N / 0°10'-0°40'W). Seasonal changes in non-trophic factors : dry cold season (DCS), dry hot season (DHS) and rainy season (RS) (A). Seasonal changes in trophic factors in the four types of rodent habitats : unrestricted habitats (UH), flooding habitats (FH), semi-arid habitats (SH) and arid habitats (AH) (B). Reproduced from Sicard (1987, 1992) and Papillon and Sicard (1995).

SEASONAL BREEDING PATTERNS IN SAHELIAN RODENTS

Results show that in unrestricted habitats (UH), where food is abundant all year round, reproduction is continuous throughout the year in *Mastomys huberti*. By contrast, *Arvicanthis niloticus* shows a short sexual rest period, which appears in the second mid-part of the rainy season in August-September (examples of data are given in Tables 1 and 2). Our laboratory investigations carried out in *A. niloticus* originating

Table 1. — Seasonal changes in plasma testosterone (Tt) in some rodent species monitored since 1984 until 1991 in the Oursi region. Tt was determined (ng/ml) by radioimmunoassay (RIA Kit, Biomérieux, France) according to a method previously used for other mammals (Maurel et al. 1981). Monthly means of Tt were calculated ((n) = number of data for each month) then all possible pairwise comparisons were performed (Wilcoxon 2-Sample test of the SAS computer statistic package) to determine statistical groups. Groups with high values of Tt has been colored (values are means \pm sem; (N) = number of data in statistical groups). The yielding Hochberg's method (which allow *a posteriori* comparisons; see Freund et al. 1986) was used to verify the significance of the differences between groups ($0,001 \leq p \leq 0,05$). 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*, Tp = *Taterillus petteri*, and Gn = *Gerbillus nigeriae*.

		J	F	M	A	M	J	J	A	S	O	N	D
UH	Mh (n)	(2)	-	(2)	(3)		(4)	(2)	(3)	(3)	-	(3)	(3)
	Tt (N)	2,28 \pm 0,15 (23)											
	An (n)	-	(2)	-	-	(3)	(2)	-	(2)	(2)	(3)	-	(3)
	Tt (N)	3,12 \pm 0,39 (13)						1,08 \pm 0,34					
FH	An (n)	(4)	(3)	(1)	(4)	(1)	(5)	(2)	(12)	(8)	(4)	(1)	(11)
	Tt (N)	3,98 \pm 0,28 (28)						1,68 \pm 0,06 (32)					
SH	Tg (n)	(2)	-	(1)	(3)	(2)	(5)	(2)	(6)	(4)	-	-	(5)
	Tt (N)	0,66 \pm 0,14 (8)						1,49 \pm 0,16 (22)					
	Me (n)	-	-	(2)	(4)	(3)	(4)	(5)	(3)	(7)	(5)	(2)	(4)
	Tt (N)	?		1,3 \pm 0,28 (18)				2,62 \pm 0,26 (28)					
AH	Me (n)	(1)	-	(2)	(4)	(5)	-	(1)	-	(4)	(4)	(1)	-
	Tt (N)	0,79 \pm 0,22 (8)		2,34 \pm 0,43 (14)									
	Tp (n)	(2)	-	(2)	(2)	-	(2)	(2)	(4)	(5)	(3)	(1)	(3)
	Tt (N)	0,46 \pm 0,2 (11)			1,71 \pm 0,22 (15)								
	Gn (n)	(5)	(6)	(2)	(3)	(6)	(4)	(5)	(10)	(9)	(6)	(4)	(8)
	Tt (N)	0,69 \pm 0,08 (31)			1,37 \pm 0,15 (37)								

from UH clearly indicate that the sexual rest period results from gonado-inhibitory effects of daylength and high temperature (non-trophic factors : NTF ; Fig. 2A).

In flooding habitats (FH), which are almost exclusively inhabited by *A. niloticus*, food is abundant all year round but rodents must face a period of flooding during the rainy season. As indicated in Tables 1 and 2, reproductive activity starts in October and stops during the dry hot season in March. Our laboratory investigations carried out in *A. niloticus* originating from FH lead us to the conclusion that the sexual rest period is induced by combined inhibitory effects of increased daylength, high temperature and dry air (non-trophic factors : NTF ; Fig. 2B). It is likely that a period of flooding is unfavourable for *A. niloticus* reproduction ; if this is the case we have a better understanding of why *A. niloticus* are always distributed in the humid habitats of the Sahelian region : they are constrained by their physiology to reproduce mainly outside the rainy season.

In semi-arid habitats (SH), where food is abundant from July to February, rodents show two breeding patterns. In *Taterillus gracilis* reproduction starts at the beginning of the rainy season while this activity starts in the middle of the rainy season in *Mastomys erythroleucus* (examples of data are given in Tables 1 and 2). Nevertheless, the cessation of reproduction occurs soon after the end of the rich-food period in the two species. In addition, these results indicate that long days induce a gonadostimulating

Table 2. – Seasonal changes in optical density of the GnRH immunostaining in median eminence (OD), in testis and seminal vesicle mass (TM and SM) and in the number of embryonic scars (ES), in some rodent species of the Oursi region. Data were recorded since 1984 (1989 for OD) until 1991. Monthly means of TM (mg/100 g BW) SM (mg/100 g BW) and ES were calculated, then all possible pairwise comparisons were performed (Wilcoxon 2-Sample test of the SAS computer statistic package) to determine statistical groups. Groups with high values of OD, TM, SM and ES has been colored (values are means \pm sem with (n) = number of data in statistical groups). The yielding Hochberg's method (wich allow *a posteriori* comparisons; see Freund *et al.* 1986) was used to verify the significance of the differences between groups ($0,001 \leq p \leq 0,05$). 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*, Tp = *Taterillus petteri*, and Gn = *Gerbillus nigeriae*.

			J	F	M	A	M	J	J	A	S	O	N	D			
UH Mh	TM		1437 \pm 80 (46)														
	SM		571 \pm 26 (46)														
	ES		14,3 \pm 0,7														
An	OD		263 \pm 30 (17)					62 \pm 8 (3)									
	TM		2204 \pm 178 (79)					375 \pm 56									
	SM		637 \pm 47 (65)					79 \pm 14 (50)									
	ES		7,2 \pm 0,3														
FH An	OD		271 \pm 36 (15)					67 \pm 9 (5)									
	TM		2176 \pm 198 (62)					538 \pm 124 (41)									
	SM		632 \pm 52 (53)					130 \pm 56 (50)									
	ES		7,4 \pm 0,4 (15)														
SH Me	OD		Insufficient data					395 \pm 59 (9)									
	TM		141 \pm 11 (19)					1350 \pm 100 (26)									
	SM		47 \pm 4 (19)					662 \pm 50 (26)									
	ES							13,8 \pm 0,5 (12)									
Tg	OD		70 \pm 14 (5)					264 \pm 42 (15)									
	TM		361 \pm 51 (21)					2226 \pm 92 (28)									
	SM		193 \pm 28 (26)					920 \pm 59 (23)									
	ES							4,7 \pm 0,3 (16)									
AH Me	TM		396 \pm 58 (28)					1675 \pm 112 (29)									
	SM		92 \pm 20 (28)					539 \pm 51 (29)									
	ES							11,4 \pm 0,5 (12)									
Tp	TM		108 \pm 16 (29)					2585 \pm 140 (32)									
	SM		54 \pm 8 (29)					518 \pm 29 (32)									
	ES							5,4 \pm 0,3 (17)									
Gn	OD		75 \pm 13 (10)					393 \pm 41 (10)									
	TM		165 \pm 13 (48)					2523 \pm 145 (54)									
	SM		82 \pm 6 (48)					617 \pm 39 (54)									
	ES							5,9 \pm 0,3 (21)									

effect in *T. gracilis* originating from SH, while *M. erythroleucus* originating from SH are not able to perceive annual changes in daylength. According to the critical photoperiod of *T. gracilis*, it may be predicted that the gonadostimulating effect of daylength appears in June in the wild, what is consistent with our field results (non-trophic factors: NTF; Fig. 2 C). Mean numbers of embryonic scars indicate that *T. gracilis* is

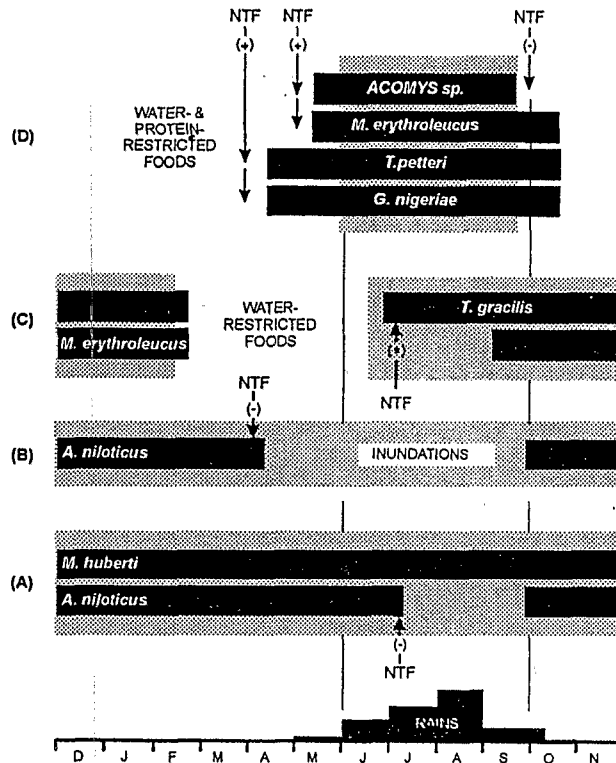


Fig. 2. – Sahelian rodents breeding patterns in the Oursi region (Burkina Faso: 14°20'-14°50'N / 0°10'-0°40'W). Breeding periods (black shaded areas) and rich-foods periods (grey shaded areas) are indicated in the four types of rodent habitats. Unrestricted habitats (A): vegetable gardens and permanent cultivations. Flooding habitats (B): low lying areas (B). Semi-arid habitats: edges of low lying areas and enclosed cultivations (C). Arid habitats (C): sand dune belt (*T. petteri* and *G. nigeriae*), dried crack in the upper part of the hydrographic system (*M. erythroleucus*) and granit islet (*Acomys sp.*) (D). Gonadostimulating (+ arrows) and gonadoinhibiting (- arrows) of non-trophic factors (NTF). Reproduced from Sicard (1987, 1992), Sicard and Gautun (1991), Sicard *et al.* (1988, 1992, 1993, 1994), Fuminier (1993), Fuminier *et al.* (1993) and Sicard and Fuminier (1994).

less prolific than *M. erythroleucus* (Table 2); thus, we can expect that a two months additional period of reproduction, due to the implication of non-trophic factors in accelerating the breeding onset, is an ecological advantage for *T. gracilis*.

All the species living in habitats where food is only abundant during the rainy season (arid habitats: AH) show a more or less similar breeding pattern: gonadotrophic activity starts before the arrival of rains (April in *Taterillus petteri* and *Gerbillus nigeriae*; May in *Acomys sp.* and *M. erythroleucus*), and stops at the end of the rainy season (September in *T. petteri* and *G. nigeriae*; October in *Acomys sp.* and *M. erythroleucus*). Examples of data are given in tables 1 and 2. Our laboratory experiments confirm in all these species, that the onset of gonadotrophic activity is mainly day-

length-dependent (non-trophic factors : NTF ; Fig. 2D), while the cessation of gonadotrophic activity is mainly related to the appearance of a restricted diet ; only *Acomys* sp. shows a strictly daylength-dependent reproductive cycle. We can expect that in arid habitats species survival is linked to the use of the short rich-food period for reproduction. Thus, the anticipation of the breeding onset according to the arrival of rains is probably a major ecological advantage for a species. Because there is no transition period between the dry hot season (end of the poor-food period) and the rainy season (beginning of the rich-food period), such a prediction is only possible for species who use environmental cues to predict the arrival of rains (Fig. 1A).

To summarize the results : (1) except for *A. niloticus*, reproduction is continuous when food is available all year round in unrestricted habitats ; (2) non-trophic factors induce a reproductive cessation before the arrival of inundations -despite food is available all year round- in flooding habitats ; (3) reproduction is related to seasonal variations in the diet when food becomes seasonally available with an annual rich-food period twice as long as the annual restricted-food period, in semi-arid habitats ; even if non-trophic factors act to accelerate the reproductive onset in *T. gracilis*, the latter do not anticipate the arrival of the rich-food period ; (4) cessation of reproduction remains related to the appearance of a restriction in the diet, while reproductive onset becomes strongly related to non-trophic factors, when available food becomes widely seasonal with a restricted-food period twice as long as the rich-food period (in arid habitats) ; as a result, the breeding onset anticipates the arrival of the rich-food period.

The common feature of Sahelian rodent breeding patterns is that they are centred on a rich-food period. Keeping in mind the effects of rainfall redistribution on seasonal variations in available foods in rodent habitats, this result is consistent with numerous other studies indicating in many African rodents living at low latitudes, that breeding patterns are related to rainfall (reviewed in Bronson 1989). It has been suggested that African rodent reproduction is related to seasonal changes in the diet *via* (i) increased water intake, (ii) variations in the quality and quantity of food, and (iii) the triggering effect of substances found in germinating plants (reviewed in Bronson 1989). Nevertheless, our results indicate that non-trophic factors (NTF) also act on sahelian rodent reproduction. Indeed : (i) NTF induce a cessation of reproduction during rains in *A. niloticus* living in UH, (ii) NTF induce a cessation of reproduction before the arrival of a flooding period in *A. niloticus* living in FH, (iii) NTF accelerate the reproductive onset in *T. gracilis* living in changing habitats, and (iv) NTF induce a reproductive onset in all the species living in arid habitats. Thus, Sahelian rodents living at low latitude, like mammals living at high latitude, can detect seasonal variations in NTF (e.g. daylength) in order to link their reproduction to the most favourable trophic period. In the species labelled "photosensitive" (reviewed in Boissin and Canguilhem 1988), the length of the day is perceived by the non-image forming system of the retina (Cooper *et al.* 1989) and leads to a stimulation or an inhibition of gonadotropic areas of the central nervous system. The "light information" is then transferred through a complex neuronal way to the suprachiasmatic nucleus (which is the main component of the endogenous circadian clock ; see Meijer and Rietveld 1989) and to the pineal gland which can modulate the photoregulation of reproduction according to a large set of environmental informations (Pevet 1987), such as temperature (Vivien-Roels and Pevet 1983), air humidity (Halder and Saxena 1988) and chemical triggers produced by germinating plants (Korn 1989).

In *A. niloticus*, individuals which live in UH have a less-marked photosensitivity than individuals which live in FH ; consequently, in the latter, cessation of reproduction occurs before the arrival of food. In *M. erythroleucus*, individuals living in SH are not

photosensitive while long days stimulate reproduction in individuals which live in AH ; consequently in the latter, onset of reproduction occurs before the arrival of the short favourable trophic period. Such a polymorphism in photosensitivity is not an isolated result. Among species of genus *Peromyscus* and *Microtus*, it has been shown that animals of the same species may differ in their photosensitivity according to altitude (Weiner *et al.* 1984), latitude (Lynch *et al.* 1981), the age of individuals (Whitsett *et al.* 1984), and the « photoperiodic history » of their mother (Horton 1985). In conclusion, the ecological significance of the implication of NTF in regulating reproduction of Sahelian rodents is probably to permit that prediction of the arrival of favourable and unfavourable periods by the endogenous circadian and circannual clocks, and thus, to permit an efficient timing of the annual breeding cycle.

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