EVOLUTION OF THE RODENT POPULATION OF A DRY BUSH SAVANNA IN THE SENEGALESE SAHEL FROM 1969 TO 1977

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ABSTRACT

An eight-year study of changes in rodent populations in a Sahel savanna habitat in northern Senegal is presented. Characteristics of population dynamics for the principal species that are most important in allowing repopulation of dry bush savanna areas include the ability to rapidly attain high population levels after an initial reinvasion. Habitat preference and resource utilization within the dry bush savanna are critical factors to successful increase in population levels and their maintenance.

INTRODUCTION

The evolution of small rodent populations was followed in a Sahel savanna in northern Senegal from 1969 to 1977. Trappings were effected at more or less regular intervals (every one to three months) for the following purposes: to determine the composition of the population and its eventual temporal variations; and to determine the most important characteristics of population dynamics for the principal species, including periodicity and magnitude of reproduction, and maximal and minimal densities during the yearly cycle.

The first part of this study, included in the International Biological Program from 1969 to 1972, occurred during an extreme drought which peaked in 1972. Rainfall since that time, although still below 30-year averages, has increased throughout the Sahel. Biological phenomena have thus undergone a renewal, illustrated by the more or less generalized outbreaks of insects and especially rodents in 1975–1976.

The purpose of the present report is to describe this latter phenomenon in a natural environment and to establish a qualitative and quantitative comparison with observations made during the period of drought. These observations were localized to the Sahel savanna of Fete-Ole, in northern Senegal (northern Ferlo).

Average yearly rainfall of about 300 mm supports a dry bush savanna, established on old dune reliefs whose topography governs the distribution of vegetation, which includes large grassy areas with occasional trees on the dunes and dense bushy undergrowth in interdune depressions.

The rainy season lasts only three or four months, between July and October. The rest of the year is dry, becoming chilly from November to March and hot from April to June. Rainfall from 1969 to 1976 is shown in Table 1. Biological activity is concentrated in the rainy season and the first part of the dry season. The majority of the animals reproduce during this period. Animals with an annual cycle, such as rodents, generally reach their abundance maximum between October and January. Population densities then decrease, reaching their minimum just before or at the onset of the rains of the following season. The characteristics of a given annual cycle are thus functions of both the minimum density of the preceding year and the peculiarities of the present reproduction (length and fecundity), all of which determine the growth level of the population and thus the maximum annual number of individuals in the population.

The rodent population of Fete-Ole was studied from 1969 to 1972 and the population dynamics of the most abundant species, *Taterillus pygargus*, was established (Poulet, 1972*a*, 1972*b*). Other studies concerning the effects of the drought were performed in 1972 and 1973 (Poulet, 1974). The spectacular change in the rodent population was studied

Table 1.—*Annual Rainfall in Fete-Ole from 1969 to 1976 (in mm).*

Year	Amount of rainfall
1969	321
1970	209
1971	202
1972	33
1973	209
1974	316
1975	311
1976	343

21 JUIL. 1980
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Bulletin of Carnegie Museum of Natural History
no 6 - 1978.

extensively from 1975 to 1977 by samplings performed during the dry season in order to obtain information concerning the fauna and demography of the region. The detailed analyses of these data are forthcoming (Poulet and Poupon, 1978; Poulet, in preparation).

DISCUSSION

Rodents of Fete-Ole

Gerbillidae.—The most common rodents on the Fete-Ole Sahel are *Taterillus*. *T. pygargus* is found in all the habitats, but this species is the only one which is capable of permanently occupying the dunes, because it is particularly adapted to the sandy habitat. *T. gracilis*, which is much more rare, inhabits only the bushy depressions. The two species coexist in these depressions, but *T. pygargus* consistently is the dominant species. This situation explains why *T. gracilis* appears to have virtually disappeared during the drought, a condition that is much more unfavorable to it than to *T. pygargus*.

Desmodilliscus braueri is a small subdesert rodent, which is very difficult to study because it does not enter the traps. Its presence is known by its occurrence in pellets of owls and, although difficult to trap, it may be stalked at night and caught by hand. Its abundance apparently varies inversely with that of all the other rodents; it is rare during periods of abundant rainfall and becomes more numerous during droughts. It seems to have dissappeared since the outbreak of the other rodents in 1975–1976.

A *Tatera* with 52 chromosomes appeared in 1976 at the latitude of Fete-Ole but its occurrence must be considered as exceptional. Its appearance seems to be exclusively related to a temporary extension of the area of distribution of the species toward the north following the outbreak of 1975–1976.

Muridae.—*Arvicanthis* and *Mastomys* are usually not found in the Fete-Ole Sahel; *Arvicanthis niloticus* normally inhabits the campsites of nomads and *Mastomys erythroleucus* is occasionally found in certain permanent settlements of the Sahel. *Arvicanthis* invaded the Fete-Ole savanna in the rainy season of 1975. Family groups inhabited all the depressions with bushy covering and often adopted a diurnal arboreal behavior. *Mastomys erythroleucus* also inhabited the depressions but was less abundant than *Arvicanthis*. The samples taken revealed only several individuals per depression.

Pullulation of Taterillus

Following the rains of 1974, thus two years after the great drought, the rodent density had risen to a level comparable to that of 1969–1971. There are no precise data for this period but the several *Taterillus* captures made indicated a considerable reproduction beginning in the months of October. The possibility of a rapid growth of rodent populations was indicated by the abundance of herbaceous vegetation as well as acridian multiplication. Population samplings were undertaken in January-February, April, and July of 1975 and then in February, April, and June 1976 (Table 2).

A maximum of population density was reached in April 1975, with approximately 40 *Taterillus* per ha. The reproduction season, at least 6 months long, resulted in the appearance of two successive generations, thus considerably increasing the population density. The period of population decrease resulting from the arrest of reproduction at the end of the dry season was very brief; from July 1975 onward, reproduction recommenced at already high densities, approximately 30 individuals per ha with an average of eight young per litter.

Considering an overall mortality rate of 15 to 20% per month and two successive litters of eight and six young with a starting density of 30 per ha, we may calculate an average maximum density of 180 (135–250) at the end of September. The demographic analysis of samplings of February 1976, show that reproduction during the rainy season of 1976 was indeed very short and that no new individuals appeared beginning with early October 1975. The period of population decrease in 1975–1976 was thus very long (October 1975–August 1976) and the population density decreased from 70 per ha in February to 30 in July, representing an overall mortality rate of 25% per month.

The 1976–1977 reproduction season began rather late, toward the end of September. The annual minimum density was reached at this time, with 20 individuals per ha, a level which is still considerable. The pullulation period could be considered as virtually terminated, because the following cycle showed neither as great a difference between minimum and maximum densities nor as rapid a variation of numbers of individuals.

The pullulation thus occurred in two stages—1) a progressive but important rise in the population

Table 2.—*Estimation of densities and biomass of* Taterillus pygargus *on the dunes of Fete-Ole during the rodent outbreak of 1975–1976. Average weight of an individual is 36 g.*

Date	Density (individuals/ha)	Biomass (g/ha)
January–February 1975	29	1,044
April 1975	40	1,440
July 1975	28	1,008
February 1976	86	3,096
April 1976	54	1,944
June 1976	28	1,008

level, due to a very long reproductive season, followed by a period of population decrease which was too short to bring the density to a low level (1974–1975); and 2) a following reproductive season characterized by a highly elevated fertility which affected the already elevated population level. The outbreak ensued and the population was quadrupled from the first litter (1975–1976).

The abrupt population increase during the second phase led to an overpopulation whose first and foremost effect was to rapidly block reproduction. Because the vegetation did not yet have the time to be degraded, the block had to be at the behavioral level; the promiscuity of individuals was reduced, thus inhibiting all subsequent gestations.

In spite of the abundance of *Taterillus*, mortality during the entire period of population decrease remained limited to a low level of 20% per month. There were no changes in the size of each age group noted between the beginning and the end of the dry season; there was thus no state of famine.

The *Taterillus pygargus*-Sahel savanna relationships appear to be especially well in equilibrium. Just as the great drought of 1972 had no irreversible consequences for the *Taterillus* population, the rapid reproduction of 1975–1976 did not lead to any considerable degradation of the habitats. It may be considered that *Taterillus pygargus* is very suitably adapted to the dry bush environment of the Senegalese Sahel. This does not, however, mean that the outbreak of *Taterillus* was without repercussions. Seed productivity in the savanna and the details of the granivorous diet of rodents are poorly known. It is not possible to precisely estimate vegetation changes, which, although not spectacular, could nevertheless be important. Furthermore, the competitive relationships among consumers were probably changed. Thus, the exceptional abundance of rodents could furnish an explanation for the disappearance of all reproduction among certain granivorous birds, which previously reproduced quite satisfactorily at the end of the dry season (the case of certain species of turtle-doves; G. Morel, personal communication).

Invasion by Arvicanthis niloticus

The invasion of the Sahel savanna by *A. niloticus* at the end of the 1975 dry season resulted from massive migrations induced by an overpopulation at the moment of the maximum population density at the first phase of the pullulation in cultivated areas and in the villages where *Arvicanthis* lives permanently.

The intense reproduction of the newcomers, inhabiting the bushy depressions, explains the spectacular increase in the number of *Arvicanthis* between October and December 1975. The dietary requirements of a population exceeding 100 individuals per ha of habitat and a resulting biomass greater than 11 kg, are such that a state of famine could not be long in developing. The consequences of this chain of events were a significant reduction in physical parameters of the individuals of a given age (size and especially weight), a lifespan not exceeding 9 months due to an intense mortality and a very clear degradation of the woody stratum. Mortality was amplified by predation resulting from abnormal concentrations of diurnal Palearctic birds of prey.

Table 3 shows the population densities in the Sah-

Table 3.—*Estimation of densities and biomass of rodent populations of "bushy depressions" in 1976.* Taterillus *sp. represents* T. pygargus *and* T. gracilis *in a 60:40 ratio. Values are given in ha of effective biotope, that is, ha of bushy depression.*

	Taterillus sp.			*Arvicanthis niloticus*		
Date	Density/ha	Average wt (g)	Biomass/ha (g)	Density/ha	Average wt (g)	Biomass/ha (g)
February 1976	66	38	2,508	100	112	11,200
April 1976	32	38	1,216	73	98	7,154
June 1976	15	38	570	17	84	1,428

Table 4.—*Maxima and minima of population densities, in number of* Taterillus pygargus *per ha of Sahel savanna, for each annual cycle from 1969 to 1977. The average value of population density is calculated from the maximum assuming a constant decrease of 20% per month until the minimum. The average weight of a* T. pygargus *is estimated as 36 g and its daily seed comsumption at 3 g. x = very low density.*

	Annual maximum		Annual minimum		Average	Biomass	
Date	Date	Density	Date	Density	density	(g)	Seed
1969–1970	April 1970	9	August 1970	4.1	6	216	6,480
1970–1971	October 1970	7.8	August 1971	0.6	3.2	115	3,456
1971–1972	November 1971	0.7	?	x	0.3	11	324
1972–1973	—	—	—	—	x	—	—
1973–1974	—	—	—	—	?	—	—
1974–1975	April 1975	40	July 1976	30	29.5	1,062	31,860
1975–1976	September 1975	180	September 1976	20	83	2,992	80,773
1976–1977	December 1976	45	July 1977	10	23.4	842	25,272

el depressions during the dry season of February to June 1976 for *T. pygargus* and *T. gracilis* (in a 60:40 ratio) and for *Arvicanthis niloticus*. The invasion was massive but was reduced very rapidly. In reality it affected only the "pond" biotope (bushy undergrowth in depressions), which represents only 10% of the Fete-Ole surface. It may be concluded that the permanence of the *A. niloticus* population in the dry bush savanna is questionable, which is fortunate for the natural environment as it can tolerate the presence of these murids for only a short time without irreversible damage.

CONCLUSIONS

The frequent droughts in the Sahel do not enable permanent populations of murids to be maintained in the dry bush savanna. The particular circumstances of an exceptional demographic outbreak are required for the murids to invade this zone. These new populations are nonetheless not capable of maintaining themselves, because of the unacceptable disequilibrium they impart to the habitats they invade. The invasion of *Arvicanthis niloticus* and *Mastomys erythroleucus* in the dry bush Sahel savanna represents the limits of their ecological potentialities; they must be considered not as normal dwellers but rather as invarders with deleterious actions.

Taterillus, especially *T. pygargus*, are the characteristic animals of the Sahel savanna. They may undergo enormous variations in abundance without producing irreversible disequilibrium in the habitats. Table 4 summarizes data gathered between 1969 and 1977 concerning minimum and maximum population densities, biomass, and seed consumption.

Biomass was increased by a factor of 300 between the drought of 1972 and the maximum population outbreak of 1976. These are extreme cases, related to climatic extremes of the Sahel. True Sahel species are those capable of undergoing large variations in population numbers in the absence of irreversible repercussions, neither to the species itself nor to the sheltering environment. This is indeed the case for *Taterillus* but not for *Arvicanthis*.

Seed productivity of 1 ha of Fete-Ole Sahel has been estimated at 29 kg (Bille, 1977). Availabilities from previous years bring the reserve to 40 to 60 kg. These figures are largely in excess of the needs of *Taterillus* during a drought, but it must be supposed that availabilities of the environment in 1976 were at least double, because the quantity of seeds required to support a *Taterillus* population estimated at 80 per ha is about 80 kg. This represents an indirect confirmation of the opinion of Bille, according to which, after the dry period, there is "a compensatory phenomenon enabling the very rapid biological rise of the ecosystem, both for the trees and grasses."

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This paper was communicated by Bernard Hubert.