

20. Ecophysiology and Chronobiology Applied to Rodent Pest Management in Semi-arid Agricultural Areas in Sub-Saharan West Africa

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Abstract

A better understanding of rodent population dynamics and strategies for surviving in various habitats can be gained from combined studies of genetics, ecology, ecophysiology and chronobiology. Each of these disciplines can contribute complementary information to improve rodent pest management (RPM).

Field studies of the ecophysiology of several species (*Arvicanthis niloticus* and *Mastomys huberti* living in wet habitats; *Arvicanthis niloticus* in easily flooded habitats; *Mastomys erythroleucus* and *Taterillus gracilis* in semi-arid habitats; *Taterillus petteri* in arid habitats) reveal a set of phase-relationships between the annual cycles of reproduction, mobility and metabolism, and the annual cycle of climate and trophic conditions in rodent habitats, defined here as the 'vital-cycle'. Improvement of RPM spatial and temporal strategies directed to control mortality, mobility and reproduction should thus be adapted to the vital-cycle according to species and habitat. Analysis of the results of field and laboratory studies in *A. niloticus* living in easily flooded habitats, allowed an understanding of the mechanisms involved in regulation of the reproductive cycle and development of models of the reproduction-dependent outbreak of *A. niloticus* in 1987 in Burkina Faso. We also describe data related to other species and discuss the advantages of integrating a chronobiological approach to the study of population mobility and mobility-dependent outbreaks.

Keywords

Tropical rodents, rodent pest management, reproduction, water metabolism, mobility, rodent outbreaks, rodent habitats, rodent population dynamics, circannual and circadian rhythms, vital-cycle

INTRODUCTION

TROPICAL RODENTS HAVE been studied in several Sahelian-Sudanese countries of West Africa in order to improve rodent pest management (RPM). Long-term investigations conducted by the French Scientific Research Institute for Development through Cooperation (ORSTOM), in the Ivory Coast, Senegal, Burkina Faso, Guinea, Niger and Mali have contributed significantly to the current knowledge of systematics, evolution, ecology, and more recently, ecophysiology and chronobiology of Sahelian-Sudanese rodents. We present here the ecophysiological and chronobiological approaches to RPM developed by Institut de Recherche pour le Développement (IRD-ORSTOM, Mammal Laboratory) in Burkina Faso (1984–1991) and Mali (1992–1997). After presenting an analysis of the relationships between RPM approaches using genetics, ecology, ecophysiology and chronobiology, we will provide some general information on methods and discuss the constraints of the ecophysiological and chronobiological approaches. Three aspects of the application of our research on RPM will then be described: (i) the characterisation of rodent habitats; (ii) the identification of temporal and spatial strategies which are specifically determined according to the 'vital-cycle' of the pest species, and (iii) the forecasting of rodent outbreaks. Lastly, some ideas will be presented on the prospects for improvement of RPM through the development of a chronobiological approach to rodent population mobility.

INTER-RELATIONS BETWEEN SYSTEMATICS, ECOLOGY, ECO-PHYSIOLOGY AND CHRONOBIOLOGY APPLIED TO RPM

Sahelian-Sudanese rodents often show a chromosomal polymorphism related to the presence of heterochromatin and various chromosomal rearrangements (*Arvicanthis*, Ducroz et al. 1997; *Mastomys*, Granjon et al. 1997; *Taterillus*, Sicard et al. 1988b; *Acomys*, Sicard and Tranier 1996 and Volobouev et al. 1996; *Gerbillus*, Maddalena et al. 1988 and Volobouev et al. 1988). In addition to its fundamental interest, knowledge of the *systematics* of Sahelian-Sudanese rodents is crucial because it allows updating of identification keys used by practitioners of agricultural development, and because biological mechanisms revealed through ecological, ecophysiological or chronobiological approaches of RPM are often species-specific or even population-specific (Sicard 1995a; Sicard et al. 1995).

Ecology applied to RPM aims to better understand species-specific demographic strategies and establishes correlations between habitat characteristics and life history traits. This approach also seeks to understand causes and mechanisms of population cycles to more accurately predict outbreaks. Outbreaks may have specific causes, or may merely represent particularly marked annual cycles of abundance. Research undertaken to predict outbreaks involved the study of factors determining rodent population dynamics, and modelling of the role of various internal (reproduction, mobility, mortality) and external (climate, predation, competition, resources, diseases) factors (Hubert et al. 1978; Poulet 1980; Hubert and Adam 1985).

To fully understand the adaptative significance of primary physiological functions (reproduction, metabolism and mobility) it is necessary to understand how homeostasis relates to ecology in the natural environment. The field of *ecophysiology* has emerged to answer this question with particular reference to species adaptation in extreme environments. Our comparative ecophysiological investigations in several Sahelian-Sudanese rodents show that adaptation to variability in arid and semi-arid environments involves precise phase relationships between primary physiological functions and seasons (Sicard and Papillon 1996). This ecophysiological approach is thus complementary to the ecological approach since primary physiological functions are the main internal factors involved in species' life history and in rodent population dynamics (Figure 1).

The majority of biological processes are expressed in the form of interdependent cycles: biochemical, anatomical, physiological, behavioural or ecological. Certain cycles referred to as 'endogenous biological rhythms' are controlled by a neuronal 'pacemaker' (a complex neural network oscillating with its own specific period; Morin 1994) involving species-specific mechanisms.

Since *chronobiology* aims to understand the mechanisms regulating such rhythms, it is interesting to approach the study of a complex cyclic phenomenon, such as rodent population dynamics, through the concepts of chronobiology. Indeed, to develop models it is necessary to determine whether agonistic or antagonistic relationships between internal (reproduction, mobility, metabolism and mortality) and external

(climate, resources, chemical signals, competition, predation, diseases) factors controlling population dynamics involve mere cycles or bona fide rhythms.

The endogenous circadian clock (ECC) in mammals is located in the suprachiasmatic nucleus (SCN) of the hypothalamus. The ECC oscillates with its own species-specific period which approximates 24 hours. The period is synchronised to the 24-hour day–night light cycle by photic information conveyed from the retina to the SCN via the retino-hypothalamic pathway (Cooper et al. 1993). The ECC is also subject to seasonal influences by two brain structures (the intergeniculate leaflet and the pineal gland) which integrate seasonal changes in daylength via direct or indirect connections with the retina (Moore 1973; Moller and Pévet 1994; Attar et al. 1995; Negroni et al. 1995). Because the day–night cycle and annual changes in daylength are precise, universal and predictable, these photic cycles are the environmental cues most used by living organisms to synchronise primary physiological functions according to seasons (Bronson 1988).

Nevertheless, particularly in small tropical mammals and depending on the species, many non-photoc factors act on primary physiological functions. Examples include temperature (Vivien-Roels and Pévet 1983; Ouarour et al. 1991), relative humidity (Haldar and Saxena 1988), food and water (Bronson 1989), chemical signals like 6-methoxy-2-benzoxazolinone secreted by plants during germination (Neal and Alibhai 1991), social factors like pheromones or rodent density, elements of the landscape structure (Delattre et al. 1992), and/or some events in the environment (Cutrera et al. 1994).

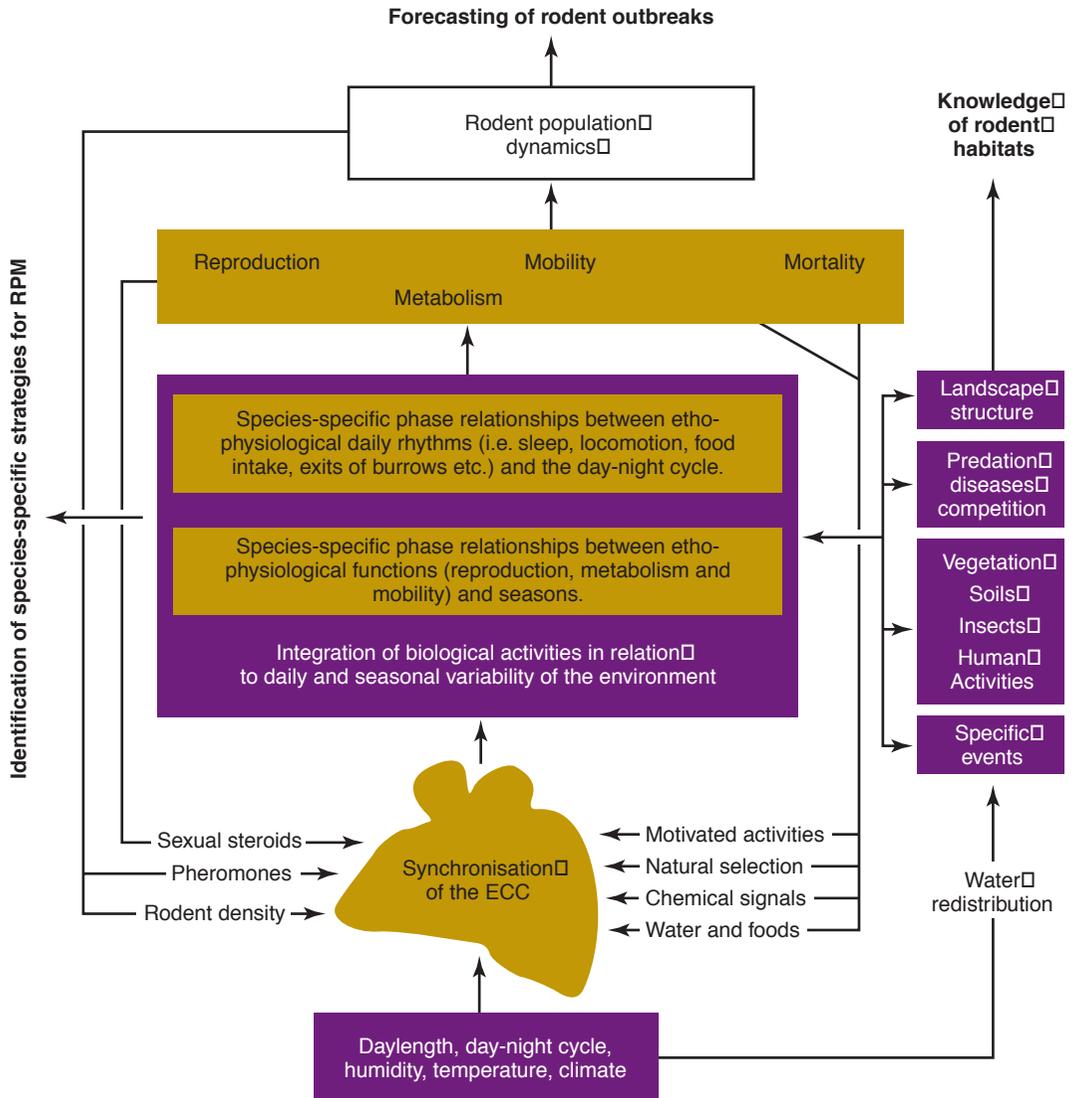


Figure 1. Ecology, ecophysiology and chronobiology applied to rodent pest management (RPM) (ECC = endogenous circadian clock; see text for full explanation).

The degree to which the ECC is directly or indirectly implicated in the physiological response to these factors is not fully known. Nevertheless, the ECC, synchronised by photic and/or non-photic factors, controls many daily and seasonal activities (Buijs et al. 1992; Pévet 1992). A specific example of the complexity of these interactions was recently observed in the inner delta of the Niger River (Mali) in which an increase in relative humidity associated with the first rain dramatically modified the normal daily activity pattern of *Arvicanthis*. The animals emerged to eat winged termites during their first occlusion in the early afternoon of the following day (Sicard, unpublished results). This change in diet has important physiological consequences for *Arvicanthis* and illustrates the adaptive significance of the role of non-photic climatic factors which can potentially affect the ECC via induced locomotor activity (Mrosovsky 1996). More generally, the importance of chronobiological rhythms for a species is illustrated by key events which occur at precise times of the day–night cycle (sleep, locomotion, food intake, exit from the burrow etc) or at precise periods of the year (reproduction, aestivation, dispersal etc). In arid environments the role of the ECC is particularly important because it allows certain behavioural or physiological functions (dispersal, reproduction) to anticipate the seasonal occurrence of predictable favourable or unfavourable conditions (Sicard and Fuminier 1996). Because the cyclic nature of primary physiological functions determined by the ECC is more or less well adapted according to predation and competition, it may be

expected that the latter factors sculpt the evolution of the ECC via natural selection. Thus, factors acting on individuals, which arise from various social and environmental levels and potentially involving the ECC, introduce feedback into the regulation of rodent populations dynamics (Figure 1).

Phenomena acting on individuals also act on populations and phenomena acting on populations are inevitably perceived, at least, by certain individuals. Ecology allows integration of individual data by taking into account the crucial adaptive role of individual variability. Ecophysiology and chronobiology allow us to understand the mechanisms involved in the response of individuals to external factors. The majority of these mechanisms are species-specific or population-specific, thus a genetic approach also seems necessary. All these approaches are thus complementary and necessary for modelling rodent population dynamics.

METHODOLOGICAL CONSIDERATIONS OF ECOPHYSIOLOGICAL AND CHRONO-BIOLOGICAL APPROACHES TO RPM

Our ecophysiological and chronobiological approaches applied to RPM use, as models, wild animals living in their natural environment and aim to identify species-specific and non species-specific mechanisms inducing the phase relationships which link external and internal factors regulating rodent population dynamics (Figure 1). These approaches include three phases: long-term field monitoring, laboratory and terrarium experiments, and modelling of the results.

Long-term field monitoring

Long-term field monitoring was carried out in Burkina Faso (1984–1991) and Mali (1992–1997) with the goal to determine the ‘vital-cycle’ of the monitored rodent populations. The vital-cycle is defined here as a set of phase relationships between annual cycles of primary physiological functions and annual cycles of climate and trophic parameters.

Daylength was calculated according to the latitude of the study region. Rains and seasonal changes in temperature and air humidity were recorded from our own meteorological stations (see Sicard 1987). The capture, mark and release method was used. Grids made up of 10 lines of 10 traps each, separated by 10 or 20 metres were established approximately every 30 days, for 7 to 10 days, during many years, in many habitats. Therefore, it was possible to calculate various abundance indices, indicators of reproduction (sex ratio, percentages of young and sexually active adults, state of testes and uterus) and mobility (home range size, home range overlap, displacement of activity centres) (Meunier and Solaris 1979; Gautun and Sicard 1986; Sicard 1987; Gautun et al. 1989).

In addition, trapping networks were placed elsewhere in each habitat to obtain data on physiological parameters. Diet was determined from analysis of stomach contents (Sicard 1987) and reproduction was estimated from numbers of embryos in pregnant females. Reproductive onset and offset were determined from an analysis of oestrous cycles using vaginal smears (Kyelem and Sicard 1994), seasonal changes in blood sexual steroids using

radioimmunoassays (Maurel et al. 1981) and seasonal changes in the gonadotrophin-releasing hormone activity of the gonadotrophic areas of the brain (which regulate reproduction), using immunohistochemical methods (Fuminier 1994). Seasonal changes in water metabolism and aestivation period were determined from analysis of total body water balance and of water turnover expressed as a percentage of total body water (WT as %TBW; Sicard et al. 1985), and from analysis of the activity of the vasopressinergic system of the brain (which regulates water intake and related behaviours) using immunohistological methods (Fuminier et al. 1993).

Experimental study of causal relationships

The aim of our experimental studies was to determine whether correlations derived from field studies were causally related. We present here the results of our study on the regulation of reproduction in *Arvicanthis niloticus* which examined the effects of all possible combinations of the various factors that regulate the reproductive cycle. We also present results obtained in other species and results obtained on the regulation of water metabolism. While reproduction and water metabolism are only expressed at the seasonal level, mobility is both expressed at daily (circadian rhythm of activity) and seasonal (dispersal and non-dispersal periods) levels. The experimental study of mobility is thus more complex and potential future approaches are discussed at the end of this chapter.

Modelling for RPM improvement

Vital-cycles, as defined here (Sicard and Papillon 1996), are species-specific and habitat dependent. They allow a better understanding of species' adaptations to environmental variability and determination of favourable and unfavourable periods (i.e. temporal and spatial strategies) for rodent control. Examples presented here concern *A. niloticus* and *Mastomys huberti* living in wet habitats; *A. niloticus* in easily flooded habitats; *M. erythroleucus* and *Taterillus gracilis* in semi-arid habitats; and *Taterillus petteri* in arid habitats.

Experimental studies allow simulations of both typical and atypical climato-trophic conditions derived from bio-climatological analysis. Comparisons between field and laboratory results then allow modelling of the regulation of primary physiological functions involved in the vital-cycle. Examples presented here concern regulation of reproduction in *A. niloticus* during typical and atypical years, allowing models to be developed of the reproduction-dependent outbreak of *A. niloticus* in 1986–1987 in Burkina Faso.

VITAL-CYCLES, KNOWLEDGE OF RODENT HABITATS AND RPM IMPROVEMENT

Certain species such as *M. erythroleucus* occupy many habitats whereas other species like *T. petteri* occupy only specific habitats (Sicard 1992). Analysis of the distribution of pest species would facilitate the definition of priorities for research and RPM, at both national and regional levels and help to answer the question: *which are the most important pest species and habitats?* Nowadays

in the Sahelian-Sudanese region, human demographic growth and climate aridification encourage man to occupy easily flooded low zones and to develop permanent crops in the vicinity of habitations in certain urban and rural areas. A sufficient knowledge of pest rodent distribution within the continuum of the agro-ecosystem would allow prediction of the consequences of these environmental modifications on the evolution of the rodent problem. Ecological and biogeographic studies in the Sahelian-Sudanese region were designed to characterise rodent habitats according to several criteria such as the type of soil and vegetation (Hubert et al. 1977), the importance and type of human activity (Sicard et al. 1995) or the landscape structure (Papillon and Sicard 1995a). Further, ecophysiological and chronobiological studies sought to understand how cyclic variations in food and water resources allow the definition of different habitats, and drive adaptive mechanisms that govern rodent distribution.

Four categories of habitats can be distinguished based on cyclic variations of food and water resources which depend on numerous factors (rains, altitude, slope, soils, vegetation, agronomical practices etc; see Papillon and Sicard 1995b and Figure 2):

- ▶ In wet but non-floodable habitats (villages and permanent cultivations located at the bottom of slopes; i.e. in the first belt of the agricultural system named *Soforo* by the Bambaras population), rodents find abundant water and food resources throughout the year.
- ▶ In floodable habitats (rice growing and natural low areas), rodents have abundant

food all year long but must face a period of flood during rains.

- ▶ In semi-arid habitats (sandy covered areas and large open fields located mid-slope), rodents must face a water-restricted food period during the dry and hot season.
- ▶ In arid habitats (granitic islets, dunes and higher parts of the hydrographic system), rodents have rich and varied foods only during rains and must face a water- and protein-restricted food period during the remainder of the year.

Rodent distribution depends on numerous etho-ecophysiological factors. Rodents adjust the openings and the depth of their burrows so that the burrow atmosphere is saturated and temperature is close to thermal neutrality. This behaviour, in addition to a mainly nocturnal activity rhythm, allows rodents to avoid the rigours of the Sahelian-Sudanese climate (Sicard 1992). The soil of the most arid Sahelian-Sudanese habitats contains an enormous quantity of seeds (Grouzis 1988) from which rodents make important food reserves. Nevertheless, water and food are the main factors limiting survival of Sahelian-Sudanese rodents and water metabolism (i.e. the aptitude of rodents to save water by reducing water losses) is a key factor in species distribution (Sicard 1987, 1992; Sicard and Fuminier 1994). Water, water redistribution and food availability are highly variable throughout seasons and years, and are dependent on many climatic and non-climatic factors.

Sahelian and Sudanese climates are often regarded as sub-desert climates, a term that misleadingly suggests that rains appear

randomly in time and space. Indeed, despite an important variability in annual rainfall (200–400 mm in the Sahel versus 500–1000 mm in the Sudan), rains almost always occur between June and September in the Sahelian-Sudanese region. Thus, from a chronobiological point of view, the rainy season is thus more predictable in Sahelian-Sudanese regions than in equatorial or temperate regions. Indeed, in the latter, the abundance and temporal pattern of rainfall is of low predictive value in the absence of a well-marked annual rainy season. In contrast, according to rainfall, the Sahelian-Sudanese climate is characterised by three well-defined seasons (the dry and hot season from March to May, the rainy season from June to September, and the dry and cool season from December to January) delimited by less well-defined transitional periods (Figure 2). These seasons are marked by a succession of potential synchronisers that include:

- ▶ a maximal rate of increase in temperature near the end of February;
- ▶ a maximal rate of increase in daylength near the vernal equinox at the end of March;
- ▶ a maximal rate of increase in air humidity near mid-May (related to a seasonal weakening of the harmattan wind);
- ▶ the arrival of rains in June;
- ▶ a simultaneous decrease in temperature, air humidity and rains near mid-September; and
- ▶ a decrease in temperature near the end of November.

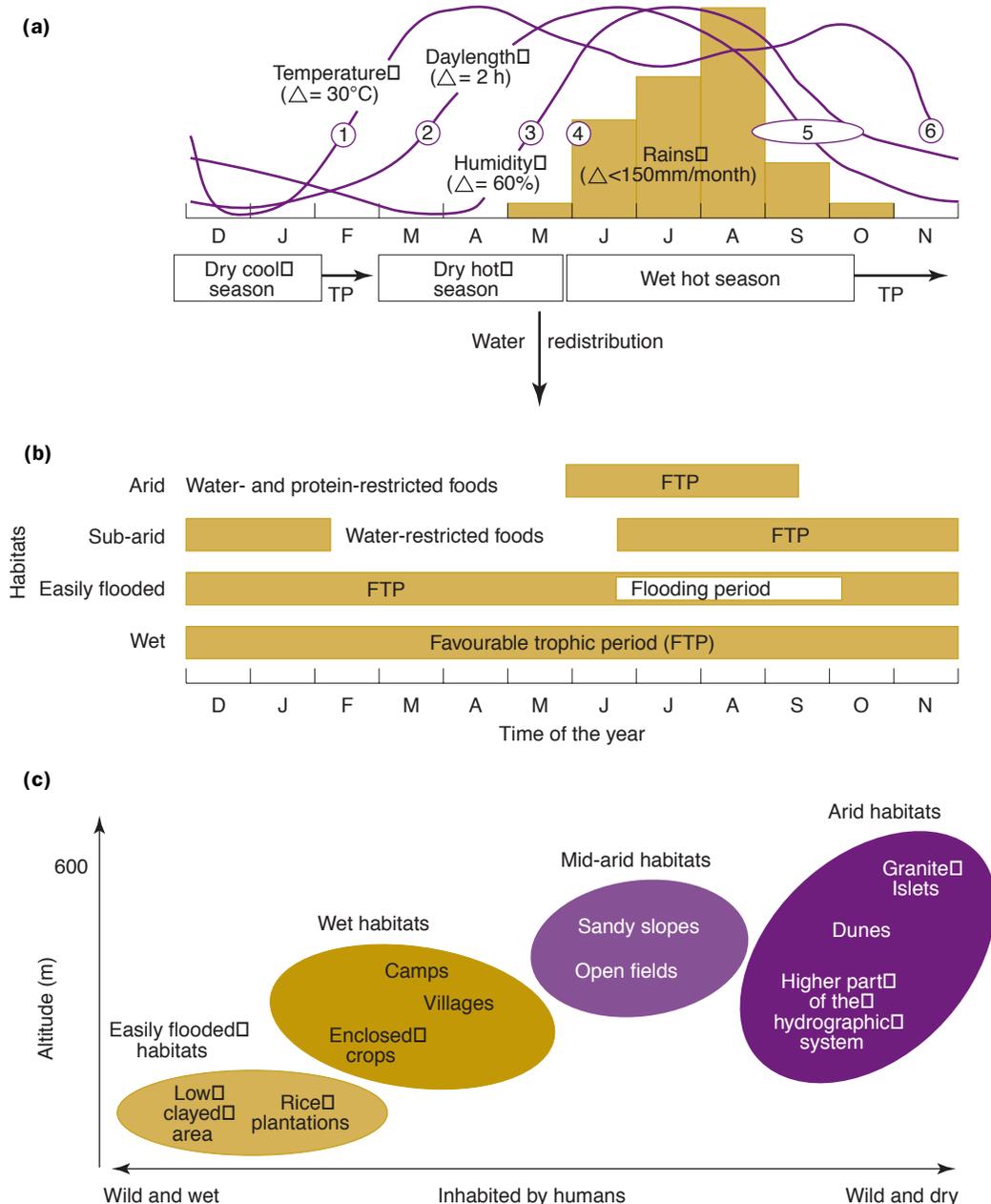


Figure 2. Climate, trophic resources and rodent habitats. (a) Sahelian-Sudanese climate (D = range of annual variations of climatic parameters; TP = transitional periods). The numbers 1–6 indicate the chronological order of appearance of potential synchronisers (see text). (b) Variability of trophic resources according to rodent habitats. (c) Diversity of rodent habitats.

Thus, the Sahelian-Sudanese climate provides reliable synchronisers that can influence the ECC of mammals for anticipatory regulation of physiological functions (Sicard 1987, 1992). The animal's capacity to predict external factors and to adjust in advance its physiology represents the adaptive advantage of endogenous rhythms. Analysis of the relationship between a species' distribution according to habitat (Sicard 1992) and reproductive timing (Sicard 1999) demonstrates that anticipatory adaptive capacity increases in increasingly arid environments.

ECOPHYSIOLOGY, KNOWLEDGE OF RODENT VITAL-CYCLES AND RPM IMPROVEMENT

Life history strategies, vital-cycles and RPM improvement

The "r- and K-selection theory" of Pianka (1970) is one of the most used models for describing demographic strategies developed by species to adapt to their environment. Other theories have been proposed (Stearns 1976, 1989; Sibly and Callow 1985; Southwood 1988) and investigations by Perrin (1989) indicate that in small mammals, temporally-dynamic selection, adversity-selection and bet-hedging theories may be more appropriate than the dualistic r- and K-selection theory to establish correlations between life history patterns and habitat characteristics (stability, predictability etc.). Knowledge of life history traits is important for RPM because pests with different life history patterns require different control strategies (Conway 1981; Stenseth 1981; Sullivan 1987). Poulet (1982), Hubert (1982) and

Sicard (1992) have shown that life history traits of Sahelian-Sudanese rodents fit more or less well to r- and K-selection theory. Muridae have a more rapid sexual maturation, a shorter generation time, larger litter sizes and a lower investment per young, than Gerbillidae. Thus, Muridae are more r-strategists than Gerbillidae which conversely are more K-strategists. Nevertheless, it is not always possible to differentiate Muridae and Gerbillidae on the basis of their size, longevity and survival. In addition, certain species such as *Gerbillus nigeriae* (which is apparently a K-strategist) are able to reach extremely high densities of the outbreak type (Sicard 1987).

The vital-cycle (see earlier definition) which characterises physiological cycles according to species, habitat and season provides fundamental insight to species' adaptation, crucial for defining the temporal schedule of RPM actions. Three types of RPM actions can affect population dynamics: actions targeting mobility, reproduction, and/or mortality (see text above and Figure 1). Our main focus in this section is to propose how to build strategies for scheduling RPM actions as a function of the vital-cycle rather than to discuss the possible modes of action.

Actions targeting mobility

Figure 3 summarises previous results indicating how home range size, home range overlap and displacements of activity centres allowed the description of an annual cycle of rodent population mobility (Sicard 1987, 1992; Papillon and Sicard 1995b; Sicard and Papillon 1996).

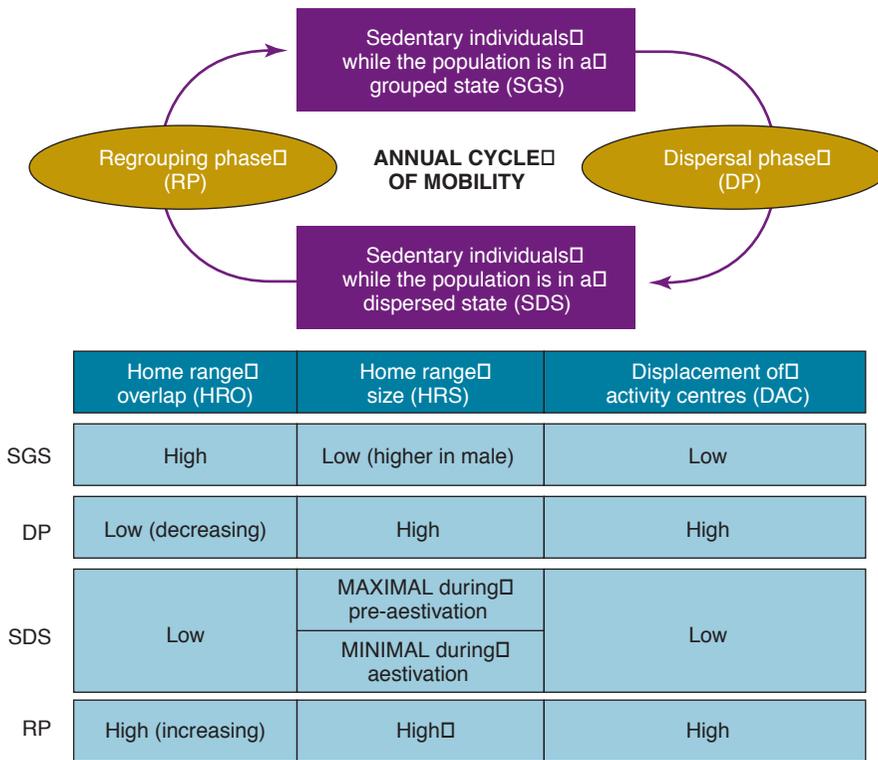


Figure 3. Annual cycle of mobility in rodents. Changes in home range size, home range overlap and displacement of activity centres between successive trapping sessions allow determination of the four stages of the annual cycle of mobility.

In its most complete expression, this cycle includes four phases:

- ▶ a sedentary phase while the population is in a grouped state;
- ▶ a dispersal phase;
- ▶ a sedentary phase while the population is in a dispersed state;
- ▶ a regrouping phase.

Sahelian-Sudanese human populations have developed some RPM strategies that consist either of attracting rodents away from habitations and crops or protecting

them using sound, physical or chemical barriers (Diarra 1996). These methods, which are aimed at affecting rodent mobility, are probably most effective during those phases of the annual cycle when animals are most likely to be actively mobile, i.e. during the dispersal and regrouping phases. The hypothesis that knowledge of the annual cycle of rodent mobility improves the timing and efficiency of these RPM methods will be tested in the near future.

Actions targeting reproduction

Strategies affecting reproduction are not yet widely used in West Africa, although

this alternative to an actions targeting mortality or mobility could be very useful in certain cases. Factors influencing rodent population dynamics are so tightly integrated that an action aiming to permanently decrease reproduction would probably elicit powerful compensatory mechanisms. Our suggestion is that since avoidance of compensatory mechanisms is preferable, a discontinuous, rather than a continuous, action aimed at inhibiting reproduction would be more effective. If this assumption—currently under experimentation in the field—is correct, it is necessary to define the appropriate period for action. Mechanisms that regulate reproduction result in young being born at the most favourable time for their development. The first half of the birth period, which is often much more favourable than the second half (Bronson 1989), is thus an appropriate period for an action targeting reproduction. Therefore, for a bait-delivered immunocontraceptive control to be an effective management strategy (see Chambers et al., Chapter 10), a high proportion of the breeding population would need to be sterilised at the beginning of the breeding season.

Actions targeting mortality

Poisoning is the most frequently used technique for rodent control in West Africa. During the dispersal and regrouping phases, spatial mobility of animals increases according to the landscape structure and certain environmental events. Since rodents cover long distances, the probability that an individual will encounter the treated area is low. This also carries an increased risk in the event that animals ingest non-lethal

amounts of rodenticide and develop resistance. Conversely, when rodent densities are low, animals are sedentary and non-reproductive, and we suggest that the use of anticoagulants is advisable, even in some r-strategist species. It is thus interesting to take into consideration the annual cycle of rodent mobility to determine favourable or unfavourable periods for chemical control.

Cases studies in sub-Saharan agriculture

***Mastomys huberti* and *Arvicanthis niloticus* living in wet habitats**

Figure 4 schematically summarises data obtained for populations of *M. huberti* and *A. niloticus* in wet habitats where a rich diet and water is available throughout the year (Sicard 1987). Investigations of the effects of water restriction on water balance show that neither species show mechanisms to reduce water losses (Gautun et al. 1989; Sicard 1992; Fuminier 1994; Sicard et al. 1994; Sicard and Papillon 1996). Analysis of home range size (HRS) shows that locomotor activity is important throughout the year with no seasonal variations (HRS \approx 400 m²). Analysis of seasonal displacement of activity centres (DAC) in consecutive months and analysis of percentage of home range overlap (HRO) indicates that displacements of populations always remain low (DAC \approx 33 m; HRO \approx 72%). In spite of the fact that both species breed all year in wet habitats (except for a short period of August–September in *A. niloticus*) outbreaks never occurred, whereas in other habitats these species showed reproduction-dependant outbreaks (in 1987 in Burkina Faso and in 1994 in Mali

for *A. niloticus*). Comparative analysis of life history traits clearly shows that populations living in wet habitats are less r-strategists than those living in easily flooded habitats. Since wet habitats are stable environments, species tend to shift their demographic strategy in the K direction of the r-K axis. Thus, a typical characteristic of the life cycle of populations living in wet habitats is the absence of a period of physiological imbalance that could offer a window of opportunity for implementation of RPM.

These features of the vital-cycles in wet habitats suggest the following strategies (Figure 4). First, we propose permanent actions targeting mobility for the two species. Second, since *A. niloticus* has a short period of sexual rest an action targeting reproduction should be focused on the period from October to March, whereas in *M. huberti* (where reproduction is continuous) this action can be achieved during any continuous six-month period of the year. Finally, due to the K demographic trends and the absence of a dispersal phase in these species, a continuous action targeting mortality is possible or could be used alternately with actions targeting reproduction.

Arvicanthis niloticus living in easily flooded habitats

Figure 5 schematically summarises data obtained in populations of *A. niloticus* in easily flooded habitats. This species has a rich diet all year, but faces a period of flooding during rains that can be regarded as an unfavourable period (Sicard 1987). In easily flooded habitats, as in wet habitats, water balance in *A. niloticus* is always in equilibrium since water losses are easily

compensated by water gains (Gautun et al. 1989; Sicard 1992; Fuminier 1994; Sicard et al. 1994; Sicard and Papillon 1996). Observed differences in water turnover between populations in wet or easily flooded habitats are partly related to the fact that locomotor activity is more important in the latter habitat during the dispersal phase. In easily flooded habitats, animals are sedentary from October to April (HRS \approx 390 m²; DAC \approx 31 m; HRO \approx 65%), and display an increase in mobility from May to September (HRS \approx 1160 m²; DAC \approx 60 m). Initially (May–August) animals show a dispersal phase marked by a decrease in overlapping home ranges (HRO \approx 23%), followed in September by a regrouping phase marked by an important increase in overlapping home ranges (HRO \approx 75%). Animals breed from October to the end of April. Thus, the dispersal period starts only when animals are in sexual rest and, conversely, sexual activity starts only when animals are sedentary. Although the role of non-trophic synchronisers (NTS in Figure 5) in reproduction has previously been characterised (Sicard and Fuminier 1996), possible effects on mobility (i.e. induction of onset and offset of dispersal and regrouping phases) remains to be determined. In addition to the direct effects of non-trophic factors, an indirect effect of sexual steroids on central mechanisms involved in the regulation of mobility cannot be excluded.

The vital-cycle in easily flooded habitats suggests (Figure 5) focusing actions on mobility during the rainy season and actions on reproduction from October to February. These proposals may be an alternative to chemical control which is not advisable since *A. niloticus* is a typical r-strategist in easily

Ecologically-based Rodent Management

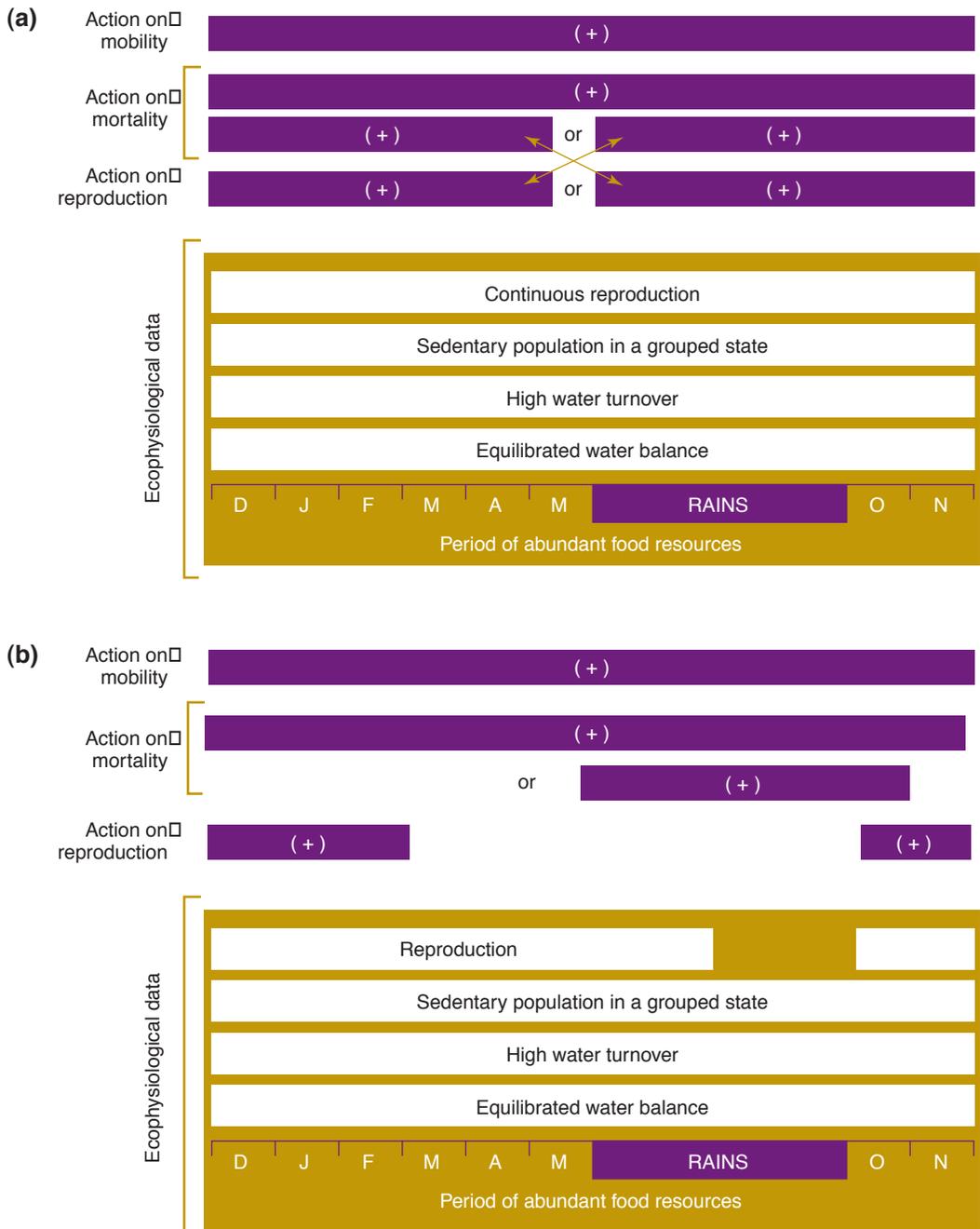


Figure 4. Vital-cycle and rodent pest management (RPM) strategies in wet habitats. Strategies for RPM (upper panels) may be deduced from an analysis of the vital-cycles (lower panels) of (a) *Mastomys huberti* and (b) *Arvicanthis niloticus* (redrawn from Sicard and Papillon 1996).

flooded habitats. Nevertheless, limited actions targeting mortality may be effective during two periods: (i) the period of low rodent densities, decreased reproduction, and prior to the dispersal phase; and (ii) during the regrouping phase at the beginning of reproduction (Figure 5).

Mastomys erythroleucus and Taterillus gracilis in semi arid habitats

Figure 6 summarises data obtained for populations of *M. erythroleucus* and *T. gracilis* in semi-arid habitats (Sicard 1987, 1992; Gautun et al. 1989; Fuminier 1994; Sicard and

Papillon 1996). In this habitat these species have a rich diet from June to the end of January and a water-restricted diet during the rest of the year. Seasonal variations in water turnover are strongly correlated with diet in the two species, but water balance is in equilibrium throughout the year.

In *M. erythroleucus*, analysis of mobility and reproduction shows that during periods of food availability, animals are sexually active and the population is in a grouped sedentary state (HRS \approx 530 m²; DAC \approx 26 m; HRO \approx 84%).

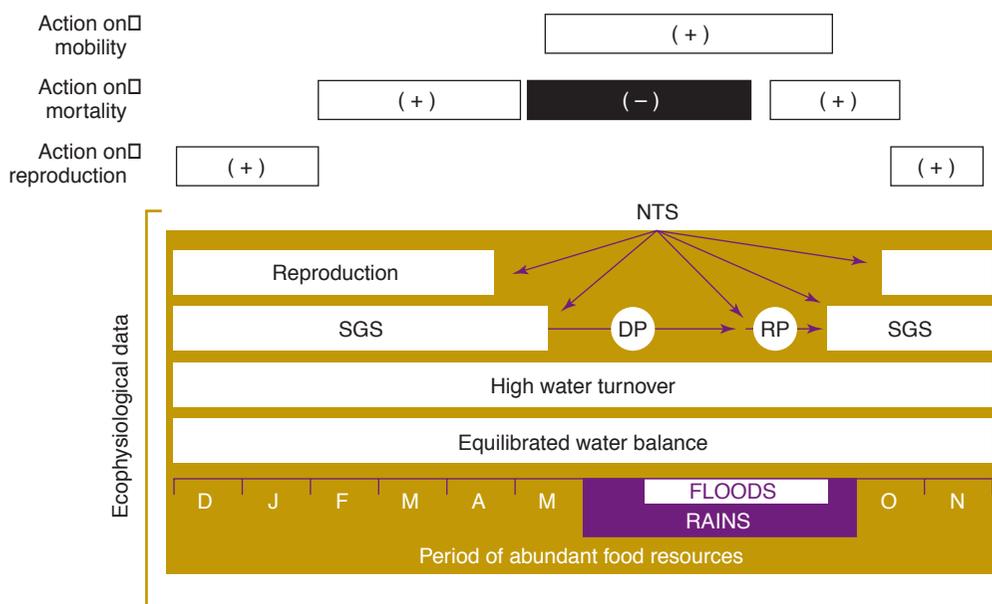


Figure 5. Vital-cycle and rodent pest management (RPM) strategies in easily flooded habitats. Strategies for RPM (upper panel) may be deduced from analysis of the vital-cycle (lower panel) of *Arvicanthis niloticus* (DP = dispersal phase; NTS = non-trophic synchronisers—daylength, temperature, humidity etc.; RP = regrouping phase; SGS = sedentary phase of individuals while the population is in a grouped state). Arrows indicate that NTS: (i) induce the cessation of reproduction and trigger the DP before the flooding period; (ii) trigger the RP then the SGS near the end of the flooding period; and (iii) trigger reproduction in October (redrawn from Sicard et al. 1995; Sicard and Papillon 1996

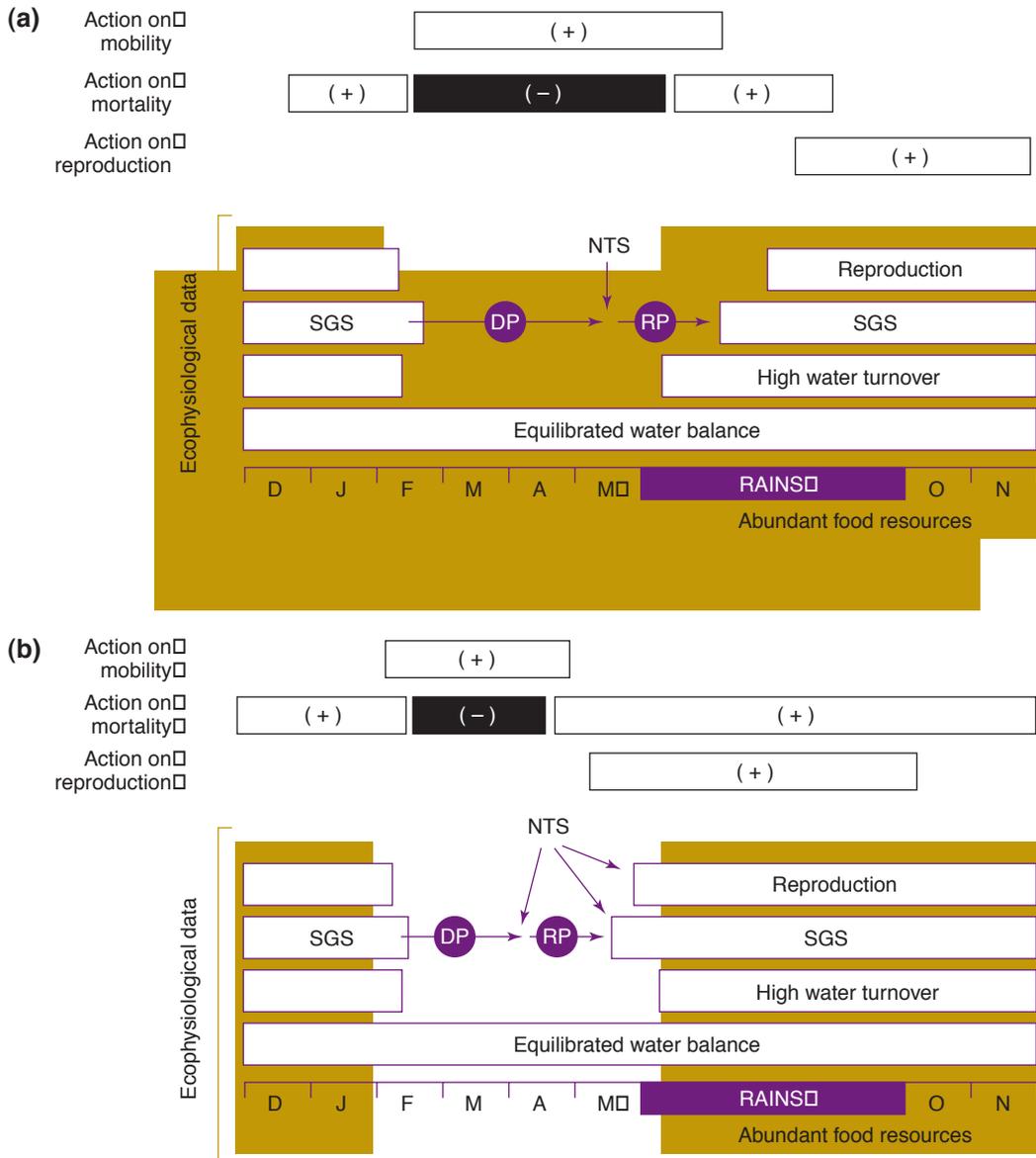


Figure 6. Vital-cycle and rodent pest management (RPM) strategies in semi-arid habitats. Strategies for RPM (upper panels) may be deduced from analysis of the vital-cycles (lower panels) of (a) *Mastomys erythroleucus* and (b) *Taterillus gracillis* (DP = dispersal phase; NTS = non-trophic synchronisers; RP = regrouping phase; SGS = sedentary phase of individuals while the population is in a grouped state). Food restriction induces a decrease in water turnover, the cessation of reproduction and triggers DP (February). NTS trigger RP in May. Changes in diet (i.e. period of abundant food resources) induce an increase in water turnover followed by the SGS phase (June–July) and subsequently trigger reproduction (August) (redrawn from Sicard et al. 1995; Sicard and Papillon 1996).

During the period of restricted foods, when animals are sexually inactive, mobility and displacements increase (HRS \approx 1,200 m²; DAC \approx 71 m). From February to the end of April animals undergo a dispersal phase (HRO \approx 22%), while in May they undergo a regrouping phase (HRO \approx 77%).

Experiments have confirmed that water restriction induces the decrease in water loss and the cessation of reproduction (Sicard 1992). We are currently investigating whether (1) this sequence of events (increase in water turnover, sedentarisation, reproductive onset) are linked by causal relationships and (2) the triggering of the regrouping phase is due to non-trophic synchronisers or to the vasopressinergic system (which is involved in physiological and behavioural regulation of water metabolism; Fuminier et al. 1993; Fuminier 1994). Although chemical control is usually not recommended for r-strategists such as *M. erythroleucus*, this species' vital-cycle suggests a precise chronological schedule for complementary (or alternative) actions targeting mobility, reproduction and mortality (Figure 6a).

In *T. gracilis*, as in *M. erythroleucus*, restricted food induces a decrease in water turnover which in turn triggers the cessation of sexual activity and the start of the dispersal phase (HRS \approx 1,250 m²; DAC \approx 78 m; HRO \approx 32%). In contrast, the sedentary phase (HRO \approx 92%) and sexual activity of *T. gracilis* start prior to favourable conditions and the increase in water turnover. Our experimental results indicate that the cessation of reproduction is mainly controlled by trophic resources whereas the anticipatory reproductive onset is mainly controlled by daylength and temperature

(review in Sicard et al. 1996). The non-trophic synchronisers triggering regrouping and sedentary phases remain to be determined. The involvement of different synchronisers in the reproductive strategies of *T. gracilis* and *M. erythroleucus* is significant. Due to the high fecundity of *M. erythroleucus* (litter size \approx 10), a short period of reproduction is sufficient to ensure reproductive success. In contrast, the low fecundity of *T. gracilis* (litter size \approx 3) requires a longer period of reproduction to reach similar productivity. The onset of reproduction before rains illustrates the adaptive significance of a physiological function that depends on seasonal factors through an endogenous rhythm. This type of adaptation is probably just as important as metabolic adaptations for the maintenance of species in semi-arid habitats. Although chemical control is usually recommended for K-strategists such as *T. gracilis*, the vital-cycle of this species suggests that such action is inappropriate during the dispersal phase. In addition, a precise chronological schedule for complementary (or alternative) actions targeting mobility, reproduction and mortality is suggested in Figure 6b.

Taterillus petteri living in arid habitats

Figure 7 summarises data obtained for populations of *T. petteri* in arid habitats (Sicard 1987, 1992; Sicard et al. 1988b; Gautun et al. 1989; Fuminier et al. 1993; Fuminier 1994; Sicard and Fuminier 1994; Sicard and Papillon 1996). These animals have a rich diet only during the rainy period. Field monitoring and laboratory results indicate that, as for many other species, restricted food induces a decrease in water turnover (WT \approx 44% TBW during rains

versus 32% TBW during cool season), which in turn induces the cessation of sexual activity and the start of the dispersal phase. Contrary to other species, *T. petteri* presents a water imbalance phase (WIP) in February (WIP \approx -3% TBW per day). As in other species, the sedentary phase while the population is in a grouped state (SGS) coincides with the rich diet period and is followed by a dispersal phase (DP), but both phases are more marked in males: SGS (HRS \approx 800 m² in males versus 500 m² in females; DAC \approx 25 m in males versus 17 m in females; HRO \approx 79%); DP (HRS \approx 1,600 m²; DAC \approx 65

m; HRO \approx 10%) from October to December. In contrast to other species, the dispersal and regrouping phases are separated by a long sedentary phase while the population is in a dispersed state (SDS) from January to May, which probably ensures a better spatial distribution of individuals during the long period of restricted food. This SDS phase comprises two stages. During pre- aestivation (PE in Figure 7) animals build a complex burrow and must increase the size of their home range to find foods for provisions (HRS \approx 2,100 m² while DAC \approx 0 m and HRO \approx 0%).

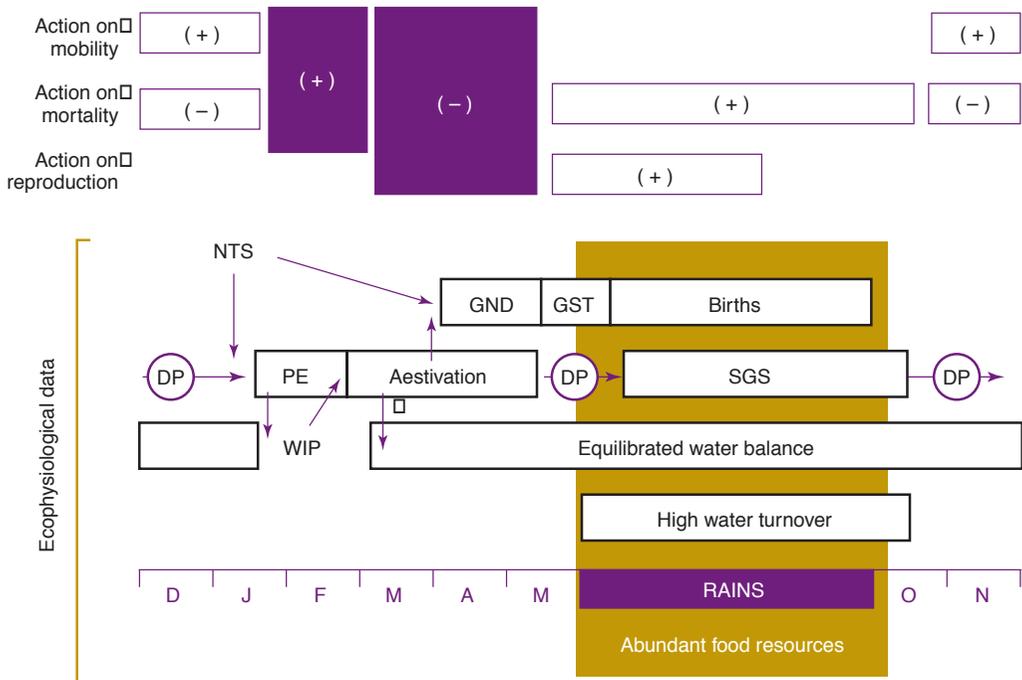


Figure 7. Vital-cycles and rodent pest management (RPM) strategies in arid habitats. Strategies for RPM (upper panel) may be deduced from analysis of the vital-cycles of *Taterillus petteri* (lower panel) (DP = dispersal phase; GND = pituitary gonadotrophic activity; GST = gestation; NTS = non-trophic synchronisers; PE = pre-aestivation; RP = regrouping phase; SGS = sedentary phase of individuals while the population is in a grouped state; WIP = water imbalance phase) (redrawn from Sicard 1992; Sicard and Fuminier 1994; Sicard et al. 1995; Sicard and Papillon 1996). See text for details.

During aestivation, animals remain in their burrow for periods of several weeks during which they only eat accumulated provisions and show daily periods of torpor (HRS ≈ 0 m²; DAC ≈ 0 m; HRO $\approx 0\%$). The end of aestivation is marked by a short regrouping phase on the grassy sandy hollows located between dunes (HRS $\approx 1,400$ m²; DAC ≈ 55 m; HRO $\approx 75\%$).

Pituitary gonadotrophic activity starts in the middle of aestivation, so that sexual coupling is possible during either aestivation or the regrouping phase. Young thus appear at the first rains. We have studied several causal relationships between these various phenomena. The dispersal phase is extremely short because it is rapidly followed by the pre-aestivation period. We propose that decreases in temperature trigger pre-aestivation (see NTS in Figure 7). During pre-aestivation, water losses decrease (WT $\approx 20\%$ TBW) in spite of the increase in home range size and the energy required to build the aestivation burrow and collect provisions. This indicates that mechanisms for reducing water losses are fully active, although a temporary water imbalance phase occurs in February. Considering the time between two recaptures using the tritiated water method, the water imbalance phase lasts approximately five days, and indicates that the water deficit is about 15% of TBW. We have previously proposed that a water imbalance phase is the internal trigger for aestivation (Sicard and Fuminier 1994). During aestivation, water balance is restored because animals become inactive and water requirements are markedly reduced. In *T. petteri*, daylength exerts a gonadal-stimulating effect throughout the year,

which is thwarted by many factors such as water restriction (Sicard and Fuminier 1994). This explains why animals are sexually inactive when they enter aestivation. We suggest that (1) animals must undergo a short period of water imbalance to enable a resurgence of gonadotrophic activity via changes in daylength and (2) the renewal of sexual activity is involved in the cessation of aestivation (see NTS in Figure 7).

The vital-cycle of *T. petteri* in arid habitats suggests focusing management actions on mobility, reproduction and mortality (Figure 7). Actions targeting mobility are appropriate during the dispersal phase, but also during the pre-aestivation phase because animals undergo a water imbalance phase and are therefore physiologically fragile. Although aestivation would theoretically be the ideal time to act on reproduction, access to the animals in their burrows is not feasible; thus actions targeting reproduction are only appropriate from June to August (the first half of the reproductive period). Although chemical control is usually recommended for K-strategists such as *T. petteri*, the vital-cycle of this species indicates that chemical control only should be implemented during pre-aestivation and/or during the rainy season.

REGULATION OF REPRODUCTION AND PREDICTION OF REPRODUCTION-DEPENDENT OUTBREAKS

Knowledge of the mechanisms involved in rodent population dynamics is very useful for RPM. Indeed, the extent of damage caused by rodents depends on annual variations in rodent population densities. Rodent outbreaks often have a major impact

on human health and agriculture in Sahelian-Sudanese regions. Forecasting of outbreaks mainly depends on an understanding of their causes and several mechanisms have been proposed to explain them. For example, in Senegal, successive years with favourable rainy seasons allow the populations of certain rodents to reach a 'pre-outbreak' level that can induce an outbreak if the following year is favourable (Poulet 1980; Hubert and Adam 1985). Analyses by Fiedler (1988a,b) indicate that in Sahelian Africa, rodent outbreaks are preceded by several years of prolonged drought, followed by years with normal or high rainfall. The increase in rodent density would be partially due to the effects of the prolonged drought on the numbers of rodent predators and competitors. It may also be that during prolonged drought the ground becomes fertilised because of the death of many animals, which would support vegetation growth in a year with a normal rainfall (Mutze 1991). In Tanzania, where there are two annual rainy periods, the risk of occurrence of *Mastomys* outbreaks is related to the aridity of preceding years and to the rainfall pattern of the current year (Leirs 1995). In temperate regions, outbreaks of *Microtus* always occur in certain type of habitats, from which they propagate, in subsequent years according to the landscape structure. At the end of this propagation period, they always reappear in the same types of habitats in a regular pattern every six or seven years (Delattre et al. 1996). By contrast, in Sahelian Africa, rodent outbreaks occur irregularly, often on a regional scale, and simultaneously in one or more species of the genera *Arvicanthis*, *Mastomys*, *Taterillus* or *Gerbillus* (Sicard

1995b). These examples show that different mechanisms can lead to outbreaks. Whatever the initial trigger of an outbreak, it must act more or less directly on reproduction, mobility and/or mortality. Mortality is an ecological function broader and more difficult to study than reproduction or mobility, which are more specific physiological functions. Below are the results relating our research on the regulatory mechanisms of reproduction in the main pest rodents of the Sahelian-Sudanese region using *A. niloticus* living in easily flooded habitats as an example. Laboratory and field results have enabled us to understand the mechanisms leading to the outbreak of *A. niloticus* in Burkina Faso in 1987. Analyses of the results and their prospects for modelling reproduction-dependent outbreaks are also presented.

Regulation of reproduction in *A. niloticus* populations living in easily flooded habitats

A. niloticus is undoubtedly one of the most important pest rodents of the Sahelian-Sudanese region. Reproductive patterns of this species have been extensively studied. In Uganda, where the climate is constant with rainfall distributed throughout the year, reproduction of *A. niloticus* is continuous (Neal 1981). In Kenya, where the climate undergoes slight seasonal variations with two rainy periods, reproduction of *A. niloticus* becomes seasonal (Taylor and Green 1976; Neal 1981). In Tanzania (Packer 1983), Ethiopia (Müller 1977), Senegal (Poulet 1982) and Sudan (Ghobrial and Hodieb 1982), where the climate shows differentiated dry and rainy seasons, reproduction begins more or less near the

end of the rainy season and ends late in the dry season. Our field studies in Burkina Faso and Mali show that the reproductive pattern of *A. niloticus* also depends on habitat variability (Sicard et al. 1994). Indeed, reproduction of *A. niloticus* is almost continuous in stable wet habitats, whereas reproduction stops from the end of the dry season to the end of the rainy season in easily flooded habitats.

Many factors can be involved in the regulation of reproduction in tropical rodents. They include daylength (Happold 1983; Khammar and Brudieux 1986, 1987), air humidity (Müller 1977; Haldar and Saxena 1988), temperature (Vivien-Roels and Pévet 1983), length of the dry season (Packer 1983), rainfall via increased water intake (Yahr and Kessler 1975; Beatley 1976; Christian 1979), rainfall via variation in the quality and the quantity of foods (Delany and Happold 1979), rainfall via a triggering effect of substances found in germinating plants (Negus and Berger 1977; Sanders et al. 1981; Alibhai 1986; Daya et al. 1990; Linn 1991; Neal and Alibhai 1991). We have studied the effects of many of these factors on reproduction, both experimentally and in animal populations monitored in the field, in Mali and Burkina Faso (Gautun and Sicard 1985; Sicard et al. 1988a, 1992, 1993, 1994; Kyelem and Sicard 1996; Papillon et al. 1996a,b; Sicard and Fuminier 1996; Sicard and Papillon 1996). In studies over the past fifteen years, *A. niloticus* populations in easily flooded habitats are those which more frequently show outbreaks. Figure 8a summarises the combined effects of daylength, temperature, relative humidity and food availability on the development and regression of sexual activity in

A. niloticus originating from easily flooded habitats and includes the following findings:

- ▶ 6-methoxy-2-benzoxazolinone does not influence reproduction.
- ▶ Water restriction *or* poor foods prevent development of sexual activity in sexually inactive animals and conversely induce regression of sexual activity in sexually active animals (situation 1 in Figure 8a).
- ▶ Long days exert a gonadal-inhibitory effect that fully counteracts any gonadal-stimulating effects of rich foods *and* unrestricted water, but only when animals are under high temperature and low humidity (situation 2).
- ▶ Gonadal-stimulating effects of rich foods *and* unrestricted water never fully counteract the gonadal-inhibiting effects, except when animals are in situation 4 (situation 3).
- ▶ Rich foods *and* unrestricted water combined with high humidity and low temperature induce the strongest gonadal stimulation (situation 4).

From these results, and from comparisons between experimental and natural conditions, it is possible to construct a scenario of gonadal-stimulating and gonadal-inhibiting effects of climatic and trophic synchronisers in easily flooded habitats throughout the year (Figure 8b). Under natural conditions and during years with a typical climate, only situations 2 and 3 exist. Situations 4 and 1 correspond to atypical climatic conditions. Situation 1, which would correspond to a massive collapse of resources in easily flooded habitats, is more improbable than situation

4, which would correspond to additional rainfall when temperatures are low (December–January) or to an exceptional decline in temperature during the rainy season (August). There is a strong inhibitory coincidence near the end of March and a strong stimulatory coincidence near the end of September (Figure 8b).

Comparisons between experimental and field results allow a clearer understanding of the regulation of reproduction in the field. In Figure 9a, the reproductive onset appears

near the end of September, when the gonadal-stimulating effects exerted by water and food, air humidity (and possibly rains) are no longer thwarted by the gonadal-inhibiting effect exerted by long days. Once reproduction has started, animals become insensitive to gonadal-inhibiting factors (refractory phase: RP1 in Figure 9). Near the end of March, the three strongly gonadal-inhibiting conditions (long days, high temperature and low humidity) concur and this coincidence induces the end of RP1, the

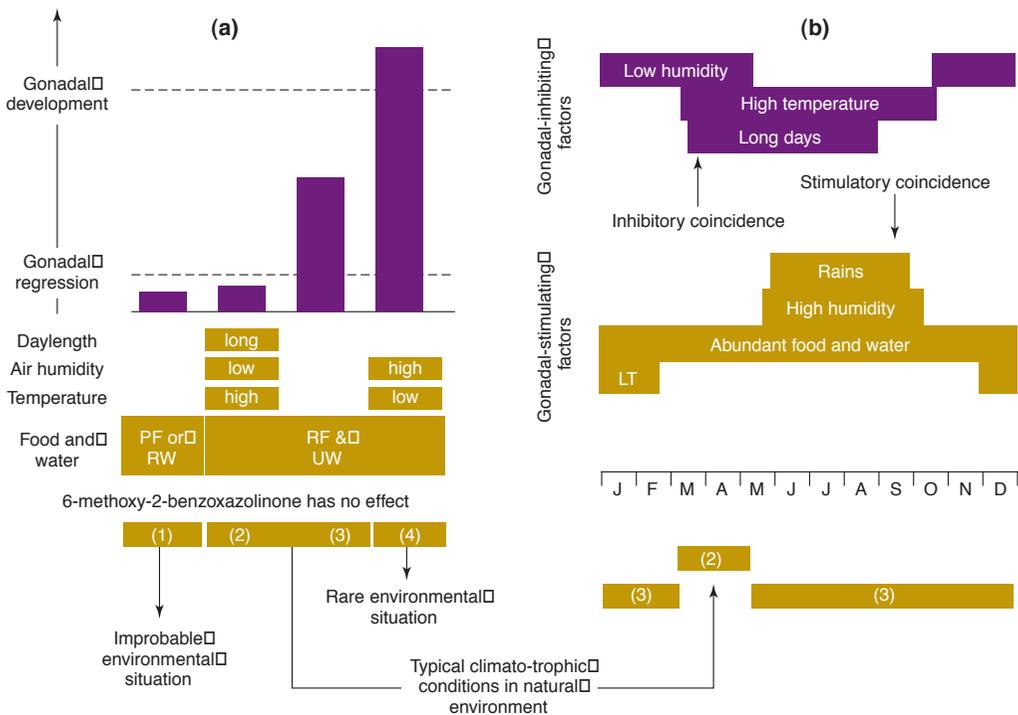


Figure 8. Regulation of reproduction in *Arvicanthis niloticus* living in easily flooded habitats. (a) Results of experimental studies on the combined effects of potential synchronisers on development and regression of gonads. Potential synchronisers include daylength (long or short), air humidity (low and high), temperature (low and high), 6-methoxy-2-benzoxazolinone found in germinating plants, foods and water (PF = poor foods; RF = rich foods; RW = restricted water; UW = unrestricted water). Comparisons between experimental and natural conditions (situations 1, 2, 3 and 4). (b) Scenario of gonadal-stimulating and gonadal-inhibiting effects of climatic and trophic synchronisers in easily flooded habitats (LT = low temperature). See text for details.

appearance of a phase of insensitivity towards gonadal-stimulating factors (refractory phase: RP2 in Figure 9a), and the regression of sexual activity. The cessation of RP2 is not possible before the gonadal-stimulating effects exerted by food and high humidity are expressed in the absence of gonadal-inhibitory effects of long days. Since investigations by Turek (1972), refractory phases have been invoked to explain seasonal variations in the sensitivity of individuals to the key factors regulating reproduction

(Pévet 1987). Refractory phases have an obvious physiological significance: a seasonal physiological activity, once started (or stopped), cannot be inhibited (or stimulated) before a certain delay.

The reproduction-dependent outbreak of *A. niloticus* in 1986–1987

Analysis of the rainfall records shows that in 1986 there was an atypical climate, not only in Burkina Faso where we studied an outbreak of *A. niloticus* and *G. nigeriae*, but also in the entire

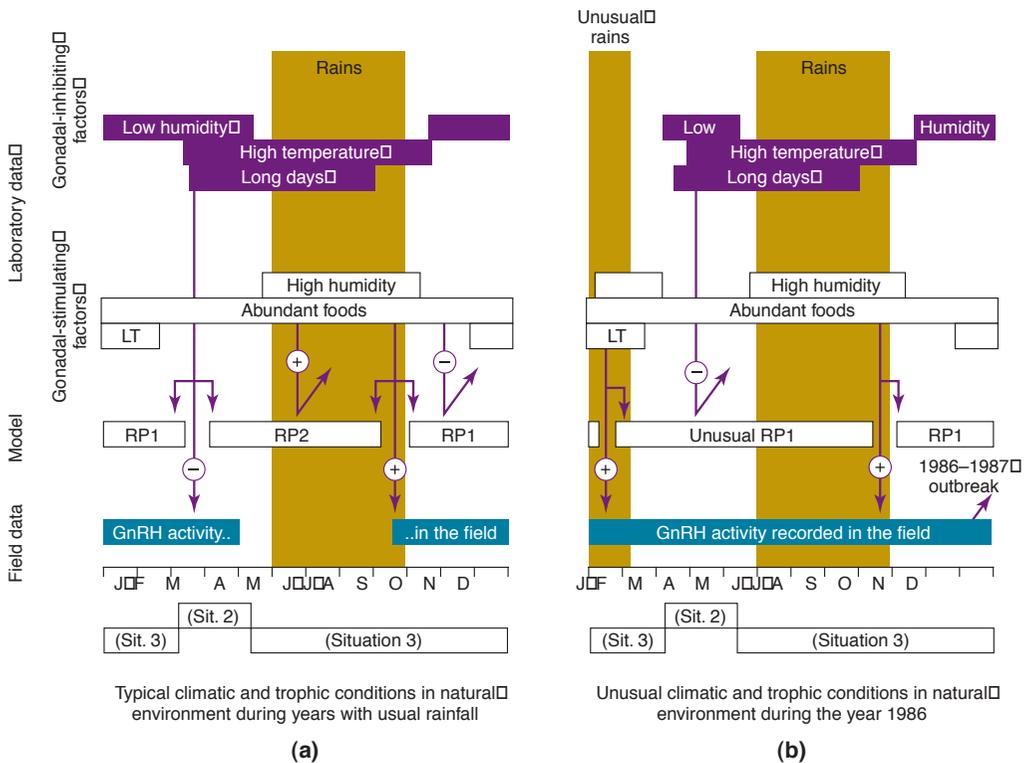


Figure 9. Reproductive cycle and reproduction-dependent outbreak of *Arvicanthis niloticus* living in easily flooded habitats. (a) Modelling of regulatory mechanisms of reproduction during a year with typical rainfall. Arrows indicate the gonadal-stimulatory and gonadal-inhibitory coincidences. RP1 = refractory phase toward gonadal-inhibiting factors; RP2 = refractory phase toward gonadal-stimulating factors (situations 2 and 3 are similar to experimental conditions in Figure 8a). (b) Modelling of regulatory mechanisms of reproduction during the year 1986 with an atypical rainfall (see text for details).

Sahelian-Sudanese region. In Burkina Faso, early rains occurred during all of January and part of February, resulting in a total of approximately 80 mm. These rains, accompanied by an unusual increase in relative humidity, allowed a transient growth of the vegetation, particularly in extreme wet and arid habitats. Indeed, the ground was not completely drained in January, and the rains caused a sufficient streaming for water to converge towards the lowest wet areas. In arid habitats, the ground is covered by graminaceous seeds that can germinate after small amounts of rainfall. This atypical climatic situation in January–February 1987 corresponded exactly to the experimental situation 4 that is described in Figure 8b and which is the most gonadal-stimulating situation studied. As shown in Figure 9b, a strong, additional gonadal-stimulating coincidence curtailed the refractory phase RP1, reinforced reproductive activity and started a refractory phase towards the gonadal-inhibiting factors that usually cause cessation of reproduction (unusual RP1 in Figure 9b). As indicated from field results, sexual activity of *A. niloticus* did not cease during the rainy season of the year 1986 and reproduction continued during the entire year, resulting in a five-month lengthening of the breeding period. Rodent density was particularly high in August 1986 and in February 1987 reached levels of the outbreak type (approximately 20 times higher than during typical years).

In the case of *G. nigeriae*, January rains in 1986–1987 prevented the water imbalance phase from occurring and induced the cessation of the refractory period to the gonadal-stimulating effect of long days (see Figure 7). Hence, reproduction started three

months in advance and resulted in an outbreak.

Thus, the experimental study of gonadal-inhibiting and gonadal-stimulating effects of climato-trophic factors associated with the descriptive study of the reproductive cycle in the field allows a better understanding of reproductive regulation during typical years as well as how atypical climatical conditions combine to remodel reproduction.

Modelling reproduction-dependent outbreaks

The preceding analyses provide a demonstration of how the timing and duration of reproduction depend on the order in which gonadal-stimulating and gonadal-inhibiting effects occur. When a set of stimulating (stimulatory coincidence) or inhibiting (inhibitory coincidence) occurs, it induces: (i) the cessation of a refractory phase to stimulating (or to inhibiting) factors; (ii) the development (or the regression) of sexual activity; and (iii) a refractory phase to inhibiting (or stimulating) factors (gonadal-stimulating coincidences—GSC; gonadal-inhibiting coincidences—GIC; refractory phase—RP; Figure 10). During years with a typical rainfall, the chronicle of GSC and GIC is typical and induces a typical breeding pattern. In contrast, during years with an atypical rainfall the chronicle of GSC or GIC becomes unusual and may induce an atypical breeding pattern, which in turn can induce a reproduction-dependent outbreak. These chronicles depend on the chronicle of environmental synchronisers during typical and atypical years, and the sensitivity of the endogenous clock to synchronisers. Thus, predictive research should take into account:

(1) species-specific influences of synchronisers on reproduction; (2) induction of refractory phases; (3) a climatic approach aiming to identify the most frequent disturbances of the Sahelian-Sudanese climate; and (4) modelling of the impacts of these disturbances on the chronicle of synchronisers.

CHRONOBIOLOGY APPLIED TO RPM AND FUTURE RESEARCH PROSPECTS

Improving the systematics of Sahelian-Sudanese rodents

Regulatory mechanisms of reproduction and endogenous rhythms are species-specific

and often population specific. For example, *A. niloticus*, which live in easily flooded habitats, show a period of sexual inactivity during the rains and are more responsive to photoperiodic changes than *A. niloticus* which live in wet habitats and reproduce continually (Sicard et al. 1992). Further genetic studies are needed to determine whether these two populations of *A. niloticus* (Burkina Faso) constitute two different species. Indeed, two species of *Arvicanthis* (*A. niloticus* Desmarest 1822 and *A. ansorgei* Thomas 1910; Ducroz 1998) have recently been shown to be sympatric in Mali and probably also in northern Burkina Faso (Sicard, unpublished data).

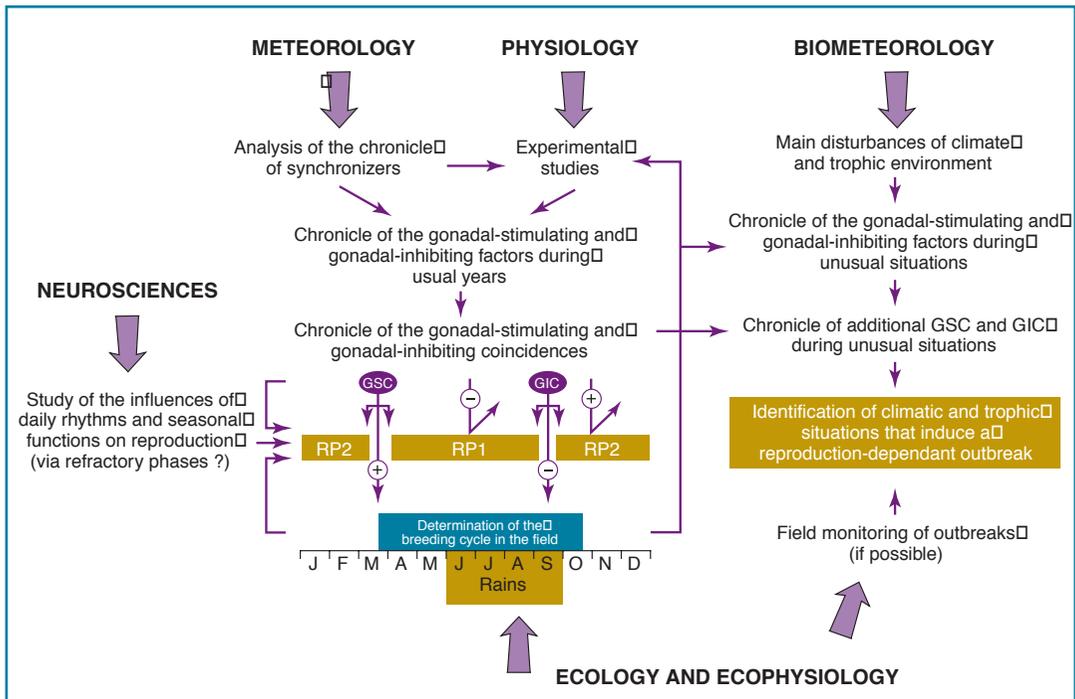


Figure 10. Modelling of reproduction-dependent outbreaks (GSC = gonadal-stimulating coincidence; GIC = gonadal-inhibiting coincidence; RP1 = refractory phase toward gonadal-inhibiting factors; RP2 = refractory phase toward gonadal-stimulating factors).

In the past few years, the genus *Mastomys* has increased from six to nine species (Lavrenchenko et al. 1998) and the genus *Arvichanthus* from one to nine species (Ducroz et al. 1997). Several new species of *Gerbillus* and *Taterillus* have recently been found in the Inner Delta of the Niger River. As shown by these examples, a large array of species, currently concealed as morphologically similar forms, remains to be described. Advancing this problem of systematics at a finer level requires several complementary tools (morphometry, cytogenetics, electrophoresis, gene sequencing).

Improving the classification of rodent habitats

Genetic and biogeographical approaches should be combined to determine internal (chromosomal rearrangements) and external (habitat structure) factors influencing population isolation. These approaches should provide a better understanding of the distribution of Sahelian-Sudanese rodents and identify areas (e.g. the Inner Delta of the Niger River) which generate biodiversity. Knowledge of these zones is important if future RPM programs are to be integrated on a more widespread regional scale covering several Sahelian countries.

Improving the concept of vital-cycles

The hypotheses raised earlier in this chapter show that a better characterisation of the vital-cycle requires further insight into the regulation of rodent mobility by external factors (i.e. climato-trophic) and internal factors (i.e. water metabolism and sexual steroids). The characterisation of the vital-cycle also necessitates a finer description of

the annual cycle of mobility. Indeed, traditional trapping methods are generally not sufficient to take into account the entire geographical range of seasonal movements of individuals and populations. Radiotelemetry techniques would allow more complete characterisation of these seasonal movements, which may occur from one habitat to another in the same agro-ecosystem. The description of the annual cycle of mobility also needs to consider the effects of the landscape structure on the activity of rodents during the dispersal and regrouping periods. Knowledge of ecophysiology, chronobiology and landscape ecology is thus fundamental for the improving our understanding of the concept of vital-cycle.

Forecasting mobility-dependent outbreaks

The analyses presented above indicate that there are at least three types of outbreaks: reproduction-dependent outbreaks (RDO), mobility-dependent outbreaks (MBDO) and mortality-dependent outbreaks (MRDO). In the Sahelian-Sudanese region, rodent outbreaks often occur on a regional scale and concern only certain species. This suggests that triggering of outbreaks directly or indirectly involves climato-trophic factors, and that the perception of these factors depends on species-specific mechanisms. The examples presented above show that additional rains in January are able to trigger a RDO in certain (*G. nigeriae* and *A. niloticus*), but not all, species.

Rainfall was abundant in 1986 (more than 400 mm) after a period of prolonged drought (annual rainfalls lower than 200 mm). It is thus possible that prolonged drought could

have played a role via previously evoked factors. The observed RDO may have been due not only to a lengthening of reproduction but also to an increase in the productivity of trophic resources. It is also possible that these RDO were partly mortality- and/or mobility-dependent. We believe that the key factors regulating population dynamics are so closely integrated that it is unlikely that one of them alone can trigger an outbreak. Thus, our distinction between RDO, MBDO and MRDO is not exclusive.

Mechanisms analysed in given examples described earlier in this chapter are species- or population-specific. Because these mechanisms are different, depending on whether *A. niloticus* live in easily flooded habitats or in wet habitats, the different reproductive cycles of these populations are differentially affected by the January rains (only the populations in easily flooded habitats were affected). *A. niloticus* did not show an outbreak in wet habitats in 1986–1987, probably because reproduction is typically continuous in this type of habitat. For this reason, we think that in wet habitats rodent populations face stronger intra- and interspecific competition than in easily flooded habitats. Consequently, even r-strategists like *Arvicanthis* or *Mastomys*, would not be able to achieve a RDO in wet habitat. This does not exclude other phenomena from triggering either MRDO or MBDO.

Our experimental studies in *M. erythroleucus* and *T. gracilis* show that regulatory mechanisms of reproduction are not sensitive to early rainfall (Sicard 1995b), which explains why reproduction-dependent outbreaks were not observed in 1986–1987. This does not exclude other types

of atypical rainfall patterns from triggering a RDO in these species.

By definition, MRDO result from a decrease in mortality. The latter can be due to natural selection (Hubert et al. 1978) or to a collapse of predation and/or competition (Fiedler 1988a,b). Competitors and predators of rodents are not very species-specific. Thus, when a MRDO relates only to certain species it is probably selection-dependent, whereas if it relates to the majority of species it is more likely to be predation-dependent or competition-dependent. Chronobiology takes into account the fact that different species do not react in the same way to disturbances in the environment because they perceive these disturbances differently. The specificity of outbreak mechanisms explains, independently of the fact that species are r- or K-strategists, why a given phenomenon evoked to account for an outbreak in a given species does not necessarily explain the outbreak of another species.

We have initiated study of the mechanisms affecting mobility and determination of MBDOs in order to address the question of how synchronisers induce seasonal changes in mobility (at the population level) via their effects on the daily rhythms (activity and behaviours) of individuals. Indeed, mobility shows daily and seasonal variations. Therefore it is necessary to continuously record rodent activity (not only at the beginning and at the end of the experiments).

It is also necessary to understand relationships between the daily expression of mobility —

which are the key components of the daily rhythm of activity of an individual?

and the seasonal expressions of mobility

which are the components of the daily rhythm of activity which change during the annual dispersal and regrouping phases of the population?

It is probable that the factors triggering outbreaks act in synergy. Modelling of the mechanisms of outbreaks thus requires comprehensive knowledge of the various factors that regulate the population dynamics of rodents in different habitats.

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