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The ecological basis of forecasting rodent outbreaks in a Sahelian agrosystem

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Taterillus pygargus in dry areas and *Arvicanthis niloticus* in wet and irrigated areas were studied in a Sahelian agrosystem in northern Senegal. Population dynamics of *Taterillus* allow simulation models to be constructed on the basis of empirical data. Densities depend mainly on natality-mortality contrast. Seasonal reproductive success is determined by the length of the breeding season, the prevalence of pregnancy and the litter size. These parameters depend on food availability, which in turn is influenced by the weather during the preceding rainy season. Predation is a constant mortality factor, and the number of predators present depends on the average rodent densities the year before. On the basis of the prey-predator relationship and the climatic conditions, it is possible to predict the rodent density in the near future. Chances for a forecast are more limited for *Arvicanthis* because of the apparent mobility of this species. Dispersal movements may follow a nomadic pattern from one temporarily favourable habitat to another, the animals being concentrated in crop fields. The diurnal behaviour of *Arvicanthis* and the presence of Palaearctic birds of prey amplify the impact of predation to an unknown degree. Under these conditions, further study is required if outbreaks of *Arvicanthis* are to be forecast.

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1. Introduction

Two rodents were studied in northern Senegal: *Taterillus pygargus* in dry areas and *Arvicanthis niloticus* in wet and irrigated areas. *Arvicanthis* is very harmful to crops because of its relatively large size and its repeated outbreaks in irrigated farmland. Unfortunately its ecology is still poorly understood. On the other hand, the population ecology of *Taterillus* is well known, and most of the examples below are based on data on this species.

The Sahelian climate is characterized by a short annual rainy season from July to September, followed by a long dry season, cool in its first part (October—January) and hot towards the end (March—June). The dynamics of rodent populations follow the climatic pattern. The breeding season extends from the rains to the middle of the dry season. Accordingly, rodent densities fluctuate from a minimum at the end of the wet season to a maximum in December—January. From then on, densities decrease until a new minimum occurs the following September. Reproduction and seasonal mortality influence the *seasonal rate of increase*, i.e. the ratio between maximum and minimum densities in a given year. Reproduction and annual mortality are manifested in the *annual rate of minimum density variations*, i.e. the ratio between population minima of two successive years. The former is an expression of the population increase during the farming period and indicates whether the threshold level of damage to crops is reached or exceeded; the latter predicts long-term trends in population fluctuations.

Natality depends on the length of the reproductive period, the litter size and the prevalence of pregnancy. The length of the reproductive period varies considerably in the Sahelian zone, depending on the climate and on the species involved. Litter size and prevalence of pregnancy vary according to species, year, and the phase of the breeding season. All reproductive parameters apparently depend on food availability, as shown by supplementary feeding experiments (Hubert et al. 1981, Poulet et al. 1981). The food available to rodents is, however, not so obviously correlated with climatic parameters as primary production itself seems to be (Rosenzweig 1968). Rodents can change their diet according to circumstances, and the quality of food available is often as important as the quantity. Sahelian rodents feed on both seeds and insects. Seed production is always abundant and hence there is an excess of seeds on the ground. Rodents take full advantage of this opportunity, whereas the actual impact of insect food is poorly known.

Mortality acts throughout the year. "Chronic" mortality produced by predation is constant, whereas "acute" mortality due to epizootics is connected with outbreaks and acts instantaneously.

2. Demographic characteristics

Taterillus and *Arvicanthis* represent two opposite types of adaptive strategy in Sahelian rodent fauna.

2.1. Taterillus pygargus

The adaptive strategy of this gerbil can be described as opportunistic with K tendency (Poulet 1982). The reproduction rate is low. The litter size is from two to eight and decreases in the course of the breeding season. The litter size of the "parent" cohort (= females adult in September) at the beginning of the breeding season varies from 2.0 to 6.9. A positive correlation ($r = 0.94$) exists between litter size and rainfall (Fig. 1). The prevalence of pregnancy is at its maximum at the beginning of the dry season, with 100 % of females breeding, and then decreases gradually. The duration of the breeding season varies from one to eight months, depending on the year. When the breeding season is long, reproduction by the young born that same year is possible, the first pregnancy occurring at an age of about three months. In this case a second annual generation appears in December or January the following year.

First-generation and second-generation young do not have an equal impact on the demography of the population. Survival of the first-generation individuals is higher than that of the second-generation onwards, and the former alone usually participate in the following year's reproduction. The density and litter size of the "parent" cohort are the two most important parameters in the population dynamics of *Taterillus*; these parameters determine the number of first-generation young, which, in turn, constitute the bulk of the population at the beginning of the following breeding season.

Predation by small carnivores and owls causes most of the "chronic" mortality in the *Taterillus* population (Poulet 1982). The predation rate fluctuates markedly from year to year and can be considered the main reason for long-term variations in the abundance of this species.

Demographic data obtained from studies on *Tarterillus* populations from 1969 to 1978 are summarized in Table 1.

2.2. Arvicanthis niloticus

This African rat is a typical r strategist (Poulet 1982). The reproduction rate of *Arvicanthis* is high. The litter size is two to eleven; the overall mean is about seven young, but the average reached by the "parents" is 7.7. The first pregnancy occurs when the female is two months old, and the production of a second annual generation is common. The duration of the breeding season varies from five to nine months. The lifespan is short, only a few individuals reaching the age of eight months. Thus the second-generation young become the "parent" cohort of the next breeding season.

Arvicanthis is prey to numerous predators, and the predation rate is always high.

Annual density fluctuations depend on the duration of the breeding season. Irrigation allows several crops during the dry season, and this, in turn, promotes population increase. When outbreaks do occur, predation can no longer limit the population growth. *Arvicanthis* disperses from one field to another, depending on food availability, colonizing only

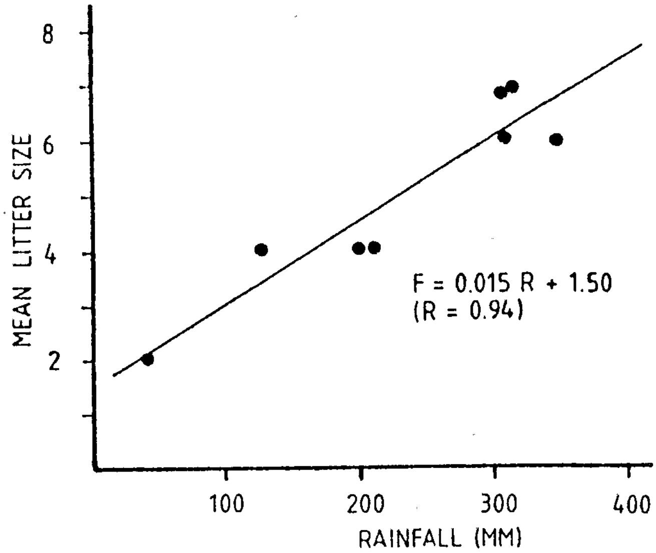

Fig. 1. Correlation between the mean litter size of *Taterillus* adults in September ("parents") and the annual rainfall.

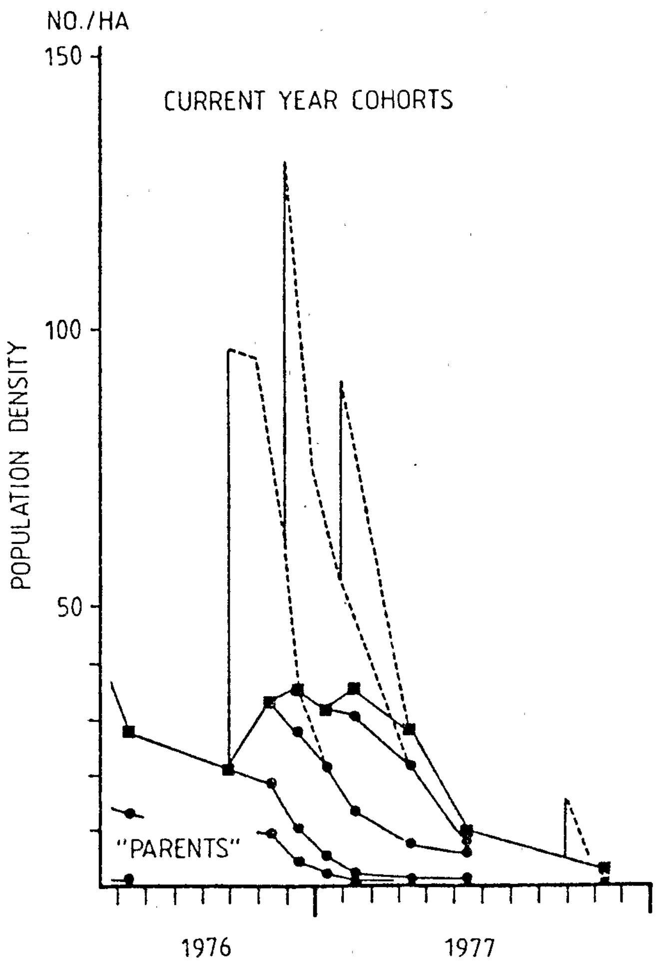

Fig. 2. Descriptive model of the 1976—77 annual population cycle of *Taterillus* in Fete-Ole, northern Senegal. For explanation, see text.

temporarily favourable habitats (Poulet & Poupon 1978). Finally, diseases intervene when a high density has been reached. The survivors are then confined to small 'nuclei' with good cover and adequate food supply (Delany & Roberts 1978).

3. The modelling approach

3.1. The descriptive model

Trapping at regular intervals gives indices of the density of a given rodent population, but only the trappable part of the population appears in the sample. The untrappable part is not known, but can be computed when natality and dispersal parameters are known. The observed curve can be modified by a calculated curve. The descriptive model then obtained permits more accurate interpretation of the ecological phenomenon under study.

Fig. 2 gives a model to explain the density changes in *Taterillus* in 1976—1977, one year after an outbreak (Poulet 1982). Solid squares connected by a line refer to observed density indices. Circles represent the current year cohort split into three bimonthly groups. Population samples indicate that reproduction occurred during six months from September 1976 to February 1977. In September—October all females were pregnant, the average litter size being 6.3 embryos. The corresponding values in November—December were 75.8 % and 5.3, and in January— February 73.6 % and 3.8, respectively. The computed number of offspring for each bimonthly period is indicated by the dashed lines. Although the age at first capture varies, the difference between the calculated and the observed numbers is mainly due to high mortality during the dry season. Monthly mortality rates of the trappable population are similar, being about 30 to 50 %. Such heavy mortality was probably caused by an epizootic, as was shown in another part of Senegal at the same time (Hubert & Adam 1982).

3.2. The simulation model

A simulation model was developed for calculating the data lacking for 1973—1974 (Table 1) on the basis of known reproductive and mortality parameters from eight annual cycles. Rainfall during the 1973 rainy season was 209 mm (13 rainy days) as in 1970. Demographic parameters of the 1970—1971 cycle are well known (Poulet 1972), but at this time the density of *Taterillus* decreased from 4.1 individuals/ha to 0.6/ha owing to the high mortality rate of 25 % per month. In 1973—1974, however, the population increased from 0.75 to 8.1 individuals/ha. The question now arises: is it possible to simulate a population cycle leading to an annual rate of minimum density variations above 10?

The characteristics of the 1970—1971 breeding season do not indicate whether this would be possible, even if the mortality was very low. So we have to assume that the 1973—1974 season was very different from that of 1970—1971, but possibly similar to 1976—1977. To be realistic, our model must have the following characteristics: (1) The mean litter size of the "parents" is 4.8, corresponding to 209 mm annual rainfall (Fig. 1). (2) The litter size must decrease from the "parent" cohort to the current-year cohort in the course of the dry season. (3) The fecundity rate must decrease in the course of the dry season. (4) Mortality must increase from the first-generation to the second-generation young in the course of the dry season.

Table 1. Principal data pertinent to understanding the demography of *Taterillus pygargus* in the Fete-Ole Savanna, northern Senegal, in 1969—1978. Predator-index: number of small terrestrial carnivores/km^2; prey/predator ratio: average number of *Taterillus* available as daily prey to small terrestrial carnivores; mortality of prey: average monthly mortality rates of *Taterillus*; densities of *Taterillus*: number of individuals/km^2 (Max. = annual maximum density, D = average annual density, and Min = minimum density), i.e. initial density of each annual cycle; SRI: seasonal rate of increase; ARMV: annual rate of minimum density variations; duration of breeding: duration of the breeding season in months; mean litter size: annual mean of litter size of all females breeding; parents' litter size: mean litter size of females adult in September; rainfall: annual rainfall in mm.

Annual cycle:		1969—70	1970—71	1971—72	1972—73	1973—74	1974—75	1975—76	1976—77	1977—78
Predator index		2.1	0.9	0.6	0.4	?	0.3	1.4	1.3	?
Prey/predator ratio		2.2	3.4	0.2	0.1	?	38.1	26.2	39.4	?
Mortality of prey		0.25	0.25	0.05	0.01	?	0.09	0.14	0.29	?
Densities	Max	900	780	70	88	?	6 300	14 350	12 710	1 420
of	(D)	(600)	(478)	(58)	(76)	?	(4 245)	(8 455)	(6 908)	(845)
Taterillus	Min	80	410	60	40	75	810	2 880	2 400	610
SRI		11.2	1.9	1.2	2.2	?	7.8	5.0	5.3	2.3
ARMV		5.1	0.14	0.67	1.9	10.8	3.6	0.83	0.25	0.16
Duration of breeding		8	6	1	1	?	8	2	6	1
Mean litter size		3.2	3.0	4.0	2.0	?	5.2	4.7	4.6	4.0
Parents' litter size		6.0	4.0	4.0	2.0	?	6.9	6.8	6.0	4.0
Rainfall (mm)		313	209	202	38	209	316	311	347	126

Fig. 3 gives a plausible model with a long reproductive period and a high production of second-generation young. Low monthly mortality rates must be assumed. Population changes predicted by the model have, in fact, been observed at certain times, but what the model does not explain is how such a long reproductive period could occur with an annual rainfall of only 209 mm.

3.3. The predictive model

This type of model is similar to the preceding one, but the objective is not fixed beforehand, the purpose being to build alternative probability patterns. The minimum starting density being known, the question is: what happens if one or other of the parameters varies? For instance, with a monthly mortality rate of 0.25, the densities of *Taterillus* decreased abruptly during the 1970—1971 cycle. But, what would have happened if mortality had been different?

Fig. 4 answers this question. Densities could become stable in one year at a monthly mortality rate of 0.12 or they could increase threefold at a mortality rate of only 0.04. Similarly, the reproductive parameters could be modified (cf. Fig. 3).

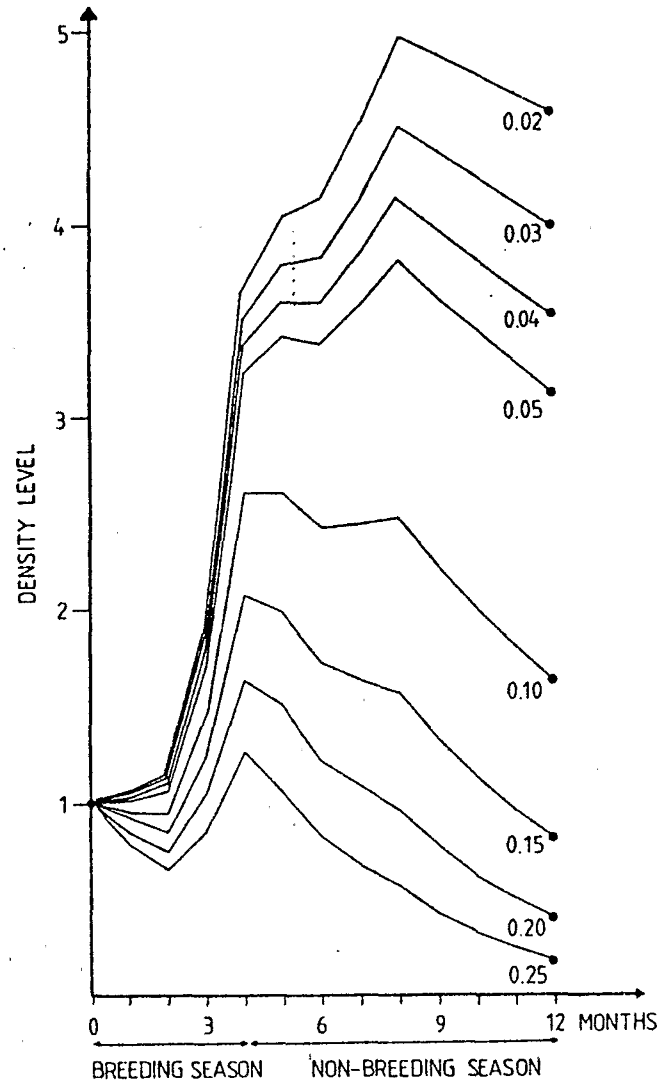

Fig. 4. A predictive model for the 1970—71 annual population cycle of *Taterillus* in Fete-Ole, northern Senegal, using the observed reproductive parameter values but variable monthly mortality rates (values indicated at the end of each curve).

4. Discussion

Some descriptive models have been developed for studying the adaptive strategies of Sahelian rodents. A mathematical formula has been adjusted for modelling the annual population cycle of *Taterillus gracilis* and *Mastomys erythroleucus* (Hubert et al. 1978). *T. pygargus* and *A. niloticus* were studied in the same way (Poulet 1982), and the information gained allows us to formulate a broad outline for pedictive models.

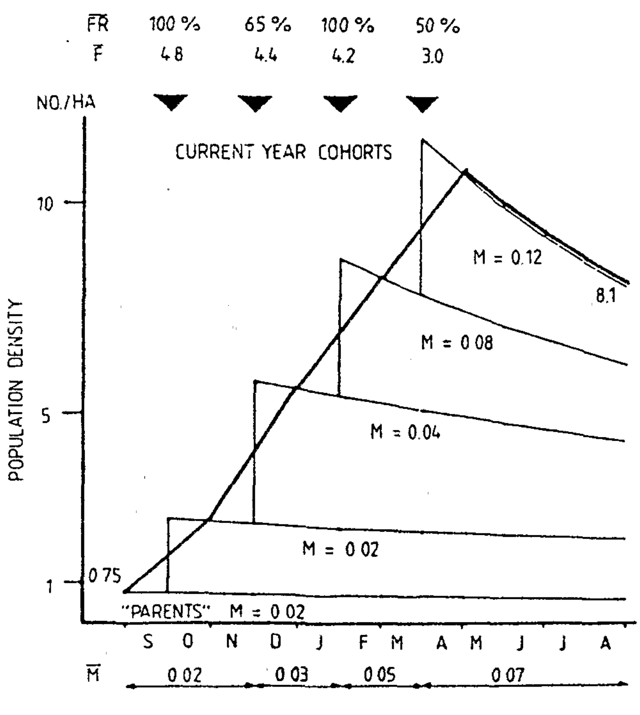

Fig. 3. Simulation of the 1973—74 annual population cycle of *Taterillus* in Fete-Ole, northern Senegal. $\overline{FR}$ = mean fecundity rate, F = mean litter size, $\overline{M}$ = average monthly mortality rate, m = cohort specific mortality rates. For further explanations, see text.

Two different starting-points can be selected: (1) the minimum initial density of the annual cycle to be predicted, or (2) the maximum density of the cycle preceding the one to be predicted. In the first case we are seeking a short-term forecast to assess seasonal population growth, and in the second case a longer-term forecast. In both cases the crucial point of the population dynamics is the annual minimum density around September. This parameter is easily determined by trapping in the first case, or it can be computed from the preceding maximum density on which mortality acts, at the end of the previous dry season and in the rainy season.

The growth rate of the population depends primarily on the level of the annual minimum density. If this level is very low, the population cannot reach a density so high that crops are damaged. In contrast, a high starting density necessarily leads to a maximum density, resulting in heavily damaged crops. The level of the initial density is generally intermediate and the pattern of the growth curve will depend on the fertility of the species concerned and on the level of mortality.

In species such as *Taterillus*, natality depends on the weather in the preceding rainy season acting through the available food (Fig. 1). Mortality can vary greatly according to the predation rate. The number of predators depends on the average level of rodent density in the previous year. This means that the development of a given annual cycle is highly dependent on the history of the population studied. The principal difficulty is in estimating the predation index and, consequently, obtaining realistic mortality rates. A crude predation index can be obtained, for example, by observing a given class of predators such as small terrestrial carnivores (Table 1).

Forecasting is more difficult with regard to *Arvicanthis* because of the apparent mobility of this animal. Population movements and dispersal can occur from a potential reservoir or follow a nomadic pattern from one temporarily favourable habitat to another, aggregations developing in crop fields. The diurnal behaviour of this species and the presence of Palaearctic birds of prey affect predation to an unknown degree. The duration of the breeding season is extended when irrigation allows several successive crops during the dry season. High initial densities, irrigation and lack of rodent control measures lead to crop damage.

Arvicanthis appears to exhibit regular peaks of abundance at intervals of about four years. In northern Senegal, *Arvicanthis* were numerous in 1964, 1967, 1971, 1975 and 1980 according to information given by farmers and our own observations. This raises the question: will the next peak be a real outbreak or only a moderately abundant phase? The answer depends on the climatic conditions of the four preceding years and on internal population parameters still unknown today.

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