Journal of Applied Ecology 2000, **37**, 603–615

The spatio-temporal distribution of a rodent reservoir host of cutaneous leishmaniasis

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Summary

1. The rodent *Psammomys obesus* is the main reservoir host for *Leishmania major*, the causative agent of cutaneous leishmaniasis in Tunisia, much of North Africa and mid-western Asia. An understanding of the population dynamics of this rodent is essential to establish a preventive control strategy based on the early prediction of rodent outbreaks.

2. The study of *P. obesus* dynamics at a regional scale requires index-based sampling. Rodent numbers were monitored twice per year at the beginning and end of the breeding season, using transects around the Sidi Bouzid region in central Tunisia.

3. Two different types of dynamics occurred in two drainage basins. Rodents living in the northern basin were at low density and those living in the southern basin were at high density.

4. At the scale of a plot, occupied burrows were generally associated with the presence of three Chenopodiaceae: *Arthrocnemum glaucum*, *Salsola tetrandra* and *Suæda fruticosa*, rarely in monospecific formations. However, in dry periods, occupied burrows drifted to *A. glaucum* formation linked with high moisture and salinity of the soil (χ^2 MacNemar = 6·26).

5. The risk of a *P. obesus* outbreak can be assessed by a simultaneous knowledge of flooding regimes in the drainage basins, the distribution of halophytic plant formations, and the progressive movements of the rodents as drying out proceeds. The transect indices of rodents are easily repeatable, economical and would be applicable in other developing countries where cutaneous leishmaniasis occurs.

6. This work illustrates that simple ecological methods can assist the assessment of spatial and temporal components of epidemiological risk such as the proximity between rodent colonies and human habitats at the time of outbreaks.

Key-words: dynamics, landscape ecology, *Leishmania major*, *Rodentia*, salt habitat.

Journal of Applied Ecology (2000) **37,** 603–615

Introduction

Zoonotic cutaneous leishmaniasis (ZCL) is a parasitic disease, caused by *Leishmania major* Yakimoff & Schokhor 1914, extending discontinuously north of the Sahara, between Morocco and Uzbekistan, and south of the Sahara, between Senegal and Ethiopia (WHO 1990). In Tunisia, ZCL has existed for many years as a stable endemo-epidemic in the Gafsa/El Guettar oases (Deperet & Boinet 1884). In 1982, an epidemic occurred for the first time in the Sidi Saad area (south of the Kairouan Governorate), close to a dam that had recently been completed (Ben-Ismail, Ben Said & Ben Rachid 1989). Since then, the epidemic has extended to 10 other governorates

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and over 70 000 human cases were recorded between 1982 and 1997 (Direction des Soins de Santé de Base, unpublished data). Studies of the reservoir hosts identified three rodent species carrying *Leishmania major*: *Meriones shawi* Duvernoy 1842 (Rioux *et al.* 1986), *Psammomys obesus* Cretzschmar 1828 and *Meriones lybicus* Lichtenstein 1823 (Ben-Ismail *et al.* 1987a). In Tunisia, the ZCL vector was identified as *Phlebotomus papatasi* Scopoli 1786 (Diptera: Psychodidae) (Ben-Ismail *et al.* 1987b), which frequently uses *Psammomys obesus* burrows for daytime resting and, possibly, breeding (Helal *et al.* 1987; Esseghir *et al.* 1993). According to observations made while the epidemic was spreading geographically, *Psammomys obesus* seems to have played a major part in amplifying the transmission. Outbreaks of this species were regularly followed by high ZCL incidence in humans. According to Ben-Ismail & Ben Rachid (1989), the more ubiquitous distribution of *Meriones shawi* and *Meriones lybicus* could allow these species to propagate the parasite between *Psammomys obesus* colonies, thus increasing the distribution of the parasite.

This set of circumstances suggests *Psammomys obesus* as the key species in the cycle of cutaneous leishmaniasis in Tunisia as well as in other countries (Gunders *et al.* 1968; Ashford *et al.* 1977). Its geographical distribution coincides with the North African and West Asian distribution of *Leishmania major* and extends from Mauritania to Saudi Arabia (Fig. 1).

Psammomys obesus lives in saline habitats where it feeds almost exclusively on natural vegetation of the family Chenopodiaceae (Daly & Daly 1973; Rioux *et al.* 1986; Kam & Degen 1989; Zaime & Gautier 1989). It is tolerated in areas close to farmland and even in human settlements. The strict feeding habits of *Psammomys obesus* have been used to develop a control strategy against ZCL, based on eliminating its food plants and on destroying the rodent's biotope by deep ploughing followed by planting trees such as *Casuarina* sp. and *Accacia cyanophylla* (Ben-Ismail *et al.* 1997). Such strategies can only be efficient around large human settlements, as was the case around the town of Sidi Bouzid, which numbers almost 35 000 inhabitants. The cost per human case prevented is, however, extremely high if this strategy is applied to scattered settlements.

The development of new control strategies for *Psammomys obesus* requires a good understanding of this rodent's dynamics and of the factors influencing its spatial distribution and population size. Such information would help to develop early warning systems for predicting ZCL epidemics.

For this paper, an index-based sampling technique, recently developed by Fichet-Calvet *et al.* (1999b), was applied at the regional scale to assess the distribution in space and time of *Psammomys obesus* in habitats favourable to the species. This technique is based on counting indices of presence (burrows, food remains and faeces) along transects, thereby yielding data on relative rodent abundance, spatial distribution, and the nature of source habitats from which outbreaks spread. It allows the spatial heterogeneity and the diversity of habitats used by *Psammomys obesus* to be assessed. The main application of this study is to estimate the epidemiological risk in three components: space, time and human population processes (Rioux, Dereure &

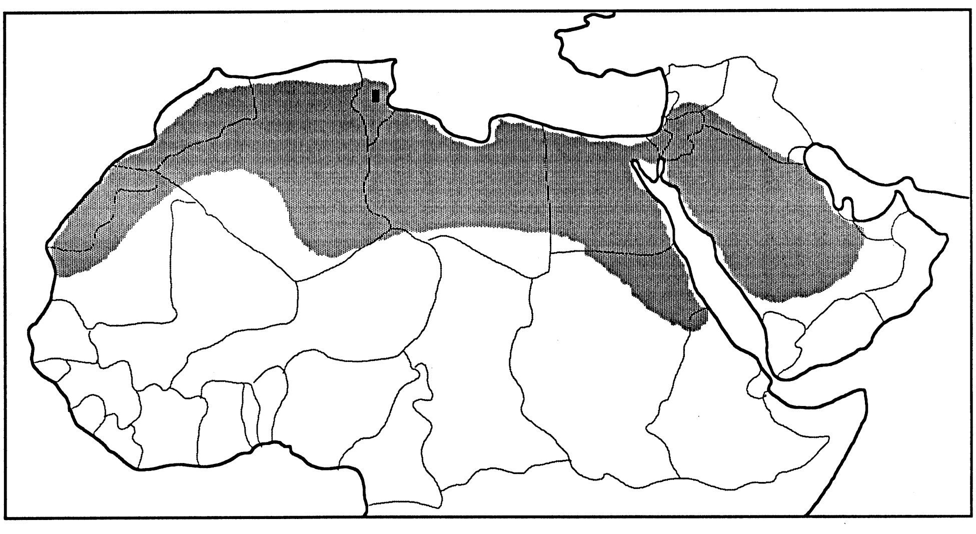

Fig. 1. Geographical distribution of *Psammomys obesus* (shaded area), modified from Le Berre (1990), and location of the study site in Tunisia (black square).

Périères 1990) by using thematic maps (maps of vegetation, land and habitat use, rodent abundance).

Materials and methods

STUDY SITE AND LANDSCAPE DESCRIPTION

Because two outbreaks of ZCL occurred in 1985 and 1987 in central Tunisia (Mbarki *et al.* 1995), epidemiological research for this work was carried out in that area. The study of the main rodent reservoir host in the same area formed an integral part of this programme. The study area covers approximately 1500 km^2 centred around the town of Sidi Bouzid (35°02′N; 9°28′E, altitude 330 m). The dominant features of the landscape are low hilly massifs (jebels) with peaks varying from 579 to 737 m in height. The characteristic plant association is that of *Rosmarinus officinalis*, *Stipa tenacissima* and *Reseda papillosa*. It has remained unchanged since Long (1954) established a vegetation map (in Le Houerou & Le Floc'h 1995), on which the zoning of the study site is based (Fig. 2). Between the jebels, very diversified fertile lowlands are distributed along a gradient of altitude and soil salinity. The periphery of the jebels, once occupied by *Artemisia campestris*, *Ziziphus lotus* and *Peganum harmala* steppes, is now occupied by planted orchards, including mainly olive, almond and pistachio trees (Or), by food crops and wheat (Wh), and a few *Opuntia* sp. plots (Op). Depending on their location, fallow plots are characterized by saltwort *Suæda fruticosa* (Sf) or *Peganum harmala* (Ph). Uncleared but overgrazed land is characterized by *Astragalus* sp. (As). Farmland currently makes up the landscape matrix in the sense of Forman & Godron (1986).

Succulent halophytic lowlands (shl), called *sebchet* in Tunisia (Le Houerou & Le Floc'h 1995), occupy the lowest areas (270–315 m) and are surrounded by farmland (Fig. 3). Two of these border the northern and eastern parts of the town (Garat An Naggada and Garat Al Akrish). In zones adjacent to the town, a pilot control project was undertaken in 1992 by ploughing 3200 ha (Ben-Ismail *et al.* 1997). One-tenth of this area was planted with *Casuarina* sp. A third *sebcha* (Garat An Njila) is located 20 km south of the town. The three *sebchet* are mainly occupied by Chenopodiaceae populations in two distinct associations; one with *Arthrocnemum glaucum* (Ag) and *Halocnemum strobilaceum*, the other with *Salsola tetrandra* (St), *Suæda fruticosa* (Sf), *Atriplex halimus* (Ah) and *Limoniastrum guyonianum* (Lg) (Plombaginaceae). These plant communities represent the most favourable habitats for *Psammomys obesus*. Communities located at the periphery have been inventoried and can act as marginal habitats used by the rodents during periods of high density. These are the halophytic plant formations mentioned above, associated with *Salsola vermiculata*, *Plantago lagopus* (Pl) or *Aristida pungens* (Ap). The shrub stratum is locally represented by *Tamaris africana* (Ta). The floras of Ozenda (1991) and Jafri & Rateeb (1978) were used for plant identification and nomenclature follows these authorities.

At the scale of a plot, structural elements in the landscape, such as artificial dykes and narrow remnant *sebcha* strips, separate fields. In cereal, mainly used for growing hard wheat, stubble fields are used for grazing but they return to fallow land when weather conditions are unsuitable for sowing.

Wet periods were defined by rainfall above 40 mm and more than 6 days of rain during the previous month.

Soil salinity was estimated for 15 stations along transects 1, 3, 4, 5 and 7 in November 1996. Two samples were taken from each station, one between 0 and 20 cm depth, the other between 20 and 40 cm. For six of the plant formations sampled, salinity was estimated by calculating the average of the recorded values (As: 1 station; Or: 1 station; St + Sf + Wh: 1 station; St + Sf: 3 stations; Ag + St + Sf: 4 stations; Ag: 5 stations).

INDEX-BASED SAMPLING METHOD: TRANSECTS

The topographic map published by the Office de Topographie de Tunisie (1993) was used to superimpose Long's (1954) map of the vegetation with the current land-use map. This map was also used to select landmarks used in the transects, such as peaks and roads.

Five transects varying from 3 to 11 km in length (numbers 1–5) were selected. They crossed all the *sebchet* and their immediate surroundings (Fig. 2). During the 2 years of the study (1995–96), the transects were covered twice per year, in spring and autumn. These periods usually coincide with the beginning and the end of the breeding season for *Psammomys obesus* (Amirat, Khammar & Brudieux 1975, 1977; Fichet-Calvet *et al.* 1999a). In the eastern portion of the Garat An Njila *sebcha*, where the rodent's demography and parasitology were studied in detail at the scale of a plot, two further transects were added in 1996 (numbers 6 and 7), each 3 km long. These transects crossed farmland, which forced us to plan fieldwork according to farming schedules (one in January 1996 and another in November 1996).

ESTIMATION OF *P. OBESUS* ABUNDANCE

Following the index-based methods developed for other rodents (Liro 1974; Delattre *et al.* 1990; Giraudoux *et al.* 1995), a semi-quantitative binary code was used to estimate *Psammomys obesus* abundance.

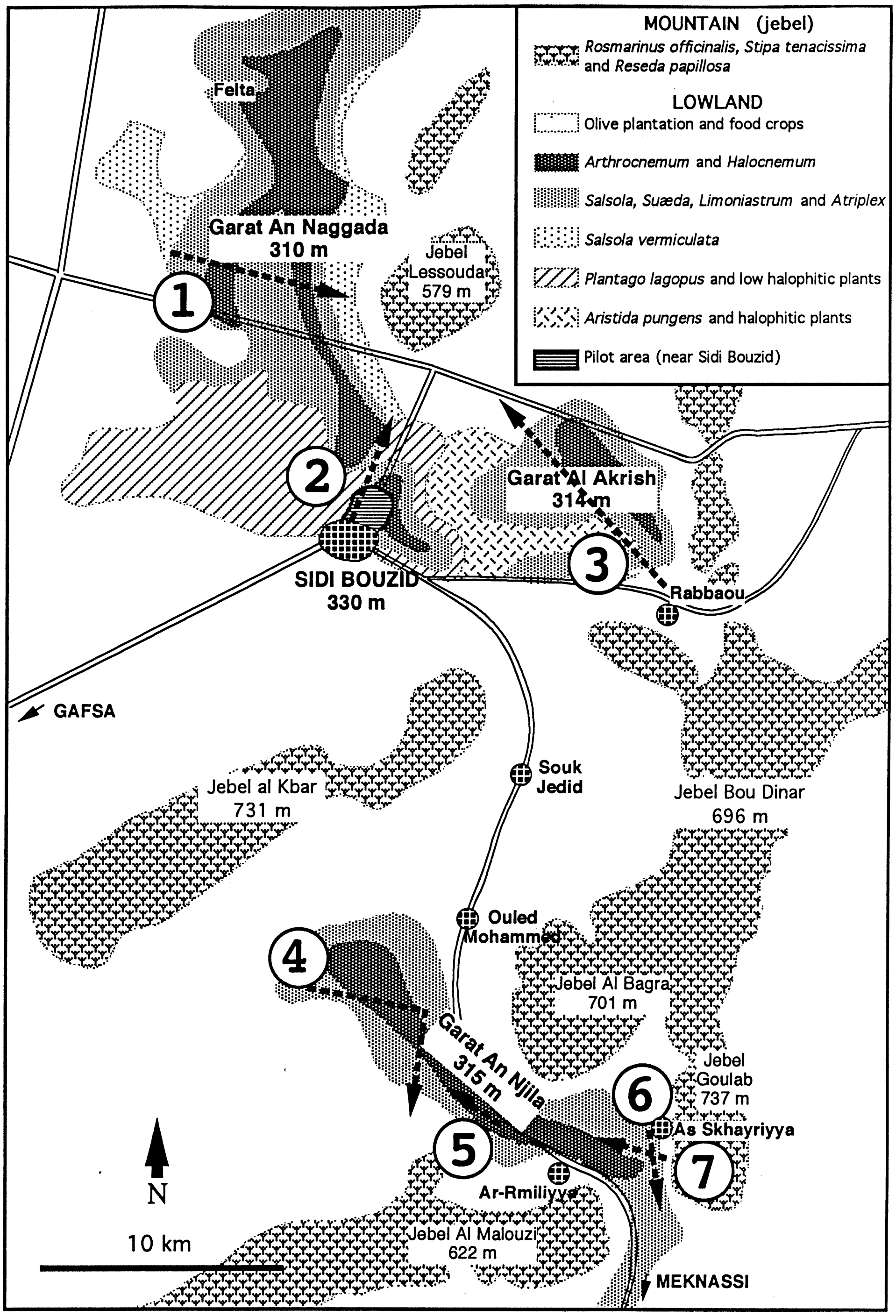

Fig. 2. Landscape description of the study site according to the map of natural vegetation established by Long (1954) between 1950 and 1954. 1–7: location of index-based recordings.

Burrow entrances, which are easily identified for this species due to their flattened aspect, were associated with more discreet indices such as Chenopodiaceae fragments and faeces (Figs 4 and 5). The abundance of these two latter indices are correlated with rodent abundance regardless of weather conditions (Fichet-Calvet *et al.* 1999b).

For data recording, burrow entrances were first counted in each 10-m length of transect and for the average field of view (i.e. a strip 2–4 m wide). Three density classes were defined; class A (0–10 entrances), class B (11–20 entrances) and class C (more than 20 entrances). Secondly, the presence of faeces or Chenopodiaceae fragments, indicating the rodent's presence, was recorded for each interval. The presence of indicators was rated '1' and absence was rated '0', although this latter observation was ambiguous regarding the rodent's presence in the

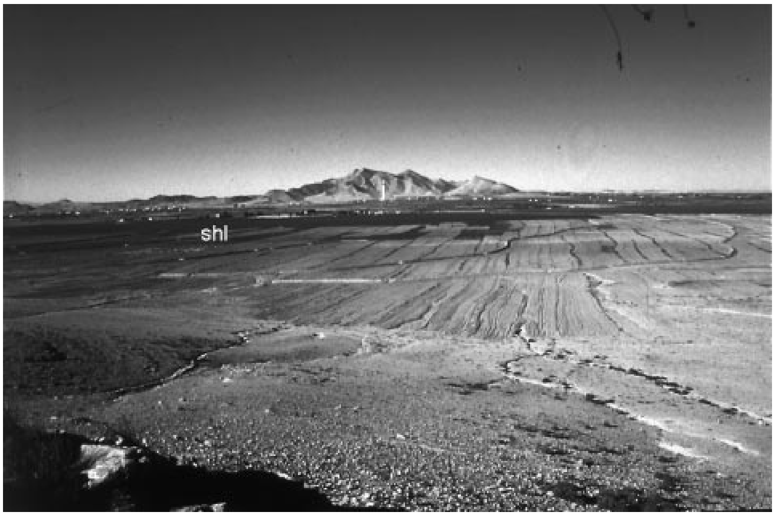

Fig. 3. Landscape around Sidi Bouzid showing jebels (j) and succulent halophytic lowland (shl). In the foreground, the shl was recently ploughed to create new farmland.

Fig. 4. Burrow occupied by *Psammomys obesus* built under *Arthrocnemum glaucum* bushes with several entrances (be) and Chenopodiaceae fragments (cf).

Fig. 5. *Psammomys obesus* on the look out at its burrow entrance. The burrow is built under a *Salsola tetragona* bush.

burrow. A pedometer, calibrated to the observer's stride, was used to measure each distance.

DATA TREATMENT

Variations in the abundance index for *Psammomys obesus* (AI) were assessed on the basis of observations carried out along a 100-m strip (i.e. 10 intervals). Each class (A1 or B1 or C1) was equal to 1. The value of AI thus varied between 0 and 10. Classes A0, B0 and C0, representing uninhabited burrows, were taken into account in studying the spatial distribution of rodent colonies, as they indicated that the species was present at one time. They provided additional information concerning the nature of habitats used occasionally.

Rodent density was thus evaluated in a semi-quantitative manner. Bar graphs illustrate seasonal spatial distribution, whereas between-season and between-year comparisons can also be made in order to examine variations in population abundance.

The MacNemar test was used for the univariate comparison of proportions between transects made in wet or dry period, respectively (Scherrer 1984).

Results

POPULATION ABUNDANCE

The results from the three *sebchet* monitored indicated that the spatial distribution of *Psammomys obesus* was irregular in what appeared, a priori, to be favourable habitat for the species. Indications of population density remained very low during 2 years in the northern area (transects 1, 2 and 3), yet overall the indications suggested that abundance remained high during the same period in the southern area (transects 5, 6 and 7) (Fig. 6).

A few burrows were distributed along transect 1 in formations including *Salsola tetrandra*, *Suæda fruticosa* and *Arthrocnemum glaucum*.

Throughout transect 2, which started in the area of the pilot control project, no occupied burrows were observed in three consecutive recordings, despite the presence of large clumps of *Salsola tetrandra* and *Suæda fruticosa*.

At its origin (Ain Rabbaou spring), transect 3 harboured a small colony of 10–20 individuals (E. Fichet-Calvet, personal observation) that remained stable during the 2 years of the study. This spot was completely enclosed by a small cliff that frequently collapsed, and halophytic plants (*Arthrocnemum glaucum*, *Salsola tetrandra*, *Suæda fruticosa*, *Limoniastrum guyonianum* and *Tamaris africana*) were abundant. The adjacent farmland along the transect never showed any trace of activity during the four recordings. The few foci observed in *Arthrocnemum glaucum* formation in September 1995 in the Garat Al Akrish *sebcha* were apparently the starting points for recolonization during 1996. At the far end of this transect, colonies could regularly be observed in the same formations as along transect 1 (i.e. formations with *Salsola tetrandra* and *Suæda fruticosa*). However, the burrows in monospecific *Arthrocnemum glaucum* formations were also located in a small hollow.

In 1995, in the northern portion of the Garat An Njila *sebcha* (transect 4), there were some small colonies in more peripheral areas with *Arthrocnemum glaucum*, *Salsola tetrandra* and *Suæda fruticosa* (burrows represented at the centre of the bar graph correspond to the portion of the transect forming a right angle). In November 1996, the southern portion of the transect, located close to transect 5, was suddenly colonized. New colonies appeared in a *sebcha* strip located between a small hill covered with *Astragalus* and grasses, and pastures and farmland at the foot of Jebel Malouzi.

All three records obtained along transect 5 indicated the continuous presence of *Psammomys obesus* during the 2 years of observations (abundance index approaching 9 on two occasions). In March 1995, population densities were high in the central portion of the transect (formations with *Arthrocnemum glaucum*). Their spatial distribution was irregular during that period. In March 1996, the distribution was more regular and all formations with *Arthrocnemum glaucum* were colonized and used at that time. In November 1996, the densest populations were located in the south-eastern portion of the transect.

Dense colonies (AI ranging from 5 to 10 over several intervals) were found along transects 6 and 7, located in the south-eastern portion of Garat An Njila at the foot of Jebel Goulab, in formations mainly made up of *Salsola tetrandra* and *Suæda fruticosa*. Between the beginning and the end of 1996, *Psammomys obesus* populations increased greatly throughout this area, and some recently cleared and cultivated land in the southern portion of transect 6 was colonized, as well as formations with *Arthrocnemum glaucum* in the western portion of transect 7.

At the scale of plots, an analysis focusing on the first 2 km of transect 6 allowed us to determine the precise location of *Psammomys obesus* burrows in relation to linear landscape features (Fig. 7). In November 1996, the distribution of rodents was a function of *sebcha* remnants and of their size. In the areas closest to the village of As Skhayriyya, abandoned plots were bordered by narrow *sebcha* strips (1–3 m) and by numerous dykes. Along this portion of the transect, *Psammomys obesus* colonies mainly occupied *sebcha* strips (93%), few dykes (9%) and some fallow land (3%). Along the portion of the transect furthest from the village (1·5–2 km), *sebcha* strips were wider (30–80 m) and were also colonized by *Psammomys obesus* (67%).

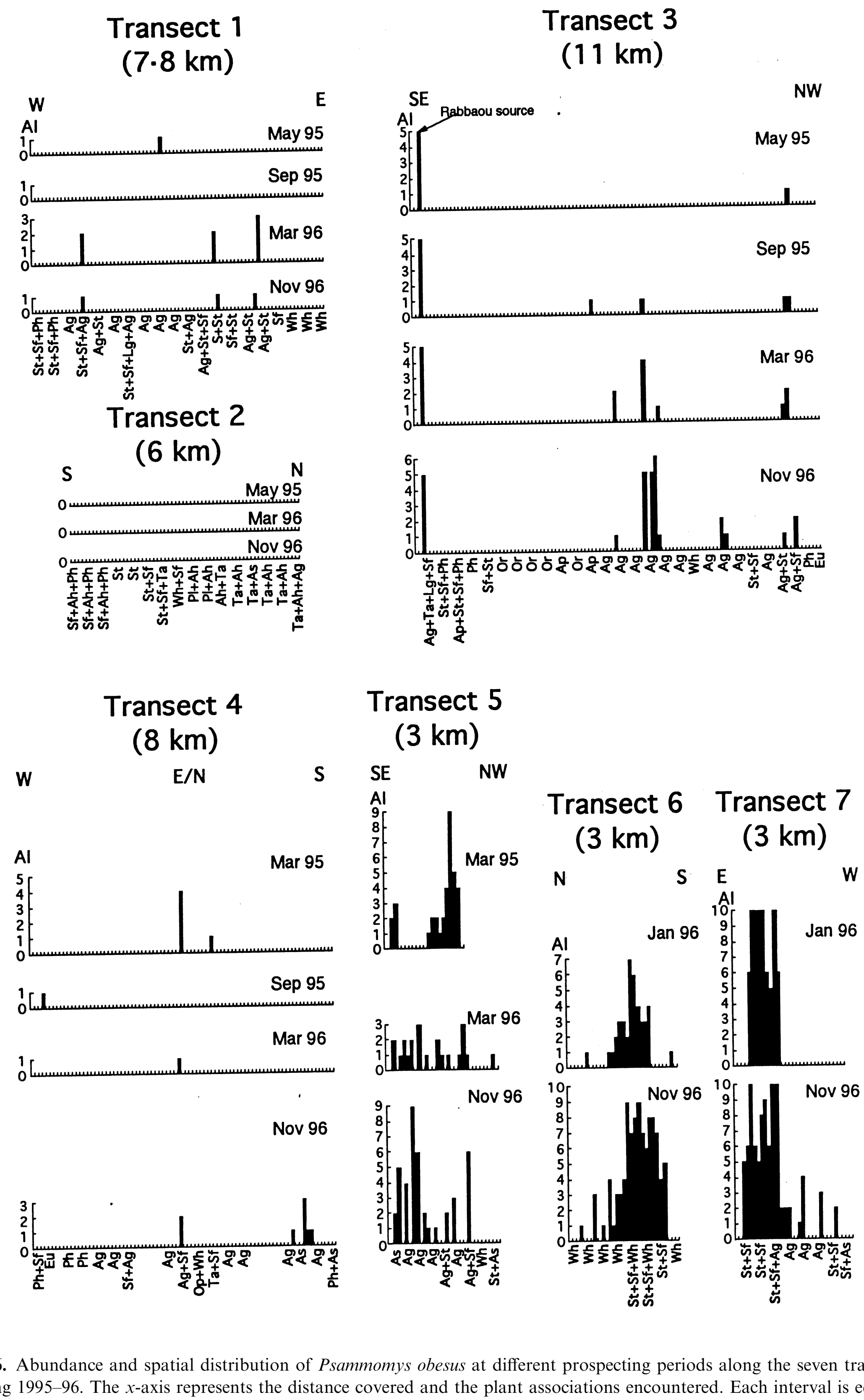

Fig. 6. Abundance and spatial distribution of *Psammomys obesus* at different prospecting periods along the seven transects during 1995–96. The *x*-axis represents the distance covered and the plant associations encountered. Each interval is equivalent to 100 m. The following plant associations were distinguished: Ag, *Arthrocnemum glaucum*; Ap, *Aristida pungens;* Ah, *Atriplex halimus;* As, *Astragalus* sp.; Lg, *Limoniastrum guyonianum*; Op, *Opuntia* sp.; Or, orchards + food crops; Ph, *Peganum harmala*; Pl, *Plantago lagopus*; Sf, *Suæda fruticosa;* St, *Salsola tetrandra*; Ta, *Tamaris africana*; Wh, wheat; Eu, *Eucalyptus* sp. The *y*-axis is AI, the abundance index: number of 10-m intervals with signs of rodent activity in each 100-m interval.

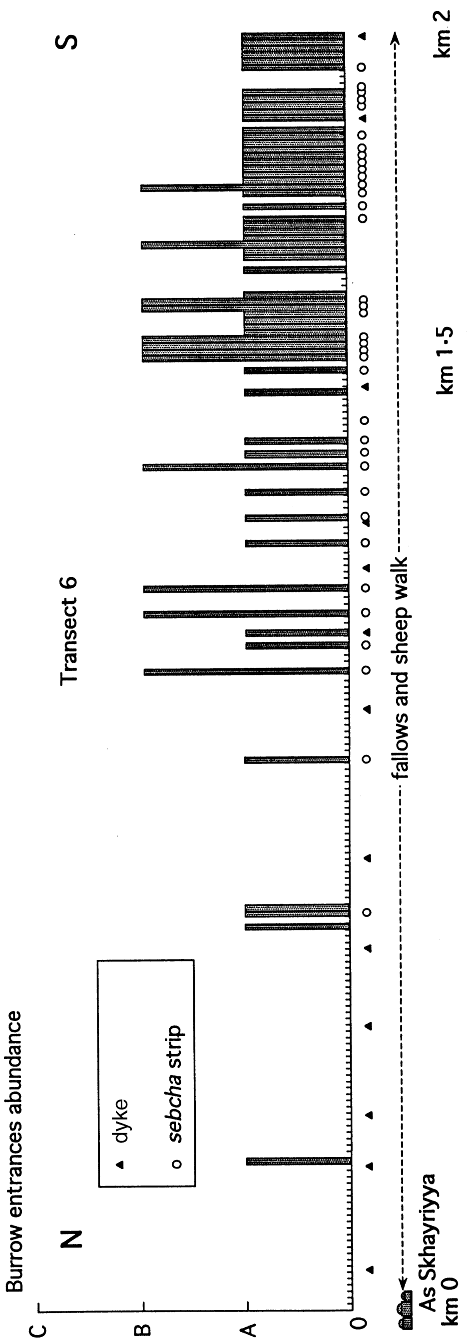

Fig. 7. Spatial distribution of *Psammomys obesus* along the first 2 km of transect 6 starting from the village of As-Skhayriyya (November 1996). On the *y*-axis, A, B, and C represent observations of less than 10, 11–20, and over 20 burrow entrances per interval, respectively. The *x*-axis represents the distance covered; each interval is equivalent to 10 m. Linear landscape features (*sebcha* remnants and dykes) and ground use (fallows and sheep walk) are indicated.

LOCAL EXTINCTION AND RODENT DISPERSAL

The juxtaposition of burrows lacking signs of activity (A0, B0 and C0) with occupied burrows yields information about the mechanisms of local extinction and recolonization (Fig. 8). Burrows that were recorded unoccupied in March 1995 along the southern portion of transect 4 indicated that this sector was densely colonized in 1994 and that local extinction occurred in late 1994 or early 1995. In March 1996, some empty burrows could still be seen. They seemed to have provided sites for recolonization by individuals present there in November 1996. Along the north-western portion of transect 5, closest to the southern portion of transect 4, a progressive movement of *Psammomys obesus* populations could be observed in parallel between March 1995 and November 1996. This movement occurred from east to west. It resulted in the colonization of the north-western portion of this sector and the progressive abandonment of the south-eastern portion. This colonization could be measured by a space-use rate (SUR) and mean abundance indices (MAI) varying between periods in the different sectors. In March 1995, SUR and MAI were four times higher in the north-west area than in the south-east area. They were almost equal in March 1996. In November 1996, they became three times higher in the south-east area than in the north-west area.

DISTRIBUTION OF RODENTS IN RELATION TO PLANT ASSOCIATIONS

In order to determine the plant associations most favourable to the arrival and maintenance of *Psammomys obesus* populations, the proportion of positive intervals (= 100 m intervals occupied by rodents) was calculated for each association during the wet period and the dry period separately (Table 1).

Globally, the spatial distribution of rodents closely fits the distribution of Chenopodiaceae formations (made up of three types of plants: *Salsola tetrandra*, *Suæda fruticosa* and *Arthrocnemum glaucum*) and the salinity gradient, regardless of the climatic period considered.

The *sebcha* area, recently cultivated and having slightly salty soils (mixed area), was colonized densely by the rodent (SUR ranging from 43% to 63%). In this area, narrow strips of formations with *Salsola tetrandra* and *Suæda fruticosa* are associated with plots of hard wheat or stubble fields. In natural wetlands with salty or very salty soils (23–35 g l^{-1}), rodents were less abundant (SUR ranging from 7% to 20%). The most favourable habitat during this period appears to have been the association made up of the three Chenopodiaceae, rather than bispeci-

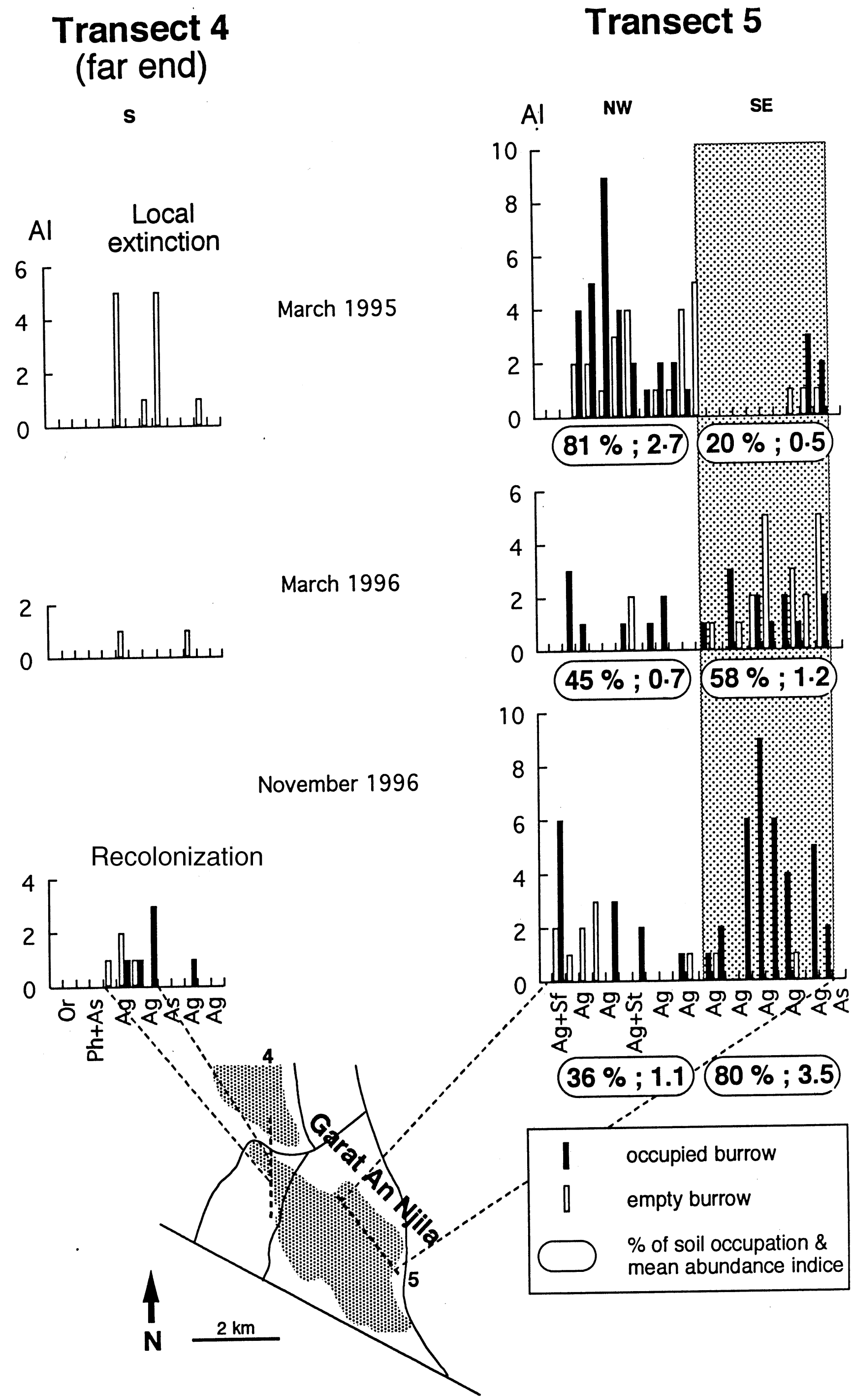

Fig. 8. Variations in the spatial distribution of occupied and unoccupied *Psammomys obesus* burrows in the central portion of the Garat An Njila *sebcha* (transects 4 and 5; March 1995 to November 1996). The *y*-axis represents the abundance index for *P. obesus*. The *x*-axis represents the distances covered and the plant associations encountered. Each interval is equivalent to 100 m. The following plant associations were distinguished: Ag, *Arthrocnemum glaucum*; As, *Astragalus* sp.; Or, orchards + food crops; Ph, *Peganum harmala*; Sf, *Suæda fruticosa;* St, *Salsola tetrandra*.

fic (with *Salsola tetrandra* and *Suæda fruticosa*) or monospecific formations (with *Arthrocnemum glaucum*).

The spatial distribution of rodents also varied according to the climatic period considered. A comparison between space-use rates during wet and dry periods particularly revealed an increase in this rate during the dry period in the mixed area and in the natural wetland occupied by *Arthrocnemum glaucum* (46% and 80%, respectively). In this last case, the difference was highly significant ($\chi2$ MacNemar = 6·26, $P = 0{\cdot}05$).

Table 1. Distribution of occupied *Psammomys obesus* burrows according to plant association encountered, climatic period (wet or dry period) and soil salinity. The following plant associations were distinguished: Ag, *Arthrocnemum glaucum*; Ap, *Aristida pungens*; As, *Astragalus* sp.; Or, orchards+food crops+*Opuntia* sp.; Ph, *Peganum harmala*; Pl, *Plantago lagopus*; Sf, *Suæda fruticosa*; St, *Salsola tetrandra*; Wh, wheat. %=number of 100-m intervals where *P. obesus* is present divided by the number of intervals crossed in the relevant plant formation ×100; km, numbers of kilometres covered

		Natural dry zones		Farmland				Mixed zone	Natural wetlands		
As	Ap	Or	Ph	Pl	Wh	St/Sf/Wh	St/Sf	Ag/St/Sf	Ag		
Wet period	%	0	0	0	0	0	1·8	43·3	6·7	19·8	6·9
	km	1·2	1·8	4·8	3·0	2·8	5·7	3·0	12·0	8·1	21·7
Dry period	%	0	0	0	0	0	0	63·3	6·9	17·3	12·4
	km	1·2	1·8	5·8	3·0	5·6	6·2	3·0	14·5	8·1	21·7
Salinity in g l^{-1}		2		6				12	23	27	35

Discussion

SPATIO-TEMPORAL EVOLUTION

Globally, the studies carried out in 1995 and 1996 show that *Psammomys obesus* populations were undergoing a low density phase in the northern part of Sidi Bouzid (Garat An Naggada and Garat Al Akrish *sebchet*) and a high density phase in the south (Garat An Njila *sebcha*). Thus, two different types of population dynamics proceeded in parallel in our study area, at a distance of a few kilometres. They could be just random variations but the fact that our study site is structured in two drainage basins, each subject to specific flooding regimes, could explain these differences in the population dynamics. The northern part of our study area is influenced by a drainage basin supplied by the El Fekka and Zerroud wadis, whereas the southern area belongs to the Oum At Teboul wadi drainage basin (Daoud & Trautmann 1994; A. Daoud, personal communication). The El Fekka wadi frequently causes spectacular floods in the Sidi Bouzid lowland. This happened in the autumn/winter of 1969, 1983, 1988, 1989 and 1990. In various portions of Garat An Naggada (in Felta and in the pilot control project area in particular) accounts given by health personnel mention high abundances of *Psammomys obesus* during 1984–86 and 1991 (R. Ben-Ismail & H. Helal, unpublished data). These two periods followed the 1983 floods in the first case, and the series of floods in 1988, 1989 and 1990 in the second case. Conversely, near total disappearance of *Psammomys obesus* was observed in 1985 and 1992; that is 2 and 3 years following the previous floods, respectively. A division into geographical surveillance units, based on the drainage basin model combined with a knowledge of flooding regimes and water levels, could thus provide an efficient surveillance system for *Psammomys obesus* abundances. In the southern part of our study (transect 5, 6 and 7), *Psammomys obesus* populations respond annually to rainfall lasting their reproduction period from September to May (Fichet-Calvet *et al.* 1999a). In the northern part (transects 1, 2 and 3), they probably need several years of high rainfall without flooding to restore high abundance, as Brown & Singleton (1999) suggested for house mouse *Mus musculus* in Australia.

Knowledge of the topography of the sites and of the infrastructures for water management could also help to determine the environments in which *Psammomys obesus* colonies initially develop (source areas), whereas knowledge of the spatial distribution of plant formations would yield indications as to how the rodent populations will disperse from these source habitats.

The locations of the foci detected in 1996 at the foot of Jebel Goulab could be explained by the slope of the mountain bordering the Garat An Njila *sebcha*. Indeed, it favours the collection of run-off water and supplies the lowland below without causing lasting floods, thus preventing rodents from drowning or being forced to disperse. The scarcity of colonies in the western portion of the *sebcha* (transect 4) during this period can be explained by the duration of the floods in this very flat area of the *sebcha*, mentioned on topographic maps as areas liable to flooding.

Proximity of the village (As-Skhayriyya) seems unfavourable to the development of *Psammomys obesus* colonies, as illustrated by the results for transect 6. A possible hypothesis is that rodent populations here are controlled by the absence of refugia such as *sebcha* strips. Indeed, at the scale of a plot the landscape structure differs from that observed 1·5 km further where *sebcha* strips are numerous and wide. Recently constructed dykes destined to retain run-off water do not favour the maintenance of rodent colonies during dry periods. A second hypothesis, complementary to the first, suggests that the omnipresent dogs in this area (E. Fichet-Calvet, personal observation) could regulate rodent populations. A ‘village effect’, comparable to the effect of domestic cats on the common vole *Microtus arvalis* in France (Delattre *et al.* 1996), could thus reflect rodent population regulation by predation. Human impact on the environment does not, however, necessarily act as a factor limiting populations, as illustrated by the presence of active burrows in areas used daily by herds of grazing sheep, despite the regular presence of humans and dogs guarding the herds.

In arid zones such as Sidi Bouzid (260 mm average annual precipitation), burrow entrances remain visible for a long time, and thus can be used to assess past abundance of *Psammomys obesus* populations at a regional or sector scale. Data from all transects show that *Psammomys obesus* is confined within the *sebchet* and never ventures into food crop areas or sandy–silty areas occupied by *Astragalus* and *Peganum harmala*. This confirms the dependence of this species on halophytic plants, as previously shown by Petter (1961) and Daly & Daly (1973) in Algeria, and by Zaime & Pascal (1989) in Morocco. The rodent seems to prefer habitats in which all three of the main halophytic species of this part of Tunisia occur together, that is *Arthrocnemum glaucum*, *Salsola tetrandra* and *Suæda fruticosa*. This association occurs mainly in the most peripheral parts of the *sebchet* and is exploited by the rodents until food resources gradually diminish (Daly & Daly 1975). The exploitation of less favourable plant formations then proceeds as the dry period progresses.

RODENT ABUNDANCE AND ZCL INCIDENCE

It is often difficult to establish correlations formally between rodent abundance and the incidence of cutaneous leishmaniasis. Indeed, the incidence of ZCL is a valid indicator of transmission rate only at the outset of an epidemic (during the first year) and for a focus previously unaffected. The immunizing effect of ZCL produces a reduction in the number of cases (except for newborn children) as a focus becomes established, even if the intensity of transmission remains high from one season to another. One method, recommended by Lysenko & Beljaev (1987), is to measure the incidence of the disease in susceptible individuals only. One such study, by Mbarki *et al*. (1995) in the Felta focus (northern part of the study area, period 1983–92), suggested a correlation between *Psammomys obesus* density and the incidence of the disease.

Nevertheless, the study should be monitored at the rodent community level to understand the global dynamics of the parasite. Thus, the role of *Meriones shawi* and *Meriones lybicus* as propagators of the disease (Ben-Ismail & Ben Rachid 1989) needs more investigation using both an index-based sampling method and a longitudinal survey of the parasite in their populations.

Conclusion

As emphasized by Rioux, Dereure & Périères (1990), searching for indicators is one of the central components of feasibility studies for control projects. Applying index-based methods, associated with the monitoring of variations in vector population densities and infection rates during transmission seasons, would show any correlations between rodent abundance, vector abundance and transmission of *Leishmania major* to humans. Index-based kilometric recordings (transects) have proven to be successful in monitoring fluctuations in abundances of *Psammomys obesus*. Indices used (burrows, food remains and faeces) are easy to identify and data collection is economical in time and means; 2–3 h of observation, repeated at 6-monthly intervals, are sufficient to reveal population increases or declines and spatial distribution over wide areas. When flooding periods are taken into account, these regular observations can be very effective in determining the temporal component of epidemiological risk.

The spatial mapping of the colonies and the description of their environment is facilitated by the use of the transects. Indeed, this method yields information about the location of source areas (types of plant formations) and about refugia for rodents (dykes in areas liable to flooding, natural microreliefs) and provides a better understanding of how outbreaks spread at different spatial scales. When these spatial data are plotted on maps simultaneously describing plant formations representing optimal habitat for *Psammomys obesus* (formations with *Arthrocnemum glaucum*, *Salsola tetrandra* and *Suæda fruticosa*), local topography, meteorology and the main hydrological structures, the spatial component of epidemiological risk can be assessed.

This method can easily be used in different areas subject to *Psammomys obesus* outbreaks associated with epidemics of cutaneous leishmaniasis. Once the areas and the periods of risk are identified, targeted operations such as ploughing of refugia or cutting of Chenopodiaceae in the vicinity of areas at risk can be recommended in order to limit epidemiological risk.

Acknowledgements

This study forms part of a project on the ecological interaction between *Psammomys obesus* and cutaneous leishmaniasis, funded by the Avicenne Programme of the European Commission, AVI CT92/0018. The Laboratoire d'Epidémiologie et d'Ecologie Parasitaire was also financed for this work by the UNDP/World Bank/WHO Special Programme for Research and Training in Tropical Diseases (TDR-RSG Grant ID: 890266) and IDRC, Canada (Project 92-0233).

Thanks are due to E. Le Floc'h and C. Gabrion for their useful comments, to J. Mathez, P. Grillas for their contribution to the identification of some plant specimens, to A. Daoud and J. Trautmann for providing information on the typology of drainage basins and their flooding regimes, and to B. Hamdi for carrying out the salinity estimates. We are grateful to an anonymous referee for the constructive comments on the manuscript. This is a contribution of the Institute of Evolution of Montpellier (No. 00.029).

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Received 18 September 1998; revision received 23 February 2000