19. Populations of African Rodents: Models and the Real World

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Abstract

The eruptive nature of African rodent populations has stimulated the development of several models, mainly to explain and forecast outbreaks. Regression models, built on the observed relation between rainfall events and rodent numbers, are quite reliable but do not provide biological explanations or allow simulations. Conceptual models combine various pieces of ecological information into an integrated representation of the species' population ecology, but they lack a numerical component; this makes it difficult to evaluate the relative importance of the different elements and the models cannot be used in practice. Writing these models mathematically allows for simulations, but realistic results are obtained only if environmental stochasticity can be included. Evaluation of a stochastic simulation model for *Mastomys natalensis* in Tanzania shows that this stochasticity is also the major drawback of this model type for use in forecasting. In conclusion, the regressive models are the best ones for prediction while stochastic population dynamics models are more appropriate for simulation. Both model types have their place in ecologically based rodent management.

Keywords

Africa, rodents, models, forecasting, simulation

INTRODUCTION

N AFRICA, RODENTS are serious pests in fields and in human dwellings, both in the countryside and in cities. They cause serious damage to crops before and after harvest, damage installations and are reservoirs or vectors of serious infectious diseases (Fiedler 1988a). Rodent damage in the field can occur during all crop stages, but often it is most serious at planting time and just before harvesting. African field rodent populations are characterised by irregular population explosions which often occur over large geographical areas (Fiedler 1988a; Leirs et al. 1996). Such outbreaks are not cyclic and therefore happen mostly unexpectedly. Damage during such outbreaks is enormous and may significantly worsen the already bad food security conditions in the affected countries. This is a direct disaster for the subsistence farmers involved, but also has national and sometimes even international political consequences. Panic-stricken authorities may quickly initiate control operations, often with very poor results and always too late. There is thus a very clear need to predict and, if possible, prevent such outbreaks (Taylor 1968; Shuyler 1977; Mwanjabe 1990; Mwanjabe and Sirima 1993).

Forecasting changes in irregularly fluctuating rodent populations relies on observed correlations with other environmental parameters and an understanding of which mechanisms are active in these populations. That information can be formalised in some way to a set of rules which is called a model (Stenseth 1977). The word model, however, covers a variety of such sets of rules which differ in the nature of input and output, the complexity of the rules that are incorporated and the language that is being used. The last can vary from vague conceptual schemes to detailed mathematical expressions.

In this chapter, I will present an overview of the different types of models that are used to predict or simulate changes in rodent populations. Although much of the following may apply to population models in general, there will be a strong focus on models that were developed for African rodent populations. I will use examples from our own work in Tanzania to illustrate the possible practical uses of different model types.

MODEL TYPES

As with all science, the current knowledge about rodent populations is based on a large collection of studies which describe or investigate different aspects of populations at various levels of detail. For African rodents, that source material is rather limited. Multimammate rats, species belonging to the genus Mastomys, are the most important rodent pests in Africa, and undoubtedly the best studied group of African rodents. Nevertheless, Leirs (1995) found only 115 references, including unpublished reports, with a direct relation to Mastomys population ecology. Even so, an overview is difficult because many of the original studies are particular and spread out over a wide geographical and ecological scale. There are only few examples where researchers have collected information on different aspects from the same African rodent population over several years

(Hubert and Adam 1985; Sicard et al. 1994; Leirs et al. 1996). In order to develop a more holistic view of the population biology of these animals, there is a need to formalise that combined knowledge in models.

Models are then simplified representations of reality - known to be different from reality, but claiming to be reasonably good at simulating some particular aspects of interest. The representation is formalised as a set of rules which can be simple or complex, depending on the model. The common line of thinking behind all models that I will discuss here is that, given a certain population state and information about the environment, they predict the state of the population at a later time. How useful such predictions are, how long beforehand they can be made and how accurate they are is different for different models. Based on the kind of data used to formulate the model, the language it uses for expressing its set of rules and the kind of information needed to feed into the model or expected to come out of it, one can differentiate between several types of models.

Regression models

Regression models are based on observed co-occurrences between certain environmental conditions and changes in the rodent populations. Properties of such models in a rodent management context have been discussed before (Stenseth 1977). They do not build on any biological concepts about the processes that affect rodent population dynamics, except a belief that unusual rodent numbers must be related to unusual environmental events. Often, there is a traditional local common knowledge of such relationships, but rarely is this knowledge explicit enough to be of practical use. The relation between outbreaks of African rodents and rainfall had been suggested for many years (see, for example, Harris 1937) but only in the 1980s was it pointed out that many rodent outbreaks were preceded by abundant rainfall at the end of a dry spell of several years. With that information, the 1986-87 outbreak in Sudan was successfully predicted (Fiedler 1988b). While the recognition of the relation between high rodent numbers and the end of a dry period basically is a regression model, it was not expressed mathematically. That was done by Leirs et al. (1996) who constructed a logistic regression curve to show the relation between rodent outbreaks in East Africa and rainfall during the early months of the rainy season (Figure 1). Such a mathematical approach is superior to a purely verbal description because it presents the observed relation in a less subjective way and allows an assessment of the associated errors by calculating a probability level.

Both the Fiedler and the Leirs models were based on records of outbreaks, often collated from the grey literature, and then relating them to a plausible environmental factor, rainfall. In both cases, there was some biological explanation to support the model. Fiedler (1988b) hypothetised that during dry years, vegetation growth would be limited and rodent populations would decrease, but so would also predators and competitors. Upon the return of the rains, an abundant vegetation regrowth would occur and rodent populations would react much faster to that than predators or large herbivores, allowing an uncontrolled explosion of rodent populations.



Figure 1.

Logistic regression curve of rodent outbreaks probability (y axis) in Tanzania between 1947 and 1977 on rainfall early in the wet season (in December–January) in Tabora, central Tanzania (x axis). Numbers on the figure represent years with or without outbreaks (redrawn from Leirs et al. 1996).

A similar hypothesis was used, and supported by data, to explain outbreaks of insect populations in Africa (Janssen 1993). The regression model used by Leirs et al. (1996) for Mastomys natalensis was biologically supported by data showing that unusually abundant rainfall during the first peak of the wet season initiated faster maturation and early reproduction, resulting in an additional generation (Leirs et al. 1993). A proximate mechanism for the effects of rainfall on reproduction, through the presence of germinating grasses, was documented (Linn 1991; Firquet et al. 1996). Nevertheless, it should be stressed that the models themselves do not rely on biological mechanisms. To some extent, this can be considered an advantage since it means that

time-consuming biological studies are not necessary to develop the model, and even if the biological hypothesis turns out to be wrong, the model would still retain its value. However, the lack of biological background in a model makes it impossible to judge its generality. As Leirs et al. (1996) pointed out, Fiedler's (1988b) model was developed for the semi-arid region of Sudan and it did not explain earlier outbreaks in south-eastern Africa. Yet, that does not change the fact that the model works for the Sudan region, neither does it prove that Fiedler's explanation for his model would be invalid. Conversely, the Leirs et al. (1996) regression model can only be used for regions with a bimodal rainy season and is therefore not useful in, for example, the Sudan region.

Even though regression models can be accurate (i.e. they predict correctly), they are not always very precise (i.e. they do not give a detailed prediction). Indeed, the model proposed by Leirs et al. (1996) provides a binary answer only: an outbreak is predicted, yes or no, but there is no information about the extent of the outbreak. In order to make models which could predict the magnitude of an outbreak on, for example, a scale from 1 to 5, one would need more detailed information about past outbreaks. Unfortunately, old reports rarely give reliable information about an outbreak's magnitude and if they do, the methodology used differs between outbreaks since they were monitored by different people, sometimes in different areas and with different technical means.

Conceptual models

Several authors have tried to organise their extensive knowledge of particular African rodent systems into a schematic model, combining the different underlying biological concepts that they observed in their studies. Based on the background work that was carried out before, these conceptual models focus on the autecology of the rodents only or use a community approach including competitors, predators and diseases as explicit factors. A common factor for all African rodent models is that climatic factors, mainly rainfall, always play a major role. This corresponds to some models developed for another eruptive species, the house mouse (Mus domesticus), in Australia (see Pech et al., Chapter 4). There is much less attention paid to intrinsic factors that are thought to be important in fluctuating

populations of holarctic rodents (Krebs 1996).

Many papers report on particular aspects of African rodent biology and several of them point towards the importance of specific factors in population dynamics. Here, however, I will briefly discuss only the few papers which explicitly combined several studies into a conceptual model. Taylor and Green (1972), in an unpublished report, stressed the importance of extended rainy seasons. They hypothesised that in normal years, cereals would be harvested at the end of the rainy season and weeds would die off because of drought; rodents would stop breeding because of food and cover limitation and their populations would remain low. When rainfall at the end of the breeding season is prolonged and heavy, harvest is delayed and weeds start regrowing. This increases food supply and reproduction continues much longer, resulting in outbreaks of populations. By contrast, in Tanzania, abnormally heavy rainfall early in the season is the key factor for populations of *M. natalensis*, according to Leirs et al. (1996). Unusual early rainfall induces faster maturation and the birth of an early generation which will reproduce during the normal breeding season; the presence of this extra generation increases the production of young so much that an outbreak follows. Leirs et al. (1996) presented their conceptual model in a flowchart diagram (Figure 2). A more complex model was developed for populations of Mastomys erythroleucus and Taterillus gracilis in Senegal (Hubert and Adam 1983).



Figure 2.

Flowchart diagram redrawn from Leirs et al. (1996) as a conceptual model to predict rodent outbreaks in Tanzania. The key factor is rainfall during the 'vuli' season, i.e. the first part of the rainy season, while rainfall during the 'masika' season, the second half of the rainy season, is less important.

Again, abundant rainfall is the central factor and the resulting improved food quantity and quality increase reproduction and survival. An outbreak occurs when predator densities are low, which in itself is a result of a longer period with low rodent densities. High rodent densities are subsequently reduced mainly by parasites and diseases, together with other factors (Figure 3). One of the most elaborate conceptual models, or rather set of models, was developed for *Arvicanthis niloticus* in West Africa (Sicard et al., Chapter 20, and references therein). Based on a very extensive knowledge of the animals' biology (with detailed information on physiology, behaviour and population fluctuations), they describe several models for different habitats and conditions. Their work is, however, an excellent example of how complex conceptual models can become.



Figure 3.

Schematic conceptual model of population dynamics of two Sahelian rodents in Senegal, redrawn from Hubert and Adam 1983.

Demographic models

Changes in population size are the net result of natality and mortality (and, in open populations, immigration and emigration). If one can express these processes as demographic rates, population size at time *t*+1 can be calculated from population size at time *t*. The problem is, of course, that these demographic processes are complex and affected by a multitude of factors. For example, rodents may die because of starvation, diseases or predation and the chances of this happening are themselves a function of other environmental factors, age of the individual and the rodent population density itself. It is exactly this complexity that one attempts to structure into conceptual models. Whereas most conceptual models stop at recognising that there is an effect of particular factors, demographic models assign values to demographic rates. These values are preferably estimates based on field data but if these are not available, theoretical approximations can be derived from the literature or they can be guessed by trial and error (e.g. French 1975; Poulet 1985).

French (1975) developed an agestructured model for *Mastomys* sp. where the timing of reproduction was synchronised with rainfall, and both natality and mortality were age-specific. This model was used for simulations to investigate the effects of different rainfall regimes, competition and predation. Unfortunately, the model was published in a medical journal and remained largely overlooked by biologists. It is worth noting that the model was developed in an attempt to understand the biology of *Mastomys* species in villages in West Africa, but the demographic parameter values were obtained from a published study on a population in a national park in Uganda. Later it was recognised that these animals belonged to a different *Mastomys* species and the model was updated with data from Sierra Leone (French 1985).

Hubert et al. (1978) estimated death rates and counted litter sizes in M. erythroleucus and T. gracilis during and after the 1975-76 outbreak in Senegal. They constructed a model with these demographic values and included some age-structure data (animals start breeding at an age of three months). Number and age structure of animals in 1976 was chosen as a starting population and the model was then run with the estimated demographic parameters for 15 months afterwards. The model performed well for that period, but since it used observed demographic rates rather than model them as response rates, it could not be used for actual predictions.

Poulet (1985) used data from an eightyear study on Taterillus pygargus in northern Senegal. He developed a demographic model, on the basis of the reproductive and mortality parameters obtained during that study period. He claimed that predation was a major driving force in mortality, but it is unclear whether and how that information was integrated in the model. He reported a linear relation between rainfall and litter size and used that to calculate natality for years when no field data were available. Using the model, he calculated the offspring produced in different cohorts and compared that with the observed numbers in order to assess cohort-specific mortality. He also simulated a number of different values for mortality

rates in order to see how that could affect a population.

Surprisingly, none of these demographic models was used to attempt simulations beyond the period for which they were formulated. The simulations that were carried out, however, contributed to a better understanding of the relative importance of different processes in the population dynamics of those species.

Leirs et al. (1997) developed a demographic model that differed in several respects to those considered above. Statistical modelling of their 1986–89 capture-mark-recapture data from a population of M. natalensis in Morogoro, Tanzania, showed that monthly survival of subadults and adults was affected not only by rainfall in preceeding months but also by density. The nature of these relations was not the same for subadults and adults. Moreover, maturation, the growth process from subadults to adults, was also dependent on rainfall and density. Therefore, they estimated these parameters, as well as natality, for different combinations of rainfall and density (see Box 1) and used this information as a set of rules to quantify a simple population dynamics model with three functional age groups (juveniles, subadults and adults). Rainfall and density were the only factors affecting parameter values and they did so in a simple non-linear way: below some rainfall or density threshold, the parameter would have one value, above that threshold, it would have another value. Thus, the model did not rely on empirical estimates for each time step, but used rainfall and density as state variables to determine the parameter values. This modelling of the demographic

rates makes this model much more general than the above ones by Hubert et al. (1978) and Poulet (1985). The major advantage is that one can use rainfall to incorporate environmental stochasticity in the Morogoro *Mastomys* model. This is particularly important since it is obvious that rodents live in a stochastic, not a deterministic, environment. Leirs et al. (1997) primarily investigated the properties of the dynamics created by their model but they also compared the predictions of their model with actual observed values in an independent data set.

THE MOROGORO MASTOMYS DEMOGRAPHIC MODEL

We continue with the Morogoro *Mastomys* demographic model (Leirs et al. 1997) to discuss the problems that are associated with the development of such a model and its use in practice. As mentioned above, the foundation must be a plausible concept of how demography is affected by other factors. This requires a sufficient knowledge of the life history of the rodent species.

The basic question is to decide which environmental factors are likely to have major impacts on demographic processes and how to include them in a model. Many different factors may play a role in this respect, but in order to make a model workable the key factors should be identified. In the case of *M. natalensis*, it was clear that rainfall in preceding months was the most important factor in the timing of the reproductive season (e.g. Leirs et al. 1989; Telford 1989 in Morogoro, and many others elsewhere as reviewed in Leirs 1995).

Box 1

For the calculation of the survival and maturation rates, we used data from a capture–mark–recapture study on a 1 ha grid in fallow land in Morogoro, Tanzania. The data were collected in monthly capture sessions of three days each between March 1987 and February 1989 and were analysed in MS-SURVIV (Hines 1994) as follows. We designed several models in which survival, maturation and capture rates could vary freely between months, were fixed during the whole period or were fixed during periods of months with similar rainfall and/or rodent density characteristics. These models were tested statistically to verify how well they represented the real data. We used the Akaike Information Criterion to select the model that gave the best representation of reality and at the same time used only a limited number of parameters. This was the model in which capture probability varied between months, while maturation and survival rates were the same for months which had similar properties with regard to density as well as precipitation (more information can be found in Leirs et al. 1997).

Based on this selected model, we estimated parameter values for survival of subadult and adult females and maturation probabilities for subadult females in six different categories of months, defined by a combination of rainfall and density properties (see table below). From removal trappings in the same area, we calculated the net reproductive rate per female for each of these categories by multiplying the mean litter size with the mean proportion of pregnant individuals among adult females in such months. These values are listed below and were used as parameter values in the population dynamics model that is described in the text of this chapter. We assumed for simplicity that male and female survival rates were equal (even though this is biologically unlikely).

	Rainfall (mm) in the previous 3 months					
	< 200	< 200	200-300	200-300	> 300	> 300
	Density (N/ha)					
	> 150	< 150	> 150	< 150	> 150	< 150
Subadult survival	0.629 ± 0.02	0.513 ± 0.053	0.682 ± 0.051	0.617±0.188	0.678 ± 0.059	0.595 ± 0.146
Subadult maturation	0.000 ± 0.015	0.062 ± 0.037	0.683 ± 0.112	0.524 ± 0.188	0.155 ± 0.111	1 ± 0.0
Adult survival	0.583 ± 0.066	0.650 ± 0.078	0.513 ± 0.074	0.602 ± 0.092	0.505 ± 0.074	0.858 ± 0.099
Net reproductive rate	1.29	5.32	0.30	6.64	4.69	5.82

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We also knew that growth and maturation of subadult animals was stimulated by rainfall, probably through an effect of growing grass (Leirs et al. 1990, 1994; Firquet et al. 1996). Therefore, it was clear that the model should include rainfall as one of the factors which would have an effect on demographic rates. As a second factor, based on general ecological theory rather than data, we selected density as an integrator of many extrinsic and intrinsic factors such as disease, predation, or social suppression of maturation and reproduction. The choice for these two factors was confirmed to be appropriate by comparing different statistical models where one or both of the factors were included (Leirs et al. 1997).

A second important question is how the population is structured. It is indeed highly likely that different parts of the population are affected in a different way by factors like predation or disease (e.g. Dickman et al. 1991). We also knew that reproductive maturation was linked to size rather than age and that individual growth was affected by rainfall (Leirs et al. 1990). For our Mastomys population, we used a very simple structure with three age groups, each with their own survival probabilities: juveniles (young animals from birth until they enter the trappable population); subadults (older animals that have not yet reached sexual maturity) and adults (animals that had reached sexual maturity).

It should be stressed that construction of a demographic model is only possible when there is enough biological information about the species. For African rodent populations other than *M. natalensis* in Morogoro, the necessary intensive and long-term studies, both descriptive and experimental, are available only for Mastomys, Taterillus and Arvicanthis species in West Africa, not surprisingly the same species for which conceptual models were developed (see above). To a lesser extent, it may be possible to construct population models for Mastomys spp. in southern Africa, where information from different authors can be collated (e.g. Sheppe 1972; Sheppe and Haas 1981; Chidumayo 1984; Bronner et al. 1988). In other places, or for other species, sporadic information may be available, but needs to complemented by generalisations from other studies before a demographic model can be designed.

Once the demographic model is designed, it needs to be parameterised, meaning that one has to make explicit the rules of how the demographic rates change with varying environmental conditions. Indeed, it is not enough to know that, for example, rainfall has an effect on sexual maturation, but one must also know how high the maturation rate is under given rainfall conditions. Although an experimental approach may provide information about the nature of these relations, the actual estimates can only come from extensive long-term descriptive studies (see also Krebs, Chapter 2).

We have not yet touched on any aspects of use of space or community ecology which may affect population ecology. Community factors, like predation, competition or disease can often be hidden in overall density-dependent variations in demography (e.g. Hansson and Henttonen 1988). Use of space is clearly very important in population dynamics (Lidicker 1975) but in the *Mastomys* Morogoro model, it has so far been neglected by assuming that immigration and emigration are insignificant or, more likely, match each other in the modelled population.

Testing the demographic model

The accuracy and reliability of a model in practice is dependent on several possible sources of error. The model design itself, and the underlying biological concepts, are fundamental and if these are faulty, good results cannot be expected of a model. The only solution is to continuously try to improve our scientific understanding but that problem is common to all biology. Looking at sources of error which are more typical of simulation/prediction models, two major problems can be identified: the quality of the model input data (the starting situation) and the quality of the parameter estimates.

In order to evaluate the model design, we used the 1986–1989 data from Morogoro, Tanzania-the same data that were used to develop the model (Leirs et al. 1997), but also the data collected between 1994 and 1998 on the same site, and thus independent of the data used for model development. This second data set comprised 14,862 captures of 4,636 individual M. natalensis during 52,400 trapping nights on a 3 ha grid in a robust capture-mark-recapture set-up with monthly sessions of three consecutive trapping nights. The study site consisted of a mixture of fallow land and small maize fields, providing typical Mastomys habitat. Population size estimates were obtained in program CAPTURE, using the jackknife estimator M(h) which allows for individual heterogeneity in capture probability (Otis 1978). For the model runs, we determined

the starting population composition (number of adults and subadults) in December of the study period and used the actual rainfall that was observed during the period of the model run. Each model was run for a 12 months simulation. Predicted population sizes were compared with actual estimates.

The runs show predicted and observed patterns which are largely parallel, although the values are sometimes quite different (Figure 4). A notable exception is the most recent year, 1998, where population size after December 1997 did not show the predicted increase. The realistic results that were obtained provide good support for the underlying concept on which the model is built, but it also raises questions as to what happened in 1997–1998. It should be mentioned that apart from the starting point in November 1986, no outbreak peaks were observed in the periods used to make Figure 4.

We investigated the model's sensitivity to changes in initial values by assuming a December starting population with 0 juveniles, 0 adults and a number of subadults varying between 20 and 300 animals of each sex. The model was run 10 times, each time with another starting number of subadults. The monthly rainfall values were chosen randomly among values observed in that month between 1970-1997 but were identical for each run. Figure 5 shows the expected large variation in the first months but a convergence of the different curves after the first year. Interestingly, however, the curves do not simply run parallel as one intuitively would expect.



Figure 4.

Model-predicted (circles) and actual estimated population (squares) sizes for a 1 ha area. Twelve-month simulations from November or December with starting values equal to actual estimated values for these months. Simulations were run with actual rainfall data (see text for further details).

It is noteworthy that smaller starting populations may, after some months, result in higher population numbers than those with a larger starting population.

The numerical values for the demographic parameters in the models (such like survival rates) are estimated from empirical data. This means that they are prone to statistical errors and rather than really knowing the exact value of the parameter, we obtain a probability distribution (normal distribution) of the parameter value, with a confidence interval around a point estimate. In order to verify how sensitive the model is to the uncertainty associated with the parameter estimates, we ran the model 100 times with identical starting conditions and monthly rainfall values, but the demographic parameter values were, at each step, chosen from a normal distribution around the point estimate.



Figure 5.

Twenty-four month model runs with 10 different starting values between 20 and 300 subadults of each sex. All parameter and rainfall values equal between runs (see text for full explanation). The resulting curves (Figure 6) show relatively minor variation during the first months but this variation accumulates and becomes very large after longer periods. Thus, while quality of input data seems to primarily affect the first months of a prediction run, the quality of estimates is more important for longer term predictions.

Predictions under environmental stochasticity

An inevitable problem for practical predictions is that the rainfall values for future months are unknown at the time of prediction (unlike the above 'a posteriori predictions'). A possible approach is to try out the several possible values that rainfall can have in the coming months and compare the model results under these circumstances. I tried this out as follows.



Figure 6.

Twenty-four month model runs (n = 100) with demographic parameter values sampled normally from around point estimate and its standard error. Sampling varies between each run, but all rainfall and starting values are equal between runs.

Starting values were chosen again from the observed populations in December in our study. Rainfall for the twelve months of each run were 'bootstrapped' from rainfall data obtained for that particular month in the period 1970-1997; that is, for each month of the run, and independently from the values for the other months, we chose a value at random from the 27 values that we had for that month. The model was run 100 times, each time with a different random seed, resulting in 100 different rainfall series of 12 months. We then compared the distribution of model outcome values for each month with the estimated population size for that month.

In most months, but not always, the observed values fall within the 95% range of predicted values (Figure 7). Unfortunately, these intervals are often so large that they do not have any practical value at all. Moreover, in order to predict real outbreaks, which are known to be related to unusual rainfall events, it may be necessary to actually look at the model results which fall beyond the 95% range. Comparing these wide confidence intervals with the relatively much better results that were obtained when the actual rainfall data were used (Figure 4), shows how important the problem of the stochasticity is for practical use of this demographic model. In order to obtain more practical results, it will be necessary to use a set of rainfall data which resembles the coming rainfall events more closely. This requires the prediction of these values themselves through separate climatological models.

AFRICAN RODENT MODELS AND ECOLOGICALLY-BASED RODENT MANAGEMENT

Stenseth (1977) expressed a clear preference for regression models as predictive tools. Although our knowledge of rodent biology has increased since then and modern computing facilities allow an easier use of numerical models, his opinion may still hold. Regression models have several important advantages. The ones that were developed for African rodent outbreaks are fairly simple with a single factor only, rainfall, and a binary response, outbreak or not (Fiedler 1988b; Leirs et al. 1996). The binary response can be associated with a certain probability, but the model does not indicate how serious the outbreak is expected to be. This makes such models intuitive to understand and easy to use. However, simplicity is not a typical characteristic of regression models (e.g. see Pech et al., Chapter 4) and although multivariate regression models may have a considerably better fit to reality, they are more difficult to understand intuitively. The major advantage of regressive models is that they attempt to give a fair representation of observed reality without the need, or risk, of having to explain the relative importance of different, sometimes hidden, mechanisms in the system. At the same time, this is a major disadvantage since these models help little in understanding the underlying biology. As a consequence, regression models can only be used within the observed data space since any simulation beyond the limits of the empirical data would require the acceptance of a plausible mechanism.



Figure 7.

Actual estimated population sizes (circles) versus median and 95%-range of model-predicted values (diamonds) for each month in 100 runs. Twelve-month simulations starting in December with starting values equal to actual estimated values for these months.

It is also impossible to use such models to evaluate the effects of pest control interactions, since that would require some knowledge about how, rather than when, populations react to changing environmental conditions.

The conceptual models, on the contrary, focus exactly on how the environment or the population itself may affect densities. They attempt to explain a complex reality by including a variety of different explanations. This complexity makes the models sometimes difficult to understand (see, for example, Figure 3 or some of the models by Sicard et al., Chapter 20). A common problem with all these models is that they are imprecise in their definitions (e.g. they talk about 'dry' or 'wet', 'low density' and 'high density') and nearly always miss a quantitative expression of the mechanisms that they include. For example, Leirs et al. (1996) recognise that there is some densitydependent mechanism, but fail to mention at what densities that should become active and how large its effect would be. Likewise, Hubert and Adam (1983) incorporated a time-lagged response of predators in their model, but were not able to say how much time was needed for that time-lag and how quickly effective densities of predators would be reached. Taylor and Green (1972) discussed the importance of field sanitation, but did not give a quantitative relation between the amount of weeds on a field and the response in the rodent population. These shortcomings make these conceptual models difficult to use in practical applications, although they may be very useful to structure an otherwise complex set of biological findings and theories.

The demographic models that were mentioned above, do allow a quantitative use. Since they are build on concepts about mechanisms that play a role in population dynamics, they can be used for simulations. The main problem with these models is the parameterisation of the demographic processes. In order to obtain a reliable model, and given that the underlying concepts are biologically all right, the parameter estimates need to be rather precise. Yet, even with large data sets, some estimates may have large confidence intervals (e.g. Leirs et al. 1997). Another problem is the determinism in these models, meant here as the absence of environmental stochasticity in the model system. The model developed by French (1975) simulated populations of rodents over several years, but assumed that each year, the same values for natality and survival would apply. This is obviously not true, and therefore such models cannot give realistic predictions. Nevertheless, they may very well simulate what the effect would be of rodent management applications.

Including stochasticity in demographic models makes them considerably more complex and less easy to understand for nonspecialists. Also, the interpretation of the results becomes more difficult since the stochasticity will cause a different result every time the model is run, even though all other parameters are the same. This means that instead of a single model outcome, a probability distribution of possible results is obtained. The practical use of stochastic demographic models will therefore, maybe paradoxically, depend on methods to reduce the amount of stochasticity.

In ecologically-based rodent management, models can play a big role as forecasting tools, indicating when problems can be expected and allowing people to organise control campaigns in a timely manner. Outbreaks that come as a surprise are a major concern for agriculture in Africa (e.g. see Makundi et al., Chapter 22). For all practical purposes of forecasting, the regression model seems to be the most simple and reliable one. As part of a national strategy, an early warning system for Tanzania can be based on the rainfall data that are being collected by the usual meteorological network. Applying the regression model to these data can be done at a central laboratory, with simple computing facilities. For more localised outbreaks, rainfall should also be collected locally; data interpretation, however, is less straightforward because it will require a comparison of the actual rainfall data with the usual rainfall data for that place; this may require input from the central laboratory.

Models can be very helpful to structure and integrate our knowledge about rodent populations. Conceptual models are useful

to get a basic understanding, but have limited practical use. For simulation purposes, demographic models are the most appropriate. Simulation itself is not an element of ecologically-based rodent management, but it may be very instrumental in evaluating what the effects could be of certain interventions in the population or how the population would react under specific conditions. Apart from advanced computer skills, their use requires detailed biological knowledge, a careful design of the simulations and a permanent critical evaluation of the output quality. It can be very attractive to explore population dynamics with these models, but because of their complexity, simulations may sometimes have side effects that do not correspond to the user's intentions. The application of demographic models is therefore not to be organised locally but they should remain a tool for the scientists who are designing strategies. Only when enough experience is gained with the model, and an intelligent user interface is provided, can such demographic models become more useful at the local level.

CONCLUSIONS

There has been, and will continue to be, a small group of scientists with good firsthand knowledge of African pest rodent populations, but if we want to make that knowledge more accessible and less' subjective, we must attempt to structure it and formulate it in the form of models. In order to be useful in practice, these models must be quantitative. For outbreak prediction purposes, regression models have the best properties and these can be easily applied. More complex, quantitative demographic models are very useful for simulation purposes, but stochasticity hampers their application for actual forecasting. Both model types are available for African rodent systems, but they have been constructed based on data from a few localities only. More and longer data series from other sites are needed to evaluate and improve the models' general validity.

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

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Abstract

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

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

Keywords

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

INTRODUCTION

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

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

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

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

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

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

Since *chronobiology* aims to understand the mechanisms regulating such rhythms, it is interesting to approach the study of a complex cyclic phenomenon, such as rodent population dynamics, through the concepts of chronobiology. Indeed, to develop models it is necessary to determine whether agonistic or antagonistic relationships between internal (reproduction, mobility, metabolism and mortality) and external (climate, resources, chemical signals, competition, predation, diseases) factors controlling population dynamics involve mere cycles or bona fide rhythms.

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

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



Figure 1.

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

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

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

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

METHODOLOGICAL CONSIDERATIONS OF ECOPHYSIOLOGICAL AND CHRONO-BIOLOGICAL APPROACHES TO RPM

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

Long-term field monitoring

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

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

In addition, trapping networks were placed elsewhere in each habitat to obtain data on physiological parameters. Diet was determined from analysis of stomach contents (Sicard 1987) and reproduction was estimated from numbers of embryos in pregnant females. Reproductive onset and offset were determined from an analysis of oestrous cycles using vaginal smears (Kyelem and Sicard 1994), seasonal changes in blood sexual steroids using radioimmunoassays (Maurel et al. 1981) and

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

Experimental study of causal relationships

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

Modelling for RPM improvement

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

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

VITAL-CYCLES, KNOWLEDGE OF RODENT HABITATS AND RPM IMPROVEMENT

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

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

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

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

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

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

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

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

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

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



Figure 2.

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

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

ECOPHYSIOLOGY, KNOWLEDGE OF RODENT VITAL-CYCLES AND RPM IMPROVEMENT

Life history strategies, vital-cycles and RPM improvement

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

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

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

Actions targeting mobility

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



Figure 3.

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

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

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

Sahelian-Sudanese human populations have developed some RPM strategies that consist either of attracting rodents away from habitations and crops or protecting them using sound, physical or chemical barriers (Diarra 1996). These methods, which are aimed at affecting rodent mobility, are probably most effective during those phases of the annual cycle when animals are most likely to be actively mobile, i.e. during the dispersal and regrouping phases. The hypothesis that knowledge of the annual cycle of rodent mobility improves the timing and efficiency of these RPM methods will be tested in the near future.

Actions targeting reproduction

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