

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 shows 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 ($HRS \approx 400 \text{ m}^2$). 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 ($DAC \approx 33 \text{ m}$; $HRO \approx 72\%$). 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 $\approx 390 \text{ m}^2$; DAC $\approx 31 \text{ m}$; HRO $\approx 65\%$), and display an increase in mobility from May to September (HRS $\approx 1160 \text{ m}^2$; DAC $\approx 60 \text{ m}$). 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 (Figure 5) suggests 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

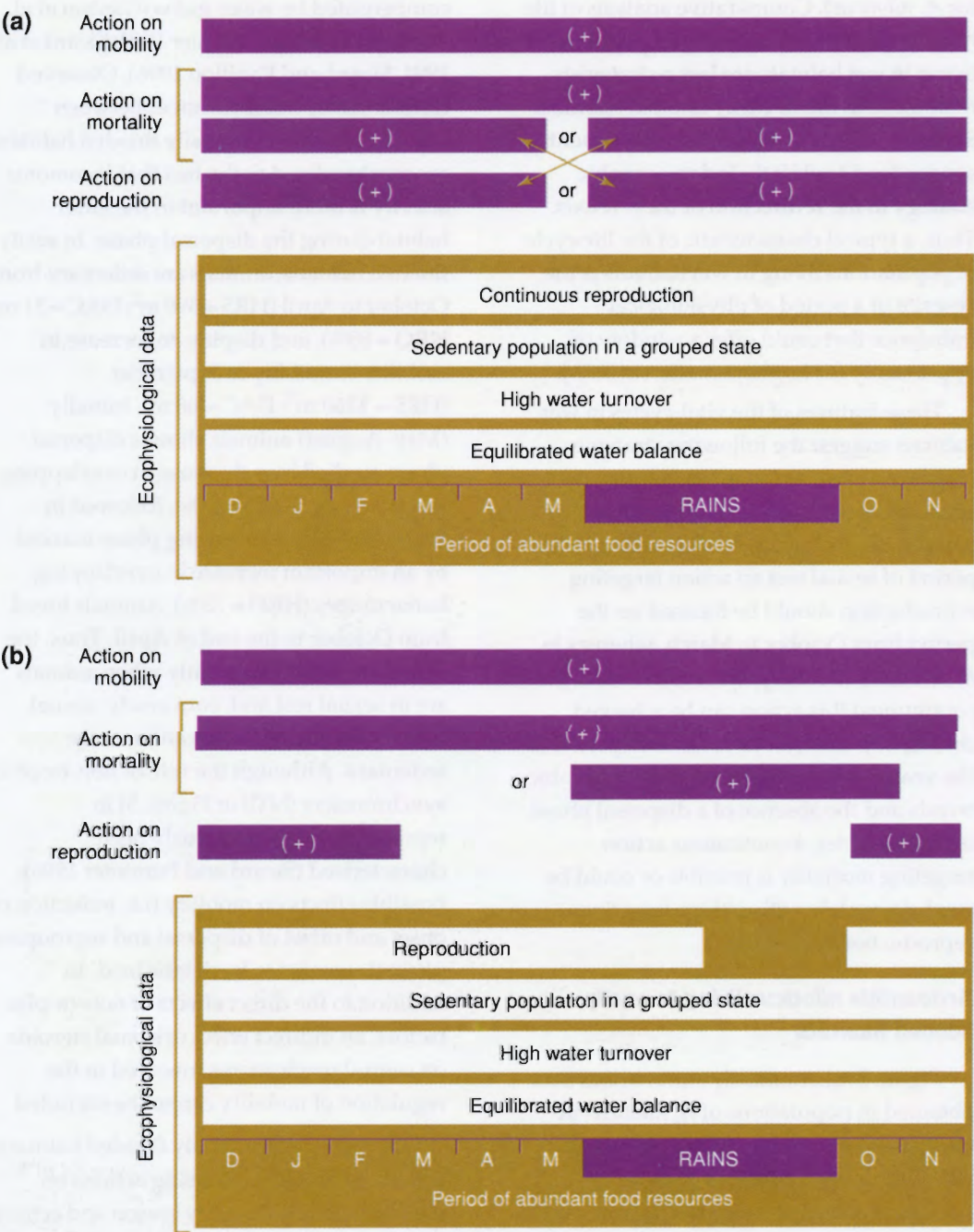


Figure 4. Vital-cycle and rodent pest management (RPM) strategies in wet habitats. Strategies for RPM (upper panels) may be deduced from an analysis of the vital-cycles (lower panels) of (a) *Mastomys huberti* and (b) *Arvicanthis niloticus* (redrawn from Sicard and Papillon 1996).

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 $\approx 530 \text{ m}^2$; DAC $\approx 26 \text{ m}$; HRO $\approx 84\%$).

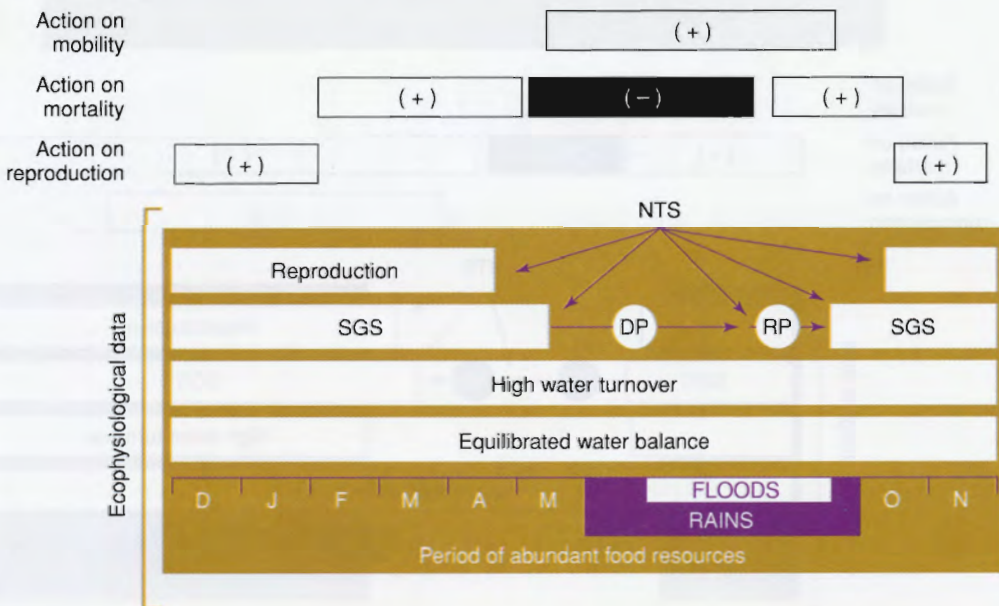


Figure 5.

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)

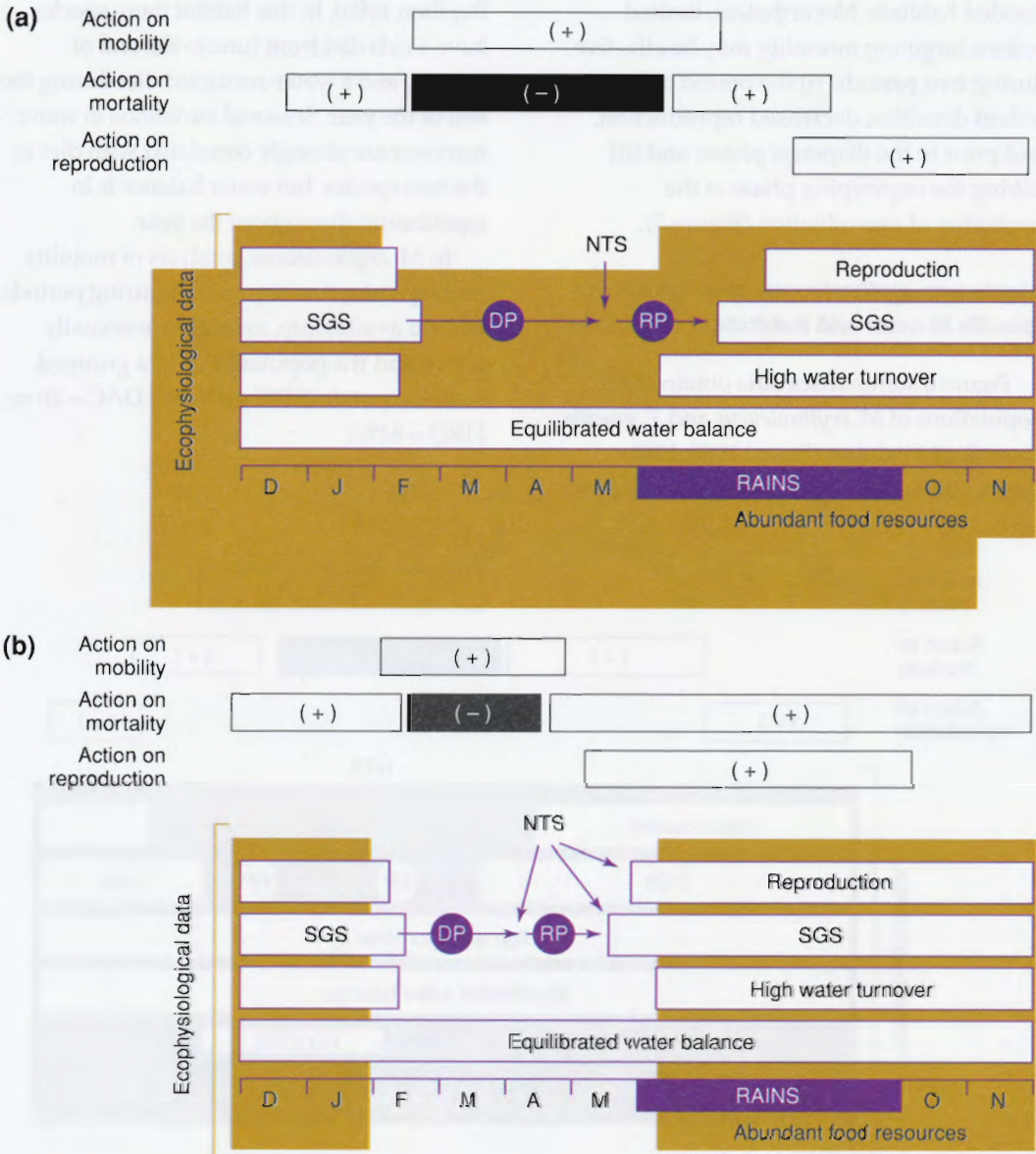


Figure 6.

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 gracilis* (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%).

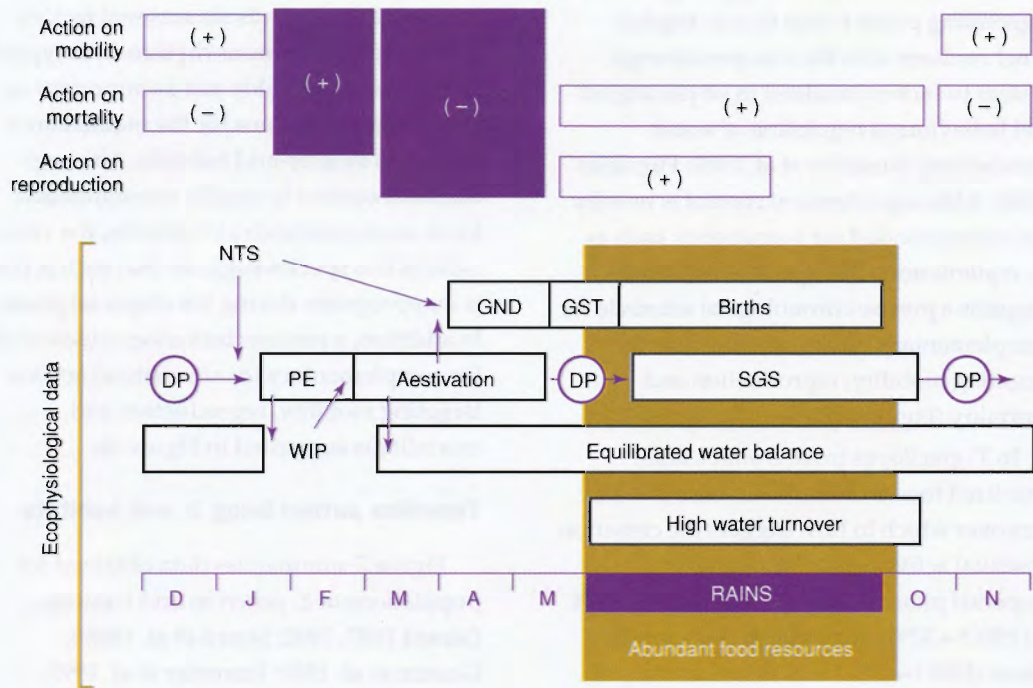


Figure 7. Vital-cycles and rodent pest management (RPM) strategies in arid habitats. Strategies for RPM (upper panel) may be deduced from analysis of the vital-cycles of *Taterillus petteri* (lower panel) (DP = dispersal phase; GND = pituitary gonadotrophic activity; GST = gestation; NTS = non-trophic 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 ($HRS \approx 0 \text{ m}^2$; $DAC \approx 0 \text{ m}$; $HRO \approx 0\%$). The end of aestivation is marked by a short regrouping phase on the grassy sandy hollows located between dunes ($HRS \approx 1,400 \text{ m}^2$; $DAC \approx 55 \text{ m}$; $HRO \approx 75\%$).

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 ($WT \approx 20\% \text{ TBW}$) 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 types 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 Brudieus 1986, 1987), air humidity (Müller 1977; Halder 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

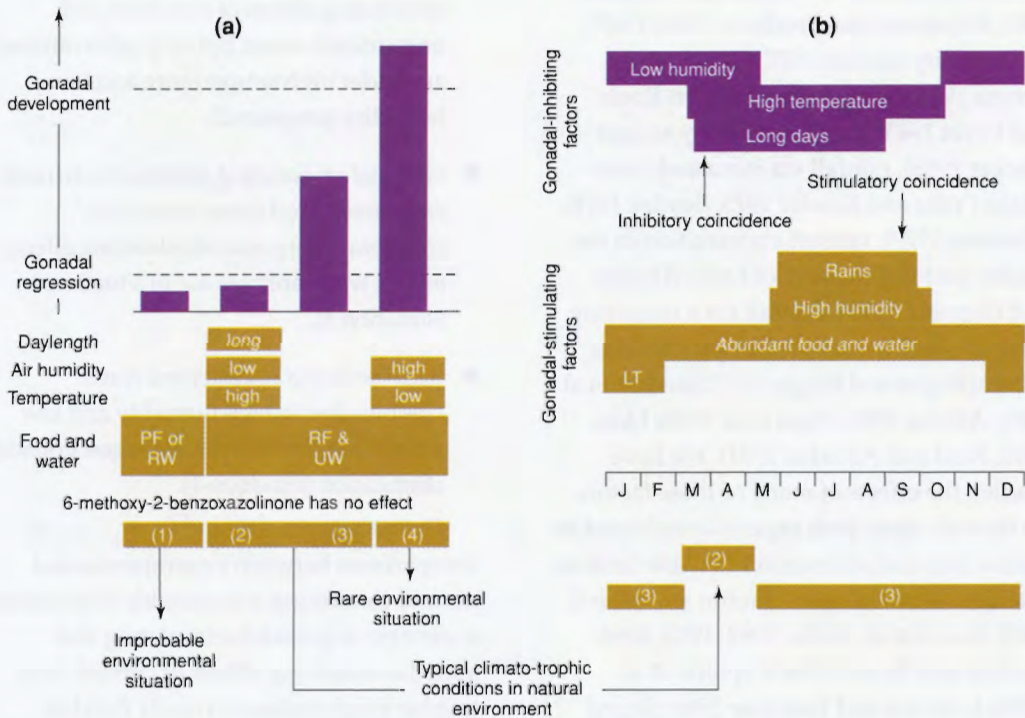


Figure 8. Regulation of reproduction in *Arvicanthis niloticus* living in easily flooded habitats. (a) Results of experimental studies on the combined effects of potential synchronisers on development and regression of gonads. Potential synchronisers include daylength (long or short), air humidity (low 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

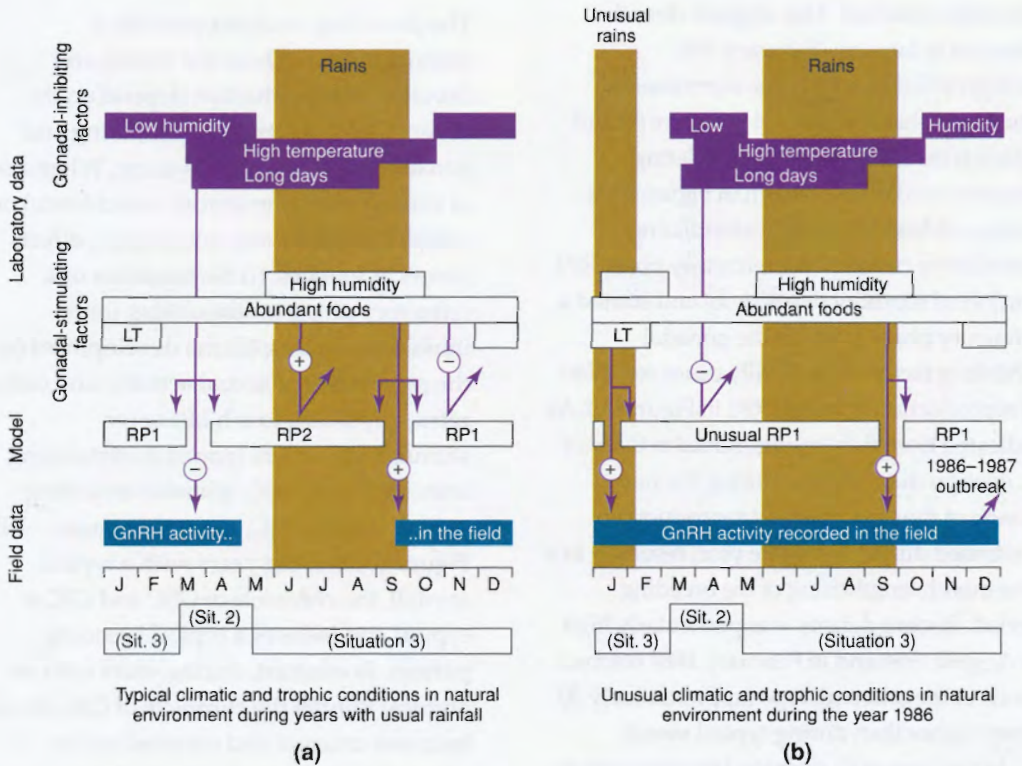


Figure 9.

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 climate 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) effects 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).

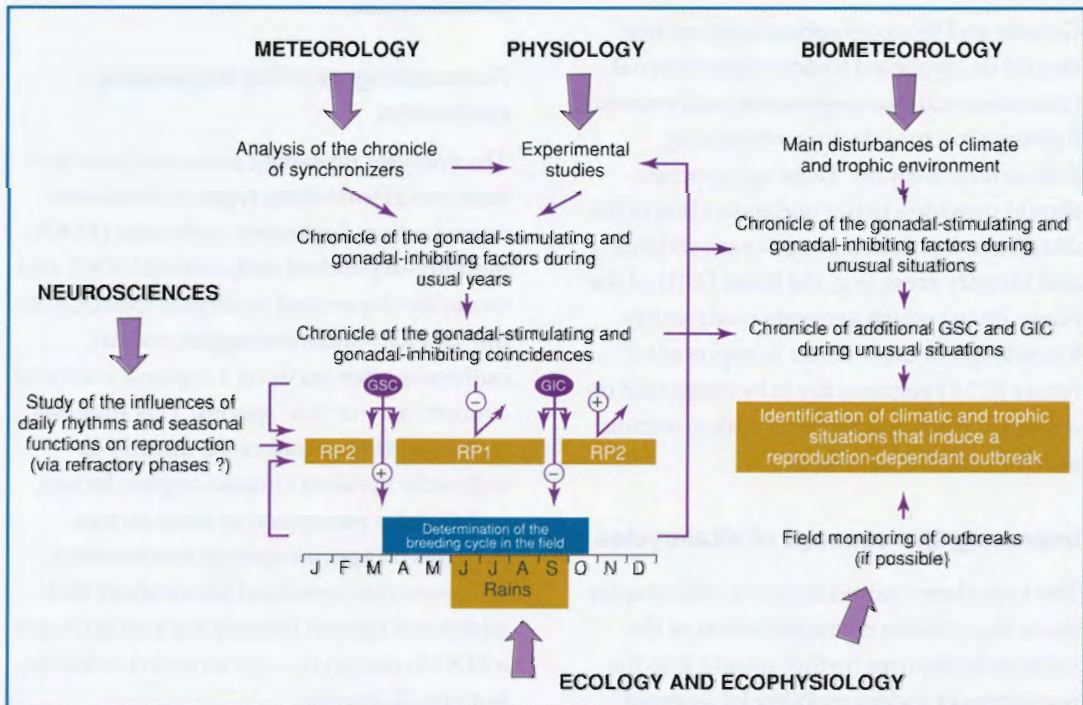


Figure 10. Modelling of reproduction-dependent outbreaks (GSC = gonadal-stimulating coincidence; GIC = gonadal-inhibiting coincidence; RP1 = refractory phase toward gonadal-inhibiting factors; RP2 = refractory phase toward gonadal-stimulating factors).

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 improving our understanding of the concept of vital-cycles.

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 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 inter-specific 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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REFERENCES

- Alibhai, S.K. 1986. Reproductive response of *Gerbillus harwoodii* to 6-MBOA in the Kora National Reserve, Kenya. *Journal of Tropical Ecology*, 2, 377–379.
- Attar, A., Merrouche, C., Kyelem, M., Sicard, B. and Cooper, H.M. 1995. Organization of the SCN and IGL in a nocturnal rodent (*Taterillus petteri*): a neuroanatomical viral tracing and neuropeptide study. *Biological Rhythms Research*, 26, 363.
- Beatley, J.C. 1976. Rainfall and fluctuating plant populations in relation to distributions and numbers of desert rodents in southern Nevada. *Oecologia*, 24, 21–42.
- Bronson, F.H. 1988. Genes, photoperiod and latitude. *Reproduction, Nutrition and Development*, 28, 335–347.
- Bronson, F.H. 1989. *Mammalian reproductive biology*. Chicago, University of Chicago Press, 325p.
- Buijs, R.M., Jouvet, M., Pévet, P., Valatx, J.L. and Wirz-Justice, A. 1992. Neurobiology of circadian and seasonal rhythms: animal and clinical studies. In: *Conférence Philippe Laudat 1991*, INSERM (Institut National pour la Santé et la Recherche Médicale), 176–229.
- Christian, D.P. 1979. Comparative demography of three Namib desert rodents: responses to provision of supplementary water. *Journal of Mammalogy*, 60, 679–690.
- Conway, G. 1981. Man versus pests. In: May, R.M., ed., *Theoretical ecology: principles and applications* (2nd edition). Oxford, Blackwell, 356–386.
- Cooper, H.M., Herbin, M. and Nevo, E. 1993. Ocular regression conceals adaptive progression of the visual system in a blind subterranean mammal. *Nature*, 361, 156–159.
- Cutrer, R.A., Ourour, A. and Pévet, P. 1994. Specific destruction of the serotonergic afferents to the suprachiasmatic nuclei prevents triazolam-induced phase advances of hamster activity rhythms. *Behavioural Brain Research*, 62, 21–28.
- Daya, S., Pangerl, B., Pangerl, A., Troiani, M.E. and Reiter, R.J. 1990. Effect of 6-methoxy-2-benzoxazolinone on the activities of rat pineal N-acetyltransferase and hydroxyindole-O-methyltransferase and on melatonin production. *Journal of Pineal Research*, 8, 57–66.
- Delany, M.J. and Happold, D.C.D. 1979. *Ecology of African mammals*. London, Longman, 434p.
- Delattre, P., Giraudoux, P., Baudry, J., Musard, P., Toussaint, M., Truchetet, D., Stahl, P. and Poulé, M.L. 1992. Land use patterns and types of common vole (*Microtus arvalis*) population kinetics. *Agriculture Ecosystems and Environment*, 39, 153–169.
- Delattre, P., Giraudoux, P., Baudry, J., Quéré, J.P. and Fichet, E. 1996. Relationship between landscape structure and common vole (*Microtus arvalis*) population kinetics. *Landscape Ecology*, 11, 279–288.

- Diarra, W. 1996. Savoir traditionnel sur les rongeurs et la lutte anti-rongeurs: application au contrôle des populations de rongeurs nuisibles. Mali, ORSTOM Laboratoire de Mammalogie, 56p.
- Ducroz, J.-F. 1998. Contribution aux approches cytogénétiques et moléculaires à l'étude systématique et évolutive des genres de rongeurs muridés de la "division" *Arvicanthis*. Thèse de Doctorat, Paris, Museum National d'Histoire Naturelle.
- Ducroz, J.-F., Granjon, L., Chevret, P., Duplantier, J.M., Lombard, M. and Volobouev, V. 1997. Characterization of two distinctive species of *Arvicanthis* (Rodentia: Muridae) in West Africa: cytogenetic, molecular and reproductive evidence. *Journal of Zoology*, 241, 709–723.
- Fiedler, L.A. 1988a. Rodent problems in Africa. In: Prakash, I., ed., *Rodent pest management*. Boca Raton, CRC Press Inc., 35–65.
- Fiedler, L.A. 1988b. Rodent pest problems in Eastern Africa. FAO (Food and Agriculture Organization of the United Nations) Plant Protection Bulletin, 36(3), 125–134.
- Fuminier, F. 1994. Influences des disponibilités en eau et de la température sur le contrôle photopériodique de la reproduction chez une espèce pullulante de rongeur sahélien (*Arvicanthis niloticus*). Thèse Doctorat, Montpellier, University of Montpellier-II, 143p.
- Fuminier, F., Sicard, B., Boissin-Agasse, L. and Boissin, J. 1993. Seasonal changes in the hypothalamic vasopressinergic system of a wild Sahelian rodent (*Taterillus petteri*). *Cell and Tissue Research*, 271, 309–316.
- Gautun, J.C. and Sicard, B. 1985. Record de fertilité de *Mastomys erythroleucus* au Burkina Faso (ex. Haute Volta). *Mammalia*, 49, 579.
- Gautun, J.C. and Sicard, B. 1986. Conditions climatiques et évolution des densités des populations de rongeurs sahéliens nuisibles aux cultures. In: Rijks, D. and Mathys, G., ed., *L'agrométéorologie et la protection des cultures dans les zones semi-arides*. Genève, OMM, 147–166.
- Gautun, J.C., Sicard, B. and Maïzy, J. 1989. Spatial distribution of a rodent population in Guinean savannah of Ivory Coast. *Mammalia*, 53, 480.
- Ghobrial, L.I. and Hodieb, A.S.K. 1982. Seasonal variations in the breeding of the Nile rat (*Arvicanthis niloticus*). *Mammalia*, 46, 319–333.
- Granjon, L., Duplantier, J.M., Catalan, J. and Britton-Davidian, J. 1997. Evolutionary systematics in the genus *Mastomys* (Thomas 1915) (Rodentia, Muridae). *Belgian Journal of Zoology*, 127, 7–18.
- Grouzis, M. 1988. Structure, productivité et dynamique des systèmes écologiques sahéliens (Mare d'Oursi, Burkina Faso). Paris, ORSTOM, 336p.
- Haldar, C. and Saxena, N. 1988. Pineal gland and humidity effects on testicular function of the Indian palm squirrel (*Funambulus pennanti*). *Journal of Pineal Research*, 5, 411–418.
- Happold, D.C.D. 1983. Rodents and lagomorphs. In: Bourlière F., ed., *Tropical savannas*. Amsterdam, Elsevier, 363–400.
- Hubert, B. 1982. Dynamique des populations de deux espèces de rongeurs du Sénégal, *Mastomys erythroleucus* et *Taterillus gracilis* (Rodentia, Muridae et Gerbillidae). I. Etude démographique. *Mammalia*, 46, 137–166.
- Hubert, B. and Adam, F. 1985. Outbreaks of *Mastomys erythroleucus* and *Taterillus gracilis* in the Sahelo-Sudanian zone in Senegal: an hypothesis. *Acta Zoologica Fennica*, 173, 113–117.
- Hubert, B., Adam, F. and Poulet, A.R. 1978. Modeling of the population cycles of two species in Senegal. *Bulletin of the Carnegie Museum of Natural History*, 6, 88–91.
- Hubert, B., Leprun, J.C. and Poulet, A.R. 1977. Importance écologique des facteurs édaphiques dans la répartition spatiale de quelques rongeurs au Sénégal. *Mammalia*, 41, 35–59.
- Khammar, F. and Brudieux, R. 1986. Variations saisonnières de l'activité testiculaire du rat des sables (*Psammomys obesus*). In: Assenmacher I. and Boissin J., ed., *Endocrine*

- regulation as adaptative mechanisms to the environment. Paris, CNRS (Centre National de la Recherche Scientifique), 49–55.
- Khammar, F. and Brudieux, R. 1987. Seasonal changes in testicular contents and plasma concentration of androgens in the desert gerbil (*Gerbillus gerbillus*). *Journal of Reproduction and Fertility*, 80, 589–494.
- Kyelem, M. and Sicard, B. 1994. Ecorégulation de l'activité ovarienne des rongeurs soudano-sahéliens; conséquences sur la modélisation des risques de pullulation. *Nuisibles Pest Pragas*, 2, 149–159.
- Kyelem, M. and Sicard, B. 1996. Population heterogeneity in regulation of reproduction in *Mastomys erythroleucus* (Rodentia, Muridae). *Mammalia*, 60, 796.
- Lavrachencko, L.A., Likhnova, O.P., Baskevitch, M.I. and Afework, B. 1988. Systematic and distribution of *Mastomys* (Muridae, Rodentia) from Ethiopia, with the description of a new species. *Zeitschrift für Säugetierkunde*, 63, 37–51.
- Leirs, H. 1995. Population ecology of *Mastomys natalensis* (Smith 1834): implication for rodent control in Africa (agricultural edition). Brussels, Belgian Administration for Development Cooperation, 35, 268p.
- Linn, I.J. 1991. Influence of 6-methoxybenzoxazolinone and green vegetation on reproduction of the multimammate rat *Mastomys coucha*. *South African Journal of Wildlife Research*, 21, 33–37.
- Maddalena, T., Sicard, B., Tranier, M. and Gautun, J.C. 1988. Note sur la présence de *Gerbillus henleyi* (De Winton, 1903) au Burkina Faso. *Mammalia*, 52, 282–284.
- Maurel, D., Laurent, A.M. and Boissin, J. 1981. Short-term variations of plasma testosterone concentrations in the european badger (*Meles meles*). *Journal of Reproduction and Fertility*, 61, 53–58.
- Meunier, M. and Solaris, A. 1979. Estimation des densités de populations à partir des captures-recaptures: application au campagnol des champs. *Mammalia*, 43, 11–24.
- Moller, M. and Pévet, P. 1994. Advances in pineal research. London, John Libbey, 320p.
- Moore, R.Y. 1973. Retinohypothalamic projections in mammals: a comparative study. *Brain Research*, 49, 403–409.
- Morin, L.P. 1994. The circadian visual system. *Brain Research Review*, 19, 102–127.
- Mrosovsky, N. 1996. Locomotor activity and non-photic influences on circadian clocks. *Biological Review*, 71, 343–372.
- Müller, J.M. 1977. Populationsökologie von *Arvicanthis abyssinicus* in der Grassteppe des Semien Mountains National Park (Äthiopien). *Zeitschrift für Säugetierkunde*, 42, 145–172.
- Mutze, G.J. 1991. Mouse plagues in South Australian cereal growing areas. III. Changes in mouse abundance during plague and non-plague years, and the role of refugia. *Wildlife Research*, 18, 593–604.
- Neal, B.R. 1981. Reproductive biology of the unstriped grass rat, *Arvicanthis*, in East Africa. *Zeitschrift für Säugetierkunde*, 46, 174–189.
- Neal, B.R. and Alibhai, S.K. 1991. Reproductive response of *Tatera leucogaster* (Rodentia) to supplemental food and 6-methoxybenzoxazolinone in Zimbabwe. *Journal of Zoology*, 223, 469–473.
- Negróni, J., Attar, A., Merrouche, C., Bennet, N., Nevo, E., Sicard, B. and Cooper, H.M. 1995. Pseudorabies virus differentially infects the visual system of normal and of blind subterranean mammals. *American Society of Neurosciences*, 21, 178.
- Negus, N.C. and Berger, P.J. 1977. Experimental triggering of reproduction in a natural population of *Microtus montanus*. *Science*, 196, 1230–1231.
- Ouarour, A., Kirsch, R. and Pévet, P. 1991. Effects of temperature, steroids and castration on daily torpor in the Djungurian hamster (*Phodopus sungorus*). *Journal of Comparative Physiology B*, 168, 477–482.
- Packer, C. 1983. Demographic changes in a colony of Nile grass rats (*Arvicanthis niloticus*) in Tanzania. *Journal of Mammalogy*, 64, 159–161.
- Papillon, Y., Kyelem, M. and Sicard, B. 1996a. Adaptation of reproductive function in *Arvicanthis niloticus* (Rodentia, Muridae). *Mammalia*, 60, 796.

- Papillon, Y., Kyelem, M., Fuminier, F. and Sicard, B. 1996b. Relationships between reproduction and other vital functions in *Gerbillus nigeriae* (Rodentia, Muridae). *Mammalia*, 60, 797.
- Papillon, Y. and Sicard, B. 1995a. Biogeography a tool to control rodent in soudano-sahelina region. *European Journal of Plant Pathology*, 101, 0545 (Abstract).
- Papillon, Y. and Sicard, B. 1995b. Comprendre la répartition spatiale des rongeurs nuisibles soudano-sahéliens. *Sahel Integrated Pest Management*, 2, 11–17.
- Perrin, M. 1989. Alternative life-history styles of small mammals. In: Bruton M.N., ed., *Alternative life-history styles of animals*. Dordrecht, Kluwer Academic Publishers, 209–242.
- Pévet, P. 1987. Environmental control of the annual reproductive cycle in mammals. In: Pévet P., ed., *Comparative physiology of environmental adaptations*. Strasbourg, Karger Basel, 82–100.
- Pévet, P. 1992. Physiological role of neuropeptides in the mammalian pineal gland. In: Foldes, A. and Reiter, R.J., ed., *Advances in pineal research*. London, John Libbey, 6, 17–36.
- Pianka, E.R. 1970. On r- and K-selection. *The American Naturalist*, 104, 592–597.
- Poulet, A.R. 1980. The 1975–1976 rodent outbreak in a northern Senegal irrigated farmland. *Biotrop Special Publication*, 12, 123–138.
- Poulet, A.R. 1982. Pullulation de rongeurs dans la Sahel. Mécanismes et déterminisme du cycle d'abondance de *Taterillus pygargus* et d'*Arvicanthis niloticus* (Rongeurs, Gerbillidé et Muridé) dans le Sahel du Sénégal de 1975 à 1977. Thèse d'état, Paris, ORSTOM, 276p.
- Sanders, E.H., Gardner, P.D., Berger, P.J. and Negus, N.C. 1981. 6-methoxybenzoxazolinone: a plant derivative that stimulates reproduction in *Microtus montanus*. *Science*, 214, 67–69.
- Sibly, R. and Callow, P. 1985. Classification of habitats by selection pressure: a synthesis of life-cycle and r/K theory. In: Sibly, R.M. and Smith, R.H., ed., *Behavioural ecology*. Oxford, Blackwell Scientific Publications, 5–90.
- Sicard, B. 1987. Mécanismes écologiques et physiologiques de régulation des variations régulières et irrégulières d'abondance des rongeurs sahéliens. Thèse d'état, Montpellier, Université de Montpellier-II, 303p.
- Sicard, B. 1992. Influences de l'aridité sur la biologie des rongeurs soudano-sahéliens. In: LeFloc'h, E., Grouzis, M. and Bille, J.C., ed., *L'aridité une contrainte au développement: caractérisation, réponses biologiques et stratégie des sociétés*. Paris, ORSTOM (Collection Didactiques), 309–333.
- Sicard, B. 1995a. Le problème rongeurs nuisibles soudano-sahéliens. *Sahel Integrated Pest Management*, 1, 17–22.
- Sicard, B. 1995b. Climate variations and outbreaks in rodent populations in the Soudano-Sahelian region. *European Journal of Plant Pathology*, 101, 0830 (Abstract).
- Sicard, B. 1999. Photopériodisme chez les rongeurs soudano-sahéliens. In: Buisson, B., ed., *Communications du 28ème congrès du Groupe d'Etude des Rythmes Biologique*. Saint Etienne, Université Jean Monnet (in press).
- Sicard, B. and Fuminier, F. 1994. Relations entre les variations saisonnières du métabolisme hydrique, l'estivation et la reproduction chez *Gerbillus nigeriae* et *Taterillus petteri* (Rodentia, Gerbillidae). *Comptes Rendus de l'Académie des Sciences*, 317, 231–238.
- Sicard, B. and Fuminier, F. 1996. Environmental cues and seasonal breeding patterns in Sahelian rodents. *Mammalia*, 60, 667–675.
- Sicard, B., Fuminier, F., Maurel, D. and Boissin, J. 1993. Temperature and water conditions mediate the effects of daylength on the breeding cycle of a Sahelian rodent, *Arvicanthis niloticus*. *Biology of Reproduction*, 49, 716–722.
- Sicard, B., Kyelem, M., Papillon, Y., Diarra, W. and Keita, M. 1995. Rongeurs nuisibles soudano-sahéliens. Paris, John Libbey, 46p.
- Sicard, B., Maurel, D., Fuminier, F. and Boissin, J. 1992. Circadian rhythm of photosensitivity and the adaptation of reproductive function

- to the environment in two populations of *Arvicanthis niloticus* from Mali and Burkina Faso. *Journal of Reproduction and Fertility*, 95, 159–167.
- Sicard, B., Maurel, D., Fuminier, F. and Boissin, J. 1994. Climate, trophic factors and breeding patterns of the Nile grassrat (*Arvicanthis niloticus solatus*); a 5-year study in the Sahelian region of Burkina Faso (formerly Upper Volta). *Canadian Journal of Zoology*, 72, 201–226.
- Sicard, B., Maurel, D., Gautun, J.C. and Boissin, J. 1988a. Activation ou inhibition testiculaire par la photopériode chez sept espèces de Rongeurs soudano-sahéliens: première démonstration d'une photogonado-sensibilité. *Compte Rendus de l'Académie des Sciences*, 307, 11–16.
- Sicard, B., Navaras, M., Jacquart, T., Lachiver, F. and Croset, H. 1985. Métabolisme hydrique de deux populations de *Mus musculus domesticus* (Rutty) et *Mus spretus* (Lataste) soumises à divers régimes hydriques. *Comptes Rendus de l'Académie des Sciences*, 300, 699–704.
- Sicard, B. and Papillon, Y. 1996. Water redistribution and the life cycle of Soudano-Sahelian rodents. *Mammalia*, 60, 607–617.
- Sicard, B. and Tranier, M. 1996. Caractères et répartition de three phénotypes d'*Acomys* au Burkina Faso. *Mammalia*, 60, 1–18.
- Sicard, B., Tranier, M. and Gautun, J.C. 1988b. Un rongeur nouveau du Burkina Faso (ex. Haute Volta): *Taterillus petteri* sp. nov. (Rodentia, Gerbillidae). *Mammalia*, 52, 187–198.
- Southwood, T.R.E. 1988. Tactics, strategies and templets. *Oikos*, 52, 3–18.
- Stearns, S.C. 1976. Life history tactics: a review of the ideas. *Quarterly Review of Mammalogy*, 51, 3–47.
- Stearns, S.C. 1989. Trade-offs in life history evolution. *Functional Ecology*, 3, 259–268.
- Stenseth, N.C. 1981. How to control pest species: application of models from the theory of island biogeography in formulation of pest control strategies. *Journal of Applied Ecology*, 18, 773–794.
- Sullivan, T.P. 1987. Understanding the resiliency of small mammals to population reduction: poison or population dynamics? In: Richards, C.G.J. and Ku, T.Y., ed., *Control of mammal pests*. London, Taylor and Francis, 69–82.
- Taylor, K.D. and Green, M.G. 1976. The influence of rainfall on diet and reproduction in four African rodents species. *Journal of Zoology*, 180, 367–389.
- Turek, F.W. 1972. Circadian involvement in termination of the refractory period in two sparrows. *Science*, 178, 1112–1113.
- Vivien-Roels, B. and Pévet, P. 1983. The pineal gland and the synchronization of reproductive cycles with variations of climatic conditions, with special references to temperature. In: Reiter, R.J., ed., *Pineal research review*. New York, R. Liss Inc., 91–143.
- Volobouev, V., Gautun, J.C., Sicard, B. and Tranier, M. 1996. The chromosome complement of *Acomys* spp. (Rodentia, Muridae) from Oursi (Burkina Faso): the ancestral karyotype of the *Cahirinus dimidiatus* group? *Chromosome Research*, 4, 526–530.
- Volobouev, V., Viegas-Pequignot, E., Petter, F., Gautun, J.C., Sicard, B. and Dutrillaux, B. 1988. Complex chromosomal polymorphism in *Gerbillus nigeriae* (Rodentia, Muridae). *Journal of Mammalogy*, 69, 131–134.
- Yahr, P. and Kessler, S. 1975. Suppression of reproduction in water-deprived Mongolian gerbils (*Meriones unguiculatus*). *Biology of Reproduction*, 12, 249–254.

21. The Rodent Problem in Madagascar: Agricultural Pest and Threat to Human Health

Jean-Marc Duplantier and Daniel Rakotondravony

Abstract

In Madagascar the rodent problem is linked to one species, the black rat (*Rattus rattus*). This chapter will describe its population dynamics in agro-ecosystems and its impact in agricultural crops, in stored grain, on human health and on the endemic rodent community. The black rat has spread absolutely everywhere: from sea level to more than 2,000 m—in houses, fields and also in the forests. It represents more than 95% of rodent catches in the fields and inside houses. Reproduction of rats living in fields stops during the cold season when their maximum annual abundance is observed. Irrigated rice crops suffer the greatest damage with losses estimated at 2.5% of the harvest. Rodent damage is also important for pluvial rice and to a lesser degree for cassava, sweet potatoes and tomatoes. Damage to cacao and sugar cane are important only in the small, poorly-maintained personal plantations. Plague is undeniably the most important disease linked with rodents in Madagascar. It is endemic to the centre of the island in rural areas located above 800 m and its prevalence is increasing. Rodent control in Madagascar is extremely complex because of the economic difficulties facing the country and because the black rat has displayed such successful colonisation in absolutely all habitats.

Keywords

Black rat, conservation biology, Madagascar, plague, rice fields, rodent control, rodent damage

INTRODUCTION

IN MADAGASCAR, the rodent problem is clearly linked to one species, the black rat (*Rattus rattus*), and concerns both agriculture and public health, as well as conservation biology. Eruptions of rat populations were reported in 1916, 1932 and 1965 (Rakotomanana 1965; Ravoavy 1966; in Zehrer 1999). After the last eruption, black rats were declared a public calamity by the Malagasy state, and agricultural pest management of rodents became state-controlled. With respect to public health, the major disease problem is undeniably the plague (caused by the bacillus *Yersinia pestis*). It spread from the seaports of Madagascar at the end of the last century and during the past 70 years permanent rural foci have existed in the central part of the island, above 800 m. Another major issue is that Madagascar's endemic rodents are threatened with extinction as a result of competition with the black rat in addition to habitat loss. This chapter will examine how this situation arose, and describe the impact of the black rat in agricultural fields, in stored grain, on human health and on the endemic rodent community in Madagascar.

Madagascar is the fourth largest island in the world (after Greenland, New Guinea and Borneo), with a surface area of 587,000 square km. It is 1,600 km long from north to south and 580 km at its widest point. It has been separated from the African continent for 160 million years. The minimum distance to Africa is now 300 km. The first human

settlements occurred approximately 2,000 years ago. Significant immigration occurred only 1,000 years ago. The human settlers are of both Asiatic (Indonesian) and African origin. A mountain range, 2,800 m high, divides the island into two from north to south (Figure 1). The east side of the country is more abrupt than the west. The effect of the monsoon and the trade winds on this relief determines the different climates and different types of vegetation within the island. Human activities have significantly changed the vegetation and now the different climatic regions can be characterised by their agricultural landscapes.

The east coast of Madagascar has no dry season and rainfall ranges from 2,000 to 3,000 mm per year. The original type of vegetation is rainforest. This type of forest is in rapid regression, due mostly to 'slash-and-burn' agriculture. The centre of the island, called the highlands, has a high altitude, tropical climate characterised by a cold and dry season from May to October and a hot, rainy season from November to April. Before human settlement, it was a mosaic of forests-savannah. Today, the landscape is totally modified by people, dominated by rice-growing in the valleys and by dry farming on the slopes (mainly corn and cassava). The primary forests are extremely rare, but there are plantations of pine and eucalyptus. The drier, west coast is less populated, and is a mixture of cultivation and pasture. The south is semi-arid with a 10 month dry season, dominated by spiny bush. It is a cattle-rearing region with some small patches of cultivated land.

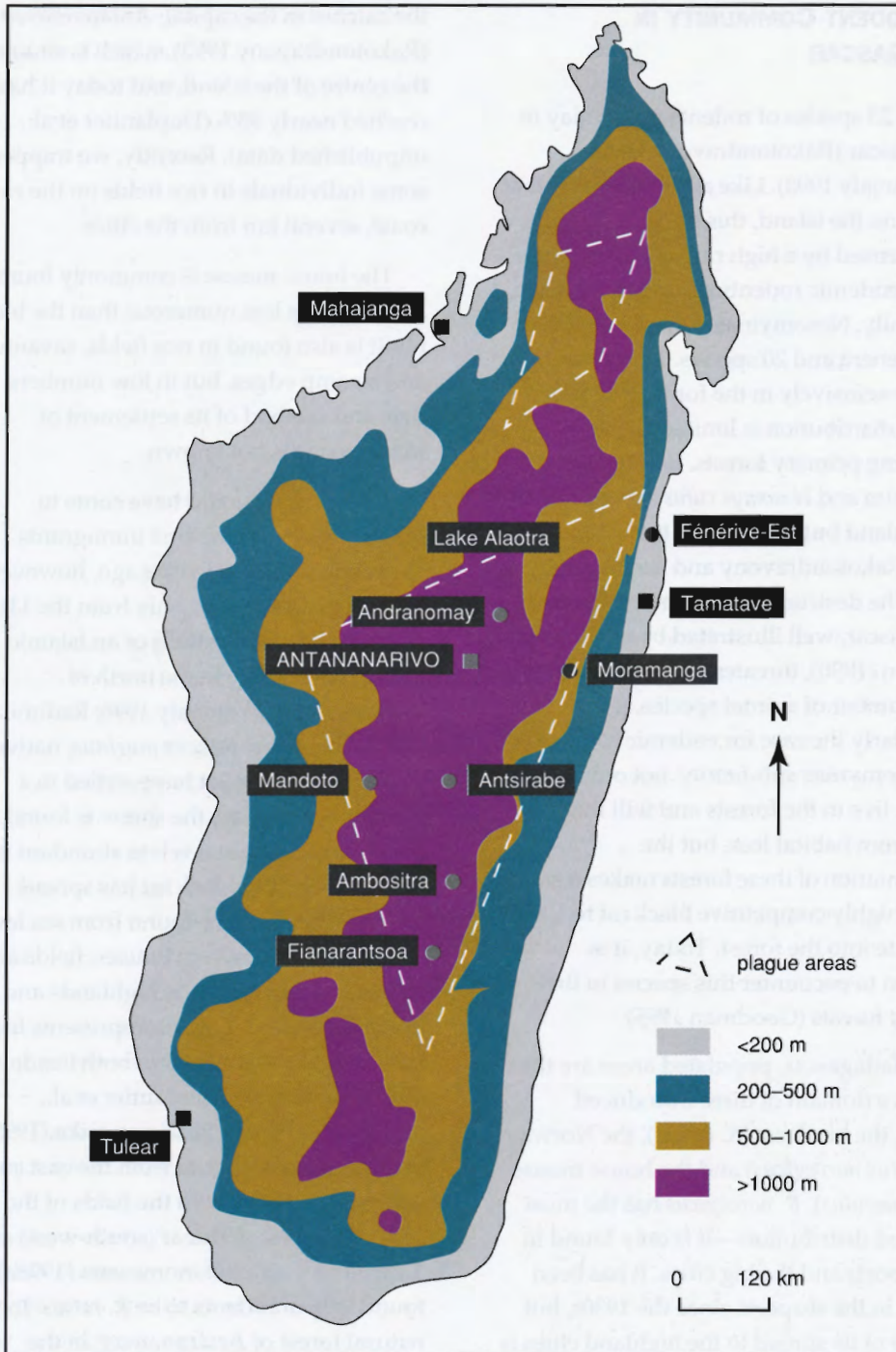


Figure 1.
Map of Madagascar: relief, localisation of plague foci, main towns and study sites.

THE RODENT COMMUNITY IN MADAGASCAR

At least 23 species of rodents exist today in Madagascar (Rakotondravony and Randrianjafy 1998). Like all animal and plant groups on the island, this order is characterised by a high rate of endemism. All the endemic rodents belong to the same sub-family, Nesomyinae, which is divided into 8 genera and 20 species. They live almost exclusively in the forest and their current distribution is limited to the remaining primary forests. *Brachyuromys ramirohitra* and *Nesomys rufus* are captured on farmland but only where this is close to a forest (Rakotondravony and Randrianjafy 1998). The destruction of primary forests in Madagascar, well illustrated by Green and Sussman (1990), threatens the extinction of a great number of animal species. It is particularly the case for endemic rodents of the Nesomyinae sub-family: not only do all of them live in the forests and will therefore suffer from habitat loss, but the fragmentation of these forests makes it easier for the highly competitive black rat to penetrate into the forest. Today, it is common to encounter this species in the primary forests (Goodman 1995).

In Madagascar, populated areas are the exclusive domain of three introduced species, the black rat (*R. rattus*), the Norway rat (*Rattus norvegicus*) and the house mouse (*Mus musculus*). *R. norvegicus* has the most restricted distribution—it is only found in the seaports and the big cities. It has been located in the seaports since the 1930s, but the date of its spread to the highland cities is unknown (Brygoo 1966). At the beginning of the 1980s, it represented more than 80% of

the catches in the capital, Antananarivo (Rakotondravony 1992), which is situated in the centre of the island, and today it has reached nearly 95% (Duplantier et al., unpublished data). Recently, we trapped some individuals in rice fields on the east coast, several km from the cities.

The house mouse is commonly found in houses but is less numerous than the black rat. It is also found in rice fields, savannas and swamp edges, but in low numbers. The date and method of its settlement of Madagascar is not known.

The black rat could have come to Madagascar with the first immigrants approximately 2,000 years ago, however its presence is confirmed only from the 11th century from excavations of an Islamic archaeological site in the north of Madagascar (Rakotozafy 1996; Radimilahy 1997). The shrew *Suncus murinus*, native to Southeast Asia, must have settled in a similar way. Today, the shrew is found all over the island, but it is less abundant than the black rat. The black rat has spread everywhere. It can be found from sea level to more than 2,000 m—in houses, fields and also in the forests. In the highlands and in the middle-west, *R. rattus* represents more than 98% of rodent catches both inside and outside buildings (Duplantier et al., unpublished data). Ratsimanosika (1995) quoted the same figure from the east coast coconut plantations. In the fields of the coastal regions of Tulear (south-west) and Tamatave (east), Rafanomezana (1998a) found 97% of rodents to be *R. rattus*. In the natural forest of Andranomay, in the highlands, *R. rattus* represented two thirds of captures from 1981 to 1982 and the

endemic genus *Eliurus* only one third (Rakotondravony 1992).

Important studies have been undertaken recently on the endemic rodents which are the most threatened order of mammals in Madagascar (Goodman 1995). However, due to their restricted distribution and scarcity, they are of minor importance to agriculture and probably also to human health.

POPULATION BIOLOGY OF THE BLACK RAT

It is a paradox that the black rat is the number one problem of agriculture and public health but little research has been conducted on this species. Different survey programs have been conducted by the Department of Plant Protection (Ministry of Agriculture), but most of the results are still unpublished except for some data on reproduction (Rafanomezana 1999). In fact, only three studies provide accurate data through at least one annual cycle: first, the study conducted at Andranomay (Figure 1) in the 1980s by D. Rakotondravony (1981, 1992) which was mostly carried out in the forest but also in slash-and-burn agriculture areas. This was followed up by a monthly survey in the fields of this locality which was conducted in 1996–97 (Rafanomezana 1999). Secondly, a monthly survey of less than a year was conducted in the Lake Alaotra region (Figure 1), which is one of the most important rice growing regions of the country (Salvioni 1989). Finally, Duplantier et al. (unpublished data) conducted a monthly two-year survey in the villages and fields of the middle-west region around the city of Mandoto (Figure 1).

Reproduction of the black rat

At the edge of the forests and within fields at Andranomay, Rakotondravony (1992) monitored reproduction in the black rat over two years (1981–1982) (Figure 2). Reproduction begins before the rainy season (November to April) with the maximum number of pregnant females occurring in the middle of this period. These data have been confirmed recently: in 1996–1997 there was an interruption to reproduction in the fields from May to August, with maximum reproduction in January (Rafanomezana 1999).

In Mandoto, reproduction of rats living in houses does not seem to be linked with season (Figure 3; Rahelinirina and Duplantier 1999). However, among the rats trapped outside, no reproduction occurs between July and December—thereafter breeding increases until May and ceases abruptly in June. In this region, reproduction seems to be linked with the harvest of crops rather than rainfall. The first rice harvest in the valleys takes place in December–January, then, from February till May–June, there follows one after another the harvest of corn, cassava, peanuts and pluvial rice on the hills. A second rice harvest can take place in the valleys in May, at the beginning of the dry and cold season (Handschumacher et al. 1999).

In Andranomay, as in Mandoto, these data are confirmed by the age structure of the rat populations: there are no young less than 50 g from May to September in Andranomay, whereas in Mandoto they are least abundant from September to March.

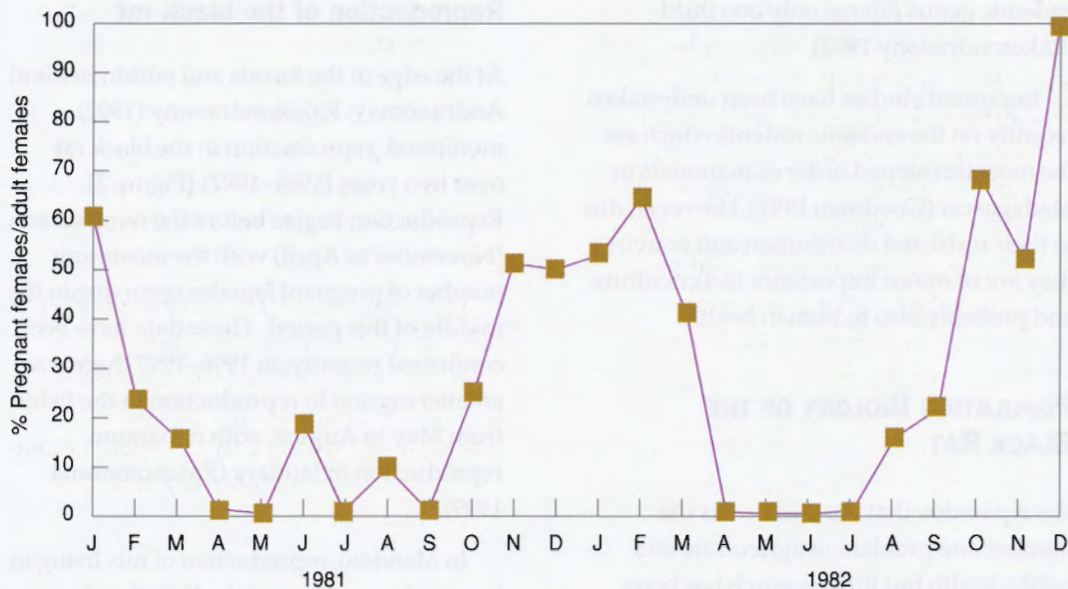


Figure 2.
Percentage of pregnant female black rats among adult females trapped monthly in Andranomay forest in 1981–1982 (Rakotondravony 1992).

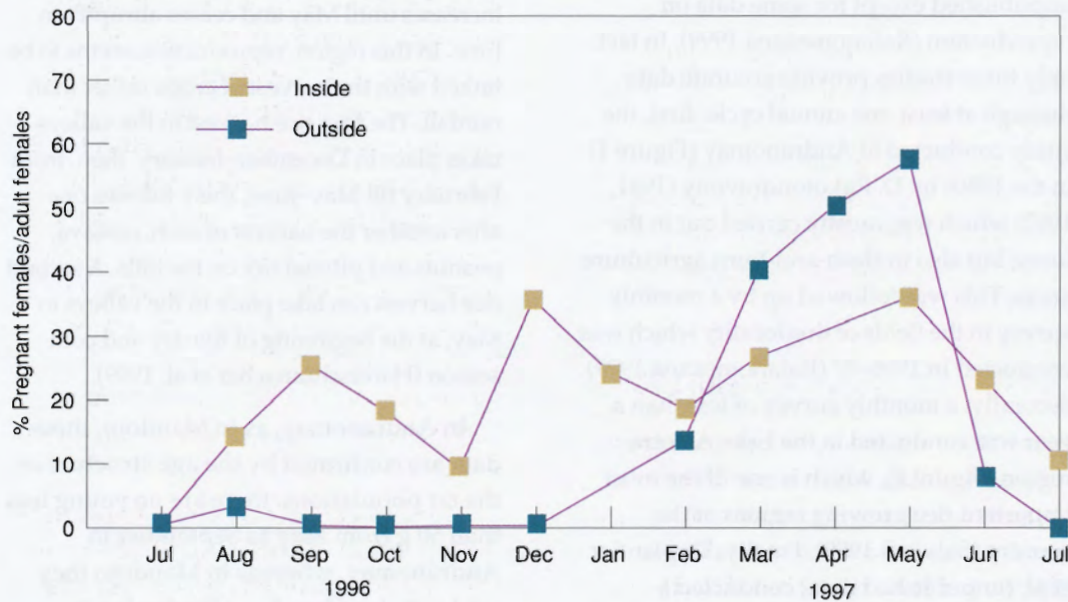


Figure 3.
Percentage of pregnant female black rats among adult females trapped monthly inside and outside houses in villages of the middle-west region around Mandoto (Rahelinirina and Duplantier 1999).

In the Lake Alaotra fields, reproduction is concentrated between March and June and seems to be linked with the availability of food in the fields (Salvioni 1989). However, in the presence of a permanent source of food and a shelter, the rats can breed throughout the year.

Differences between these localities are probably linked with the different landscapes and crop types. In the less modified landscape of Andranomay (small slash-and-burn agriculture areas surrounded by forests), rainfall seems to be the most important factor influencing the season of reproduction. By contrast, where irrigated fields are predominant (Mandoto and Lake Alaotra), the seasonality of harvests seems more important.

The aforementioned sites are in the highlands. In coastal regions, specifically Fénérive-Est on the East coast (Figure 1), the minimum number of pregnant females is observed from July to October and the maximum from December to March. In the Tulear region (Figure 1), on the south-west coast, the maximum rate of pregnancy occurs approximately over the same period (January to March) while the minimum occurs earlier, from May to August (Rafanomezana 1999).

Variations in abundance with habitat

In the Mandoto region, we compared four different habitats: houses; sisal fences around cattle pens; dry farming on the hills; and the irrigated fields in the valleys (Duplantier et al., unpublished data). The black rats were most abundant in the sisal fences. The permanent and spiny canopy of the fences provides a good, permanent

refuge and in addition, they are situated near—or even sometimes against—houses where supplies of food are available. Conversely, their abundance is lowest in the dry farming areas because these provide food for rodents only for a short period and the fields are often burned by fire once a year.

In Andranomay, trap success is higher in fields than in the forest (Figure 4; Rakotondravony 1992). Data collected around Lake Alaotra confirm that environments with abundant vegetation and near farms host a high density of rats (Salvioni 1989).

Seasonal variation in abundance

In the fields of Mandoto, we observed a well-marked, seasonal variation in the abundance of rodents with a maximum in July–August in the irrigated fields as well as in the dry farming areas on the hills (Figure 5; Duplantier et al., unpublished data). This was also noted by Salvioni around Lake Alaotra (Salvioni 1989). On the other hand, the fluctuations in population abundance observed in the villages, inside houses and in the sisal fences do not show any marked seasonal variation. In the Andranomay forest, populations peak earlier between February and April (Figure 4; Rakotondravony 1992). Rafanomezana (1999) observed a similar pattern in fields in the same locality.

Thus, the annual maximum abundance of rat populations occurs in the middle of the cold and dry season on the borders of the highlands (Mandoto and Lake Alaotra), and earlier, at the end of the rainy season, in the centre of the highlands (Andranomay).

Inter-annual variation

Only one long-term study has been undertaken: from 1980 to 1986, in Andranomay (Figure 6; Rakotondravony 1992). Inter-annual variation in the populations of black rats in the forest is low, but there is high variation in the fields, with the maximum abundance about eight times higher than the minimum. In these slash-and-burn fields, harvest differs greatly from one year to another, being especially reliant on the distribution and the total rainfall. However, it is important to note that at the same time, Rakotondravony (1992) observed similar inter-annual variations among urban populations of black rats. During the 1980s, their abundance in the capital (Antananarivo) was double that of normal densities in each of 1981, 1985 and 1989.

DAMAGE IN THE FIELDS

A survey conducted throughout the country showed that 86% of the farmers considered that they had suffered important damage from rats during the previous year. Rodent control was used by 82% of farmers, mostly in the rice fields (29%) and in the granaries (27%); 41% used rodenticides and 27% used traps (Rafanomezana 1998b).

According to Zehrer (1998), it is the irrigated rice that suffers the greatest damage. From surveys conducted in the different rice-producing regions of the country, rodent damage affects around 2.2% of cut stalks, which is equivalent to a loss of 2.5% of the harvest (Raobsoamanitrandrahana 1998). For all the country, the overall annual losses caused by rats are estimated at 62,500 t of rice paddy or 40,000 t of marketable rice.

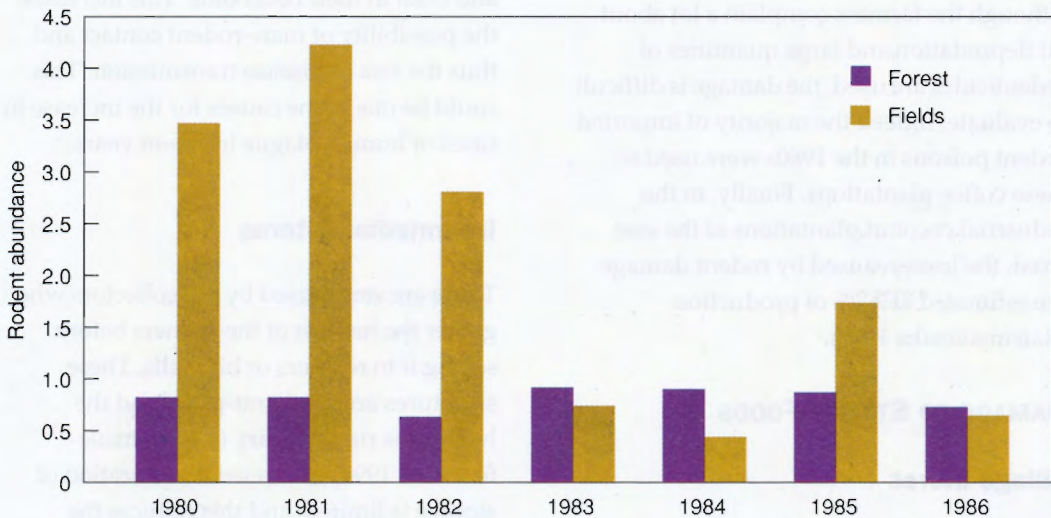


Figure 6. Annual variations of black rat abundance in Andranomay from 1980–1986 in forest and field habitats (Rakotondravony 1992).

Rodent damage is also important on pluvial rice cultivated on the hills or on slash-and-burn areas (Zehrer 1998). Other cereals (wheat, barley and oats) seem to be less affected. With respect to tubers, little damage is observed in potato crops, whereas rodents damage cassava and sweet potatoes. In market garden farms, the more important damage is to tomatoes and, to a lesser degree, to green beans, peas, cabbages and cucumbers.

Among the fruits, the most damage caused by rodents is to pineapples. Damage to jackfruit and papaya has also been observed, but only rarely to bananas. Damage to cacao is important in the small, poorly-maintained personal plantations, but low in industrial plantations—a similar situation applies to sugar cane plantations. According to Rasolozaka (1998), damage caused by rodents is estimated at 19% of the production in the coffee plantations of the east coast. According to Zehrer (1998), although the farmers complain a lot about rat depredation and large quantities of rodenticides are used, the damage is difficult to evaluate. Indeed the majority of imported rodent poisons in the 1980s were used in these coffee plantations. Finally, in the industrial coconut plantations of the east coast, the losses caused by rodent damage are estimated at 2.2% of production (Ratsimanosika 1998).

DAMAGE TO STORED FOODS

Village stores

In rural areas, according to surveys conducted in four of the six provinces of the country, the damage caused by rodents is considered by rural respondents as similar

to that caused by insects (37.5% versus 36.1%). It is only in the south (Tulear region) that the damage caused by rodents is low compared to insect damage (24% versus 58%) (Andriantsileferintsoa 1998). Most harvested crops are stored in heaps, except rice which is generally held in sacks. In the centre, the north and the west of the country, approximately 74% of the rural respondents assert that rodent attacks are continuous. In the south only 21% of farmers feel this to be the case.

With respect to health, the abandonment of traditional granaries by the farmers is a problem. Traditionally, different types of independent granaries, set apart from human houses existed according to the regions (huts built on stilts, cavities dug in the earth etc.) (Rasamoel 1998). Nowadays—for security reasons and for fear of robberies—a great number of farmers prefer to store their cereals in their houses and even in their bedrooms. This increases the possibility of man–rodent contact and thus the risk of disease transmission. This could be one of the causes for the increase in cases of human plague in recent years.

Intermediary stores

These are stores used by the collectors who gather the harvest of the farmers before selling it to retailers or big mills. These structures are rarely rat-proof and the hygiene is rudimentary (Andriantsileferintsoa 1998). However, the duration of storage is limited, and this reduces the importance of damage despite the lack of protection.

Industrial stores

In Madagascar, only the national silo (where seeds are stored) and the warehouses of big commercial companies are rat-proof. According to Andriantsileferintsoa (1998), these companies do not have any serious problems caused by rodents. Their warehouses are new and well-kept, and they regularly use the services of rodent/insect control companies that exist in the capital.

RODENTS AND HEALTH

Buck and Courdurier (1962), as well as Ribot and Coulanges (1982), established the first lists of the main zoonoses in Madagascar. A synthesis of rodent-borne zoonoses was completed recently (Duplantier 1999). The most well known disease linked with rodents is the plague, but rodents are also involved in the transmission of viruses, including hantaviruses. The importance of rodents in the transmission of other diseases in Madagascar is either poorly known (e.g. intestinal bilharziasis), or less important (e.g. rabies). Due to the isolation of the island and its particular community of rodents (a single endemic sub-family with a very restricted distribution), a number of diseases linked with rodents and important elsewhere in the world are unknown on the island (Brygoo 1972). However, the invasion of all the habitats by the black rat allows for rapid propagation of any rodent-borne epidemics throughout Madagascar.

Plague

Plague is undeniably the most important disease linked with rodents in Madagascar (Brygoo 1966). It reached the largest seaports of Madagascar between 1898 and 1907,

during the third pandemic. During the 1920s it reached the highlands, but disappeared from the coastal regions. Thus, the plague became endemic to the centre of the island in rural areas located above 800 m and is now on the increase (Chanteau et al. 1998b). From 1925 until the Second World War, more than one thousand human cases occurred annually. A maximum of more than 3,000 cases was reached in 1935. Mass vaccination campaigns, insect control and the arrival of antibiotics caused an important regression in morbidity and mortality; for more than thirty years, an average of only about fifty cases were reported annually. However, in 1978, the plague reappeared in the capital after a 28-year absence. Since the end of the 1980s, in the country as a whole, the number of human cases increased to more than 100 per year, reached 200 in 1994, and 459 in 1997. In 1991, the human plague reappeared in the seaport of Mahajanga after an absence of 63 years (Chanteau et al. 1998a,b). These official figures include only the cases confirmed by a bacteriological test. Serological tests indicate the number of cases to be two to three times higher (Chanteau et al. 1998a).

The real situation is difficult to estimate. On the one hand, important regions are out of reach of health services, and on the other, information campaigns of the national program of plague control set up since 1991 clearly increased the number of declarations. Despite a low number of official cases compared with other diseases, the economic cost of plague is very high for the Malagasy state government, which must cover all the medical expenses in the treatment of this disease. Due to the slowness of the bacteriological diagnostics (several days are

necessary), all cases suspected from clinical examination must be immediately treated. In addition, all persons in contact with those suspicious cases must also undergo an antibiotic treatment. The houses inhabited by people with suspected cases, as well as all the neighbouring houses, must be treated with insecticides by the health services. Therefore, several thousand people are treated every year.

The plague is transmitted from one rodent to another, and from rodents to humans through haematophagous flea vectors. In most of the plague foci in the world, the reservoirs are wild rodents resistant or less sensitive to the plague bacillus (*Yersinia pestis*). They generally belong to the Sciuridae family (marmots, prairie dogs) and to the Gerbillinae sub-family (gerbils, *Meriones* etc.). The black rat is sensitive to plague and thus cannot be, in principle, the reservoir. It is a commensal rodent which is the link between the wild rodents and humans and hence provokes urban epidemics. The distinctive feature of the Malagasy foci lies in the absence of a wild reservoir; the black rat is involved in all kinds of foci, urban as well as rural (Brygoo 1966). It must also be noted that different fleas are involved depending on the different habitats: *Xenopsylla cheopis* occurs inside houses and *Synopsyllus fonquerniei*, an endemic species, occurs outside. Thus, it seems that in Madagascar the black rat is at the same time the reservoir and the main victim of plague. This paradoxical and unique situation is the result of a balance between the mortality due to plague and the re-colonisation abilities of the black rat, which is spread all over the island, while the plague occurs only in very localised outbreaks.

A program set up in 1996 by the Ministry of Health (DLMT), the Institut Pasteur de Madagascar (IPM) and the Institut de Recherche pour le Développement (IRD, ex ORSTOM—the French Scientific Research Institute for Development through Cooperation) has made it possible to better understand the mechanism of the Malagasy foci. The beginning of the human plague season in the highlands (November) coincides with the minimum abundance of rats outside houses and the annual maximum abundance of fleas. We have shown that particular habitats seem to be important for transmission; i.e. the sisal fences around the cattle pens, situated inside or on the edge of villages. These are where the rodents and the fleas are most abundant, and it is also where the highest antibody seroprevalence against *Y. pestis* was noted among rats. The rural plague occurs only above 800 m, yet the black rat is widespread throughout the island from sea level to more than 2,000 m, and it is the same chromosomal form ($2n = 38$) regardless of the altitude. Inside houses *X. cheopis* is also present independent of the altitude. However, below 800 m, outside the houses, as well as on the rodent fur and in their burrows, we found almost no fleas, while an average of two fleas per rodent was observed during the same season above this altitude (IRD/IPM/DLMT, unpublished data). Thus, it seems that the distribution of the plague in Madagascar is limited by the factors that influence the geographical distribution of the endemic vector, *S. fonquerniei*, which parasitises exclusively rats living outside. It will be important for plague control to monitor the evolution of its distribution for a possible extension of plague foci below the present limit.

Other diseases linked to rodents in Madagascar

Murine typhus is relatively important in Madagascar because Mayoux and Coulanges (1970) found positive serologies in 20% of the rats tested in Antananarivo.

Borreliosis (or relapsing fever) is a disease transmitted by ticks living in the rodent burrows. It has been well known in the west of the country since the 18th century, but there have been no human cases described since the 1950s (Brygoo 1972).

Leishmaniasis is unknown in Madagascar, although infested dogs have been imported (Brygoo 1972) despite *R. rattus* being a known reservoir in Italy, and *R. rattus* and *R. norvegicus* being suspected reservoirs in many other countries (WHO 1990). According to Brygoo (1972), it was the absence of vectors that has prevented the occurrence of this disease in Madagascar. However in 1982, Ribot and Coulanges reported the discovery of a potential vector, an anthropological phlebotome. Nevertheless, no human cases have been reported.

The absence of leptospirosis in Madagascar is undoubtedly a paradox, as it is a disease which is characteristically associated with rice fields, sugar cane plantations and pig rearing (major farming activities in Madagascar), and *R. rattus* and *R. norvegicus*, as well as *S. murinus* (a very widespread shrew in Madagascar), are well known reservoirs (Faine 1987). In addition, this disease occurs in the neighbouring island of Reunion.

Intestinal bilharziasis is widespread in humans, especially in the highlands, but has not been reported in rodents (Breuil et al.

1982; Ribot and Coulanges 1982). Yet, recently a *Schistosoma mansoni* adult worm was found in one of ten black rats trapped in the Antananarivo suburbs (E. Sellin, pers. comm.). Larger surveys and more sensitive techniques of detection (work in progress: Ministry of Health/ Institut Pasteur/IRD-ORSTOM) will determine if the black rat is a wild reservoir, as is the case in the West Indies and South America (Rey 1993).

The only known reservoir of rabies in Madagascar is the domesticated dog. No rodent has been found to be a rabies carrier (Ribot and Coulanges 1982).

Until now, no human case of haemorrhagic fever with renal syndrome, due to hantaviruses, has been reported in Madagascar. Since 1985, however, antibodies of hantavirus have been reported in rodents (H. Zeller, pers. comm.). More extensive studies are under way (Institut Pasteur/IRD-ORSTOM) to determine the importance of these viruses in black rat populations trapped in different environments.

RODENT CONTROL IN MADAGASCAR

Organisation of rodent control

Big cities, and the administrative centres of the provinces (with more than 100,000 inhabitants) have a Health Municipal Office, dependent on the mayor. This department is responsible for keeping the town clean, monitoring epidemics and controlling insects and rodents. In the largest cities of the highlands, it is this department that is in charge of plague control. The Health Municipal Office is also in charge of control of plague (by trapping) among rodent

populations in the capital, Antananarivo, and since 1998, in the seaport of Mahajanga.

In small towns and villages, the Department of Communicable Diseases (Ministry of Health) intervenes as soon as human plague cases are reported and organises the control of fleas and rodents in collaboration with the basic health care units.

In rural areas, it is the Department of Plant Protection (Ministry of Agriculture) which leads the farmers in rodent control in the fields and in and around food stores.

Activities of the Department of Plant Protection

After the 1965 outbreak of the plague, rodents were declared a public calamity by the Malagasy state, which meant that the state covered all the expenditure incurred in rodent control. Then in 1976, a division inside the Department was created and dedicated to rodent control. Until the 1980s, this division provided free rodenticides to the farmers, who in turn provided the baits. Zinc phosphide was first used in the seventies and progressively replaced by anticoagulants, mainly chlorophacinone and coumatetralyl. Plant protection technicians determined the abundance of rodents by trapping in different regions and crop types and then, according to the trap success in each particular situation, decided whether to use rodenticides. However, this practice was abandoned due to the deterioration of the economic situation. Nowadays, the farmers are in charge of rodent control with only supervision provided by technicians of the Department of Plant Protection.

In collaboration with GTZ (Deutsche Gesellschaft für Technische Zusammenarbeit — the German Technical Cooperation), the Division of Rodent Control carries out three types of actions:

- ▶ a survey of the population dynamics in experimental stations situated in the different agricultural regions of the country;
- ▶ the promotion of snap-trap use by demonstration in experimental stations and through selling at a low price; and
- ▶ training and communication on health matters, cleanliness and promotion of rat-proofing methods.

Activities of the Division of Communicable Diseases

This division is responsible for the national program of plague control and hence rodent control. The agency supports the local health structures during epidemics and usually provides some training and information.

In collaboration with the municipal health office, a survey of the prevalence of plague in rat populations has been set up in the two most important urban foci: Antananarivo and Mahajanga. This division has distributed two thousand live-traps to the health centres located in the plague endemic zones. These traps are for use in epidemics, and thus promote this type of rodent control.

The aim of these training and information campaigns is to improve the hygiene within habitations. Information posters written in Malagasy on the plague—also highlighting rodent control methods in plague foci—are posted in all health centres within the plague

areas. A technical guide, which is regularly updated and includes rodent control methods, is given to all the doctors working in the plague endemic zones (Division de la peste 1990).

The particularities of rodent control in plague foci

The control of rodent populations in plague foci must follow certain rules. One must always remember that the main problem is not the rodent itself but the fleas. To avoid proliferation of the disease, it is imperative to kill the flea before killing the rodent. During the plague season, rat poisoning must not be done without prior insect control. Live-traps are better than snap-traps, because the latter encourages the dispersion of the fleas immediately after the rodent's death. For the same reason, in the case of chemical control, one must not use acute rodenticides but anticoagulants that work only after a few days, thus giving time for an insecticide to kill the fleas before the rodent dies. Until now, anticoagulants have been little used in Madagascar, so no resistance problems have been reported. However, resistance to insecticides is multifaceted and very widespread in fleas (Ratovonjato et al. 1998). The annual use of preventive insect controls in some cities is mainly responsible for this situation and has had to be abandoned. In rural areas, the problem is also encountered due to resistance to the insecticide DDT, which has been used extensively for malaria control. All these factors indicate the need for a regular survey of the efficiency of the different insecticides and for a rotation in the use of these products.

Improving rodent control

As described above, until recently, few studies of black rats had been performed. Rodent control in Madagascar took place when damage was significant but rarely took into account knowledge of the biology of the black rat. Since the beginning of the 1990s, with the creation of a national program of plague control by the Ministry of Health and the project "Promoting integrated protection of crops and stored foods" by GTZ and the Department of Plant Protection, new studies have begun with the aim of improving rodent control.

Since 1993, twelve monitoring stations have been established throughout the national territory by the Department of Plant Protection. For various reasons, only eight stations have operated correctly to provide reproductive data and two have monitored abundance. As soon as this program becomes fully efficient, it will provide useful data which will enable an adequate control schedule for each region to be established. Two long-term studies of the black rat are being undertaken on the east and north-west coasts and these will provide important additions to our knowledge of population dynamics, which today, is restricted to the central part of the island.

Concerning plague control in the highlands, the monthly survey carried out over the past two years already allows us to propose that rodent control should be focused on a particular area and season. We have demonstrated that sisal fences are the most important refuge area for rodents, fleas and plague. According to the maximum annual abundance of rats and fleas and taking into account the agricultural