LANDSCAPE EFFECTS ON THE POPULATION DYNAMICS OF SMALL MAMMAL COMMUNITIES: A PRELIMINARY ANALYSIS OF PREY-RESOURCE VARIATIONS

F. Raoul[1], R. Defaut[2], D. Michelat[1,3], M. Montadert[1,3],
D. Pépin[4], J.P. Quéré[5], B. Tissot[4], P. Delattre[5], P. Giraudoux[1]

RÉSUMÉ

L'objectif de cette étude est d'estimer l'effet de la composition du paysage sur les variations de disponibilité en biomasse de micro-mammifères pour les prédateurs, à l'échelle sectorielle ($n \times 1$ km^2). Quatre sites d'étude représentatifs d'un gradient d'intensification agricole ont été choisis dans l'est de la France en fonction de la composition du paysage.

Les fluctuations de biomasses de *Microtus arvalis* et *Arvicola terrestris* (espèces prairiales), de *Clethrionomys glareolus* et *Apodemus* sp. (espèces de milieux fermés) ont été suivies de 1992 à 1996 par méthodes indiciaires et piégeage. Les synchronies entre les populations de *M. arvalis* et celles de rongeurs de milieux fermés ont été recherchées.

Les fluctuations de biomasse de *M. arvalis* et *A. terrestris* sont stables dans les sites où la proportion de prairie permanente est la plus faible. Les populations de *M. arvalis* présentent les plus larges amplitudes de variation de biomasse et les déclins les plus prononcés dans les sites où la proportion de prairie permanente sur la surface agricole est supérieure à 50 %. Les populations d'*A. terrestris* ne sont instables que dans un site, là où la proportion de prairie permanente sur surface agricole est supérieure à 85 %. Les déclins de populations de rongeurs de milieux fermés (*Clethrionomys glareolus* et *Apodemus* sp.) sont concomitants de ceux de *M. arvalis* dans les sites à fortes variations de biomasse de cette dernière espèce.

Ces résultats suggèrent deux types de fonctionnement, en terme de variation de disponibilité en proies pour les prédateurs : (i) stable dans les paysages à faible proportion de prairie permanente, et (ii) instable, avec des déclins prononcés et rapides des populations d'espèces prairiales, entraînant des déclins synchrones du peuplement de micro-mammifères étudié, dans les paysages à forte proportion de prairie permanente.

Aucune synchronie dans les dynamiques de population de ces micro-mammifères n'est observée entre les sites d'étude, éloignés de quelques dizaines de kilomètres seulement.

SUMMARY

This study aims at estimating the effect of landscape composition on the availability of small mammal preys (in terms of biomass) to predators on a sectorial scale ($n \times 1$ km^2). Four study sites, representative of different stages of agriculture intensification, were selected in eastern France according to landscape composition.

[1] Laboratoire de Biologie et Écophysiologie, EA3184 MRT, UC INRA, Université de Franche-Comté, 25030 Besançon Cedex, France. E-mail: francis.raoul@univ-fcomte.fr; fax: +33(0)381 665 797.

[2] FRDEC-DRAF-SRPV, 191 rue de Belfort, 25043 Besançon Cedex, France.

[3] GNFC, 3 rue Beauregard 25000 Besançon, France.

[4] Maison de la Réserve 25160 Labergement-Sainte-Marie, France.

[5] Campus International du Baillarguet, CBGP-Equipe "Biologie et Gestion des Pullulations", CS30016 Montferrier-sur-lez, 34988 Saint-Gély-du-Fesc Cedex, France.

The population dynamics of *Microtus arvalis*, *Arvicola terrestris*, *Clethrionomys glareolus* and *Apodemus* sp. were monitored from 1992 to 1996 by using index methods and trapping.

M. arvalis and *A. terrestris* population biomasses were stable in landscapes with low percentage of permanent grassland. *M. arvalis* populations displayed greater biomass variations with sharp declines in the sites where the proportion of permanent grassland to farmland was greater than 50 %. *A. terrestris* populations were very unstable in one study site where the proportion of permanent grassland to farmland was greater than 85 %. Synchronic patterns between *M. arvalis* populations and the populations of hedgerow rodents were suspected at sites with large fluctuations of *M. arvalis*: every decline of the populations of hedgerow rodents was concomitant with the *M. arvalis* decline.

These results suggest that two kinds of ecological systems in terms of prey-resource variations for mammalian predators can be distinguished: (i) stable in landscapes with lower proportion of permanent grassland, and (ii) unstable, with grassland species crashes and synchronous declines of the rodent community, in landscapes with higher proportion of permanent grassland.

Moreover, the population dynamics of small mammals were asynchronous between the four sites situated at relatively short distance (some tens kilometres).

INTRODUCTION

Organisms are sensitive to spatial array of their optimal habitat within a landscape (Gorman & Reynolds, 1993; Lidicker, 1994; Lidicker, 1995; Sanchez-Zapata & Calvo, 1999). One aspect of these landscape influences is their impact on the population dynamics of small mammal species. In Eastern France, empirical data support the importance of landscape composition on population dynamics of two grassland arvicolid species, *Microtus arvalis* and *Arvicola terrestris*. At regional scale, large outbreaks occur where the proportion of permanent grassland exceeds 50 % or 85 % of farmland for *M. arvalis* and *A. terrestris* respectively (Delattre *et al.*, 1988; Delattre *et al.*, 1992; Delattre *et al.*, 1996; Giraudoux *et al.*, 1997). At local scale, Oksanen *et al.* (1999) have shown that the amplitude of fluctuations of microtines in a Fennoscandia tundra is higher when habitat is dominated by highly productive habitat.

Predation can interfere with the rodent population dynamics *via* landscape structure (for review, see Korpimaki & Krebs, 1996). Predator communities are more diverse in heterogeneous landscapes (Ryszkowski, 1982) and are dominated by generalist predators (*e.g.* Fox, *Vulpes vulpes*, Stone marten, *Martes foina*). Andersson & Erlinge (1977) have postulated that in such systems, rodents densities are low and the amplitude of population variations are small. By contrast, homogeneous landscapes are dominated by resident specialist predators (*e.g.* Stoat, *Mustela erminea*, Weasel, *Mustela nivalis*). Such predator communities are assumed to destabilize rodent populations: they frequently reach high densities and sustain large variations in population densities. Moreover, synchronous fluctuations for similar-sized small mammals are often recorded in such system (Hornfeldt, 1994; Korpimäki, 1986; Linden, 1988; Oksanen & Henttonen, 1996; Pruitt, 1969; Shanker & Sukumar, 1999). This synchrony is generally attributed to predation switches by predators during the decline phase of the numerically dominant prey species (*e.g.* Andersson & Erlinge, 1977; Norrdahl, 1995). Giraudoux *et al.* (1994) have shown that in a landscape of mid-altitude mountain, in Franche-Comté, France, where virtually all farmland is grassland, high density phases (Krebs & Myers, 1974) of *Microtus arvalis* occured. During those phases the density of this species reached hundreds of animal per ha (a biomass exceeding

10 kg/ha). In hedges, the populations of rodents (the bank vole, *Clethrionomys glareolus*, and the yellow-necked mouse, *Apodemus flavicollis*) remained relatively stable, and never exceeded 0.1-0.2 kg/ha. However, the population decline of *C. glareolus* and *Apodemus flavicollis* was synchronous with the decline of *M. arvalis*. Those results suggest that landscape composition and structure could determine not only the population dynamics patterns of grassland rodents, but also, the dynamics of the whole rodent community. In short, landscape composition and structure determine both the diversity of predator communities and the variations in prey-resource abundance.

Small mammals are vectors or hosts of many pathogens impacting public health (*e.g.* haemorragic fever viruses, leishmanioses, alveolar echinococcosis). Differences in biomass fluctuations of small mammal species in the community of hosts may therefore play an important role in transmission dynamics (Combes, 1995; Gratz, 1994) and influence the risks of transmission to humans (see for instance Giraudoux *et al.*, 1996; Viel *et al.*, 1998).

Few studies, to our knowledge, have addressed the question of the influence of landscape on the population dynamics of rodent communities (Oksanen *et al.*, 1999), especially focusing on prey-resource availability for predators. Those landscape—prey-resources interactions may however be important in the population dynamics of two-hosts-life cycle parasites (the more food is consumed, the higher the probability of parasite recruitment, Esch & Fernandez, 1993). It is therefore important to document the relationships between landscape composition and the variations in rodent biomass available for predators.

Current research generally emphasizes at local scale on detailed capture-recapture studies of small rodents within fairly limited patches (1 to a few hectares; Heinsohn & Heinsohn, 1999; Kozakiewicz *et al.*, 1999; Lima *et al.*, 1999), based on sophisticated demographic models (Batzli, 1999; Saitoh *et al.*, 1998). Factors governing large-scale and long-term variations in average density and magnitudes of fluctuations should however take care of specific sampling methods in landscapes or regions with different dynamics. It is quite evident that it is impossible to apply the same methods at these very different scales. Index methods, calibrated against more exact density estimates, are usually employed at the large scale (Delattre *et al.*, 1999; Delattre *et al.*, 1996; Delattre *et al.*, 1990; Fichet-Calvet *et al.*, 1999; Giraudoux *et al.*, 1997; Giraudoux *et al.*, 1995; Hansson, 1979; Quéré *et al.*, 2000).

The aim of this study is to establish a baseline to compare the dynamic patterns of rodent communities in four agricultural landscapes, and to assess the main features of prey-resources variations in term of biomass availability. Two parameters were studied, based on trapping and index methods: (i) the fluctuations of population biomass, and (ii) the synchrony between populations.

MATERIAL & METHODS

STUDY SITES

Four study sites were selected in Franche-Comté (47.11°N, 6.24°E, Fig. 1) according to landscape composition. Land use was studied on the basis of data

from the 1988 General Agriculture Census (RGA) and the National Forest Census, both from the Ministry of Agriculture. Each site was representative of a stage of agriculture intensification along an altitude gradient.

Figure 1. — Location of the study sites in eastern France.

— Chemin: farmland comprised 75 % of total land, and dominated by cultivated areas (ploughed fields). Grassland (17 % of total surface, 22 % of farmland) was limited to some meadows/pastures, field margins and road sides. Virtually no hedgerow networks (0.3%) were present.

— Mouthe: farmland comprised 22 % of total land, and permanent grassland 22 % of total land (100 % of farmland). Forest was the dominating feature of the landscape, covering 57 % of total land, and grassland was mainly open areas. The hedgerow network area accounted for 2.3 %.

— Sancey: farmland comprised 55 %, and permanent grassland 33 % of total land (68 % of farmland). Grassland was featured by highly connective hedgerow network (2.9 %).

— Le Souillot: farmland comprised 57 % of total land, and permanent grassland 51 % of total land (89 % of farmland). The area of the hedgerow network was 3 %. The area of optimal habitat for grassland rodents was here the largest in this study.

To sum up, high risk of *M. arvalis* outbreaks was likely at Sancey (proportion of permanent grassland to farmland between 50 % and 85 %), whereas the risk was high for both *M. arvalis* and *A. terrestris* at Le Souillot (proportion of permanent grassland to farmland higher than 85 %).

RODENT SAMPLING

The sampling of rodents was undertaken in farmland only, which excluded large forests. Giraudoux (1991) has shown that the density of rodents is generally low and stable in those forests and that consequently, foxes (*Vulpes vulpes*), for

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instance, forage mainly in open habitats (85 % of their faeces, taken as an index of their activity are deposited in farmland). Snow tracking in winter confirms this activity pattern.

Three sampling methods were used to estimate the biomass of rodent populations:

Grassland rodents

Microtus arvalis was sampled by using an index method, based on surface indices (Delattre *et al.*, 1990). It consisted of transects of 5.3 to 9.4 km walked in spring and autumn. Along each transect the presence-absence of vole droppings within every ten paces was noted. The abundance index was the ratio of positive intervals to the total number of intervals. This index is well correlated to an ordinal scale of densities using specific coefficients (Delattre *et al.*, 1990; Quéré *et al.*, 2000).

An index method for assessing relative densities of *A. terrestris* has been developped (Giraudoux *et al.*, 1995) based on a relation between the number of *A. terrestris* tumulus in intervals and the number of individuals captured by standard trapping. This method has been used in earlier studies to monitor travelling waves and long term changes in *A. terrestris* populations (Giraudoux *et al.*, 1997), and is still used by the Regional Crop Protection Service for outbreak prevention and control, though only three classes of densities can be statistically recognized. Every autumn, every commune (French administrative division) of the study sites was visited and *A. terrestris* colonies were recorded according to the following categories: 0: no detectable sign of presence, 1: some isolated colonies, 2: colonies present in many pastures or meadows, 3: very numerous colonies and serious damage to grassland (Giraudoux *et al.*, 1997; Giraudoux *et al.*, 1995). The average score of each commune of a site was computed. For comparative purposes, density was estimated from this score according to categories proposed in Giraudoux *et al.* (1995). They correspond to statistically different density classes: 1: 50 ind/ha, 2: 150 ind/ha, and 3: 400 ind/ha, and give the order of magnitude of density only.

Hedgerow rodents

Hedgerow rodents were sampled by using 5-18 standard INRA trap lines. Each line was set in the beginning of spring (March-April) and in autumn (October). For a given season the positions of the trap lines were identical from year to year. Trap line position was changed from one season to another to avoid overtrapping. At Le Souillot rodents were collected after every night for three consecutive nights (34 traps × 3 nights = 102 trap.night) and after one night only at Chemin, Sancey and Mouthe, for logistical reasons. In order to compare sites, a regression of the number of rodent trapped after one night was computed against the total number of rodent trapped after three nights based on the data collected at Le Souillot. The regression equation was then used to correct the number of rodents trapped at the other sites. Then, the average number of rodents trapped by line was weighed by specific corrective factors which integrate species movements (2 and 5 for *Apodemus* sp. and *C. glareolus*, respectively, see Spitz *et al.* (1974)). The scores of both *Apodemus* sp. and *Clethrionomys glareolus* were pooled to compute the overall density of hedgerow rodents.

Our aim was to estimate the biomass of each sampled rodent population in the whole site (grams of individuals per "hectare of landscape") in order to estimate the general distribution of small mammal biomasses available for predators in non-forested habitats. Therefore, density scores for each species were weighed by (i) the ratio of their specific habitat in a landscape, and (ii) the average weight of each species: 80 g. for *A. terrestris*, 15 g. for *M. arvalis*, 15 g. for *C. glareolus*, and 20 g. for *Apodemus* sp.

DATA ANALYSIS

The Wilcoxon-Mann-Whitney U test was used to compare the average biomass of populations between 2 sites. Differences in average rank among more than 2 sites were tested by using the Kruskal-Wallis statistics, possibly followed by a comparison between average ranks (Siegel & Castellan, 1988).

Biomass variations were characterized by their amplitude (maximum score-minimum score).

Spearman's rank correlation was used to measure synchrony between population biomass variations (Siegel & Castellan, 1988). Only autumn data were considered in order to avoid correlation due to seasonal variations in population biomasses.

RESULTS

POPULATION BIOMASS

Table I shows the average biomass of *M. arvalis, A. terrestris* and hedgerow rodents (*Apodemus* sp. and *C. glareolus*), and the amplitude of population variations (maximum index - minimum index) at the four study sites.

AVERAGE BIOMASSES

Differences in *M. arvalis* average biomasses among sites were statistically significant (H = 13.62, p = 0.001). The score at Sancey was higher than at Chemin

TABLE I

Average biomass index and amplitude of biomass of each rodent species population at the four study sites from 1992 to 1996 (: autumn data only).*

	M. arvalis		A. terrestris (*)		Hedgerow rodents	
	average biomass	amplitude	average biomass	amplitude	average biomass	amplitude
Chemin	119	212	0	—	2	4
Mouthe	0	—	1 487	4 347	9	17
Sancey	680	1 309	2 406	6 045	13	30
Le Souillot	283	1 334	8 493	15 259	18	49

(comparison of average ranks, p < 0.05). The average biomass at Le Souillot was not statistically different from Chemin for this species though punctually much larger biomasses were recorded at Le Souillot in 1992-1993 and 1996 in comparison to Chemin.

No statistical differences in *A. terrestris* average biomasses were recorded.

The average biomass of *M. arvalis* recorded in autumn at Le Souillot was 19 times lower than of *A. terrestris* (U = 1, p = 0.008). This highlighted a clear dominance of the latter species in term of biomass. This was also the case at Sancey (U = 5, p = 0.021), but differences were not as large (twice higher).

The average biomass of hedgerow rodents was lower than for *M. arvalis* at Chemin and Sancey, not statistically different at Le Souillot, despite a score 16 times higher for *M. arvalis* at the latter. It was lower than for *A. terrestris* at Sancey and Le Souillot (U = 0, p = 0.001), and not different at Mouthe.

AMPLITUDE OF VARIATIONS

Figure 2 shows the variations of *M. arvalis* and *A. terrestris* population biomass at the four study sites. The time span of the study did not permit any consistent statistical analysis. One can however observe the followings:

The amplitudes of *M. arvalis* biomass variations at Sancey and Le Souillot were similar, and both 6 times higher than at Chemin. Higher biomasses occurred three times at Sancey (autumn 93 and from autumn 95 to autumn 96), and once only at Le Souillot (autumn 93). *M. arvalis* populations were virtually extinct at Le Souillot from autumn 94 to autumn 95.

Arvicola terrestris underwent the higher biomass variations at Le Souillot (amplitude about three times higher than at Mouthe and Sancey). At Le Souillot, lower biomasses of *A. terrestris* were recorded when the population of *M. arvalis* was extinct.

SYNCHRONY BETWEEN POPULATIONS

A statistically significant correlation between the population of *M. arvalis* and the populations of hedgerow rodents was recorded at Sancey only ($r_s = 0.771$, p = 0.05).

Moreover, figure 3 shows that the three important declines that occurred in the *M. arvalis* population during the study period (from autumn 1993 to autumn 1994 and from autumn 1996 to autumn 1997 at Sancey; from autumn 1993 to autumn 1994 at Le Souillot) were all concomitant with a decline in the populations of hedgerow rodents.

DISCUSSION

Landscape effects on rodent populations have been studied from the point of view of species richness or community composition (Canova & Fasola, 1991; Giraudoux *et al.*, 1998; Stanko, 1994), or of mean densities of a focal species according to the size and quality of habitat (Adamczewska-Andrejewska *et al.*, 1979; Canova *et al.*, 1994; Dooley & Bowers, 1996; Fernandez *et al.*, 1996;
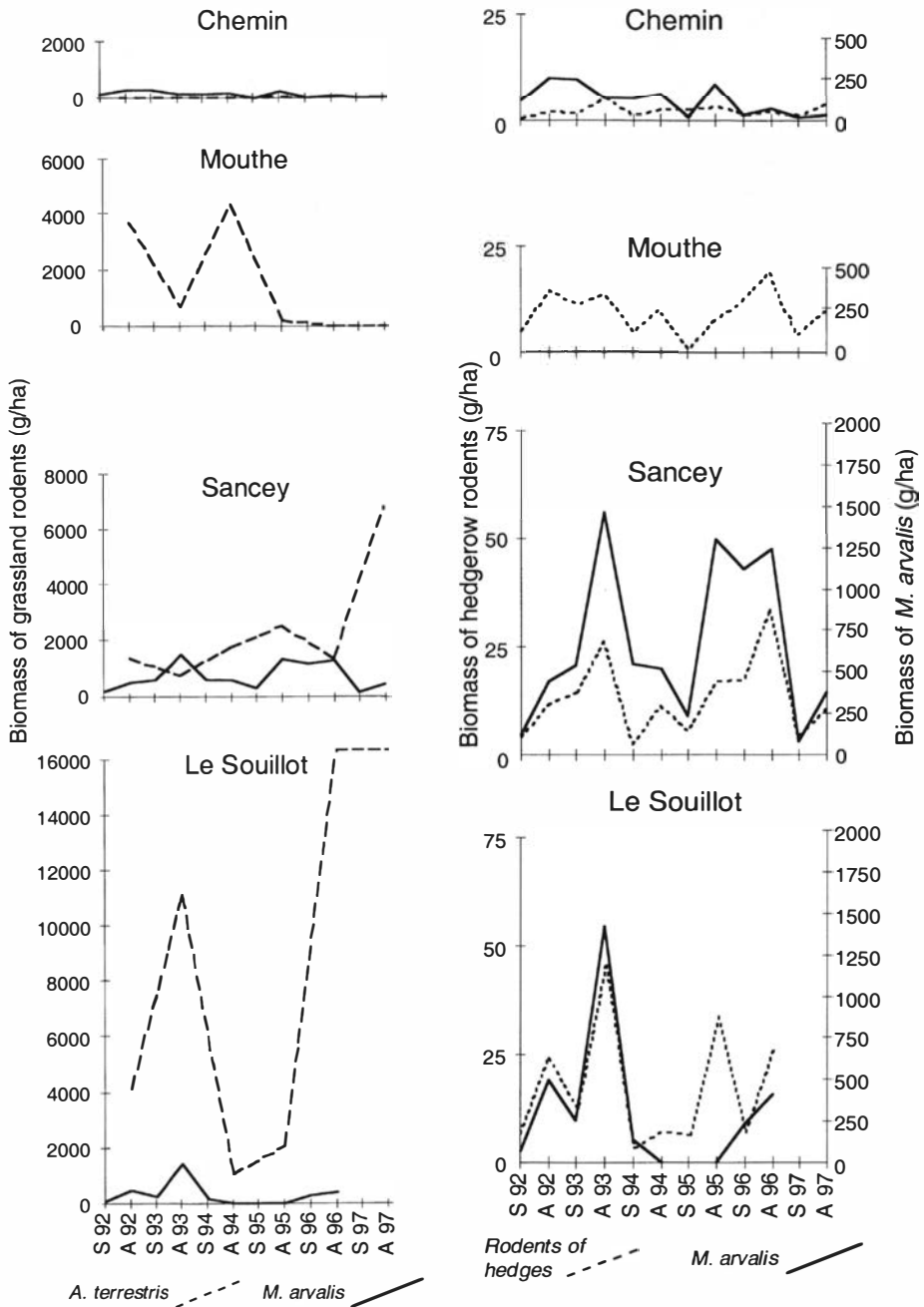
Figure 2. (left) — Variations of *M. arvalis* and *A. terrestris* population biomass at the four study sites (biomass is expressed in g/ha; S 92 = spring 92, A 92 = autumn 92).

Figure 3. (right) — Variations of hedgerow rodent (*C. glareolus* and *Apodemus* sp.) and *M. arvalis* population biomass at the four study sites (biomass is expressed in g/ha; S 92 = spring 92, A 92 = autumn 92).

Kotzageorgis & Mason, 1997; Mazurkiewicz, 1994; Rogers & Gorman, 1995; Ryszkowski, 1982). The effect of landscape on population dynamics has been investigated in single-species empirical studies: for *M. arvalis*, Delattre *et al.* (1986), Delattre *et al.* (1992); for *C. glareolus*, Paillat & Butet (1996); for *A. terrestris*, Giraudoux *et al.* (1997). Giraudoux *et al.* (1994) compared the population dynamics of rodent species of different habitats in a community at Le Souillot.

Few studies addressed the question of the effect of landscape on population dynamics of rodent communities (Oksanen *et al.*, 1999). Our aim was to assess patterns of prey-resource variations, at the scale of the whole landscape, according to landscape composition.

SAMPLING METHOD AND BIOMASS ESTIMATION

The methods used for the estimation of rodent biomass give only a rough estimate of population biomasses for the whole site. They however provide an ordinal scale suitable when densities are highly contrasted, and thus provide a first estimate of the biomass of rodent available for predators. This allows only careful comparisons between species and should be considered valid only when large differences of densities occur.

Five years time span should encapsulate the duration of most rodent cycles if any (Delattre *et al.*, 1992; Giraudoux *et al.*, 1997; Giraudoux *et al.*, 1994; Saucy, 1994), however, it still cannot be considered as a long statistical series. Definitive conclusions cannot be driven for lack of power efficiency in statistics for obvious logistic reasons. This is why those results and the following discussion must be considered preliminary. They would however pave the road to further long-term studies on landscape factors deciding the size and fluctuations of rodent populations and their possible effects on predator ecology.

LANDSCAPE COMPOSITION AND RODENT POPULATION DYNAMICS

The results of the present study indicate that, for each species, the patterns of population dynamics varied with the study areas (Table I).

In the Jura mountains, high population densities of *M. arvalis* rarely occur above 1 000 m of altitude. Population density was constantly low during the study period at Mouthe (only a few rare vole colonies were recorded). *A. terrestris* was absent from Chemin: the very small proportion of grassland seems unfavourable to the species.

The amplitude of biomass variations of *M. arvalis* at Chemin was 6 times lower than at Sancey and Le Souillot. Delattre *et al.* (1992) have shown that outbreaks of *M. arvalis* populations are more likely to occur when the proportion of permanent grassland (P.G.) to farmland is greater than 50 %. This proportion is 68 % in Sancey, and 89 % at Le Souillot. Our data show that *M. arvalis* populations reached high biomasses with high amplitude variations at Sancey. At Le Souillot, the amplitude of fluctuation of this species was as high as at Saneey but large biomasses were not reached so regularly (close to 1 400 g/ha in 1993) though Giraudoux *et al.* (1994) recorded high variations in densities during the period 1982-1990 with peaks of 300 ind/ha (eq. to 3 000 g/ha of total landscape) in grasslands. The vicinity of the sampling area to forest or dense hedgerow

network may dampen the population dynamics of this species at this site (Delattre *et al.*, 1999). Outbreaks of *A. terrestris* populations were expected at Le Souillot since the proportion of P.G. to farmland is over 85 % (Giraudoux *et al.*, 1997). The amplitude of biomass fluctuation was 3 times higher at Le Souillot than at Sancey, and biomass exceeded 10 000 g/ha in 3 autumns out of 6. Scores over 5 000 g/ha were rarely noted at Sancey and Mouthe where populations were comparatively more stable.

Despite much higher proportion of suitable habitat for grassland species at Sancey and Le Souillot than at Chemin and Mouthe, average biomass of *M. arvalis* at Le Souillot was not statistically different from Chemin, and no differences in average biomass of *A. terrestris* were recorded. These results suggest that unstability of grassland rodent populations (amplitude of biomass variation) was dependant on landscape composition. These data are in concordance with the study of Oksanen *et al.* (1999) who showed that the unstability of a microtine community was higher when the proportion of productive habitats (annual primary production) in a landscape was important.

Hansson & Hentonnen (1985, 1988), Henttonen *et al.* (1985) claimed that pronounced downturns in populations leading to very low biomasses, as well as summer declines, are features of the population dynamics of cyclic and unstable northern rodent populations. The precision of sampling method was not enough to detect summer declines of low amplitude. Several pronounced declines were recorded: a sharp decline of *M. arvalis* population started in autumn 93 at Le Souillot and the population was almost extinct until autumn 95 (here, extinction means that no rodent was detectable with the sampling method and therefore might correspond to local extinctions). At Sancey, the population also declined between autumn 93 and spring 95, and another decline started in autumn 96. The *A. terrestris* population also declined markedly between 93 and 94 at Le Souillot (the amplitude of the decline was almost 10 000 g/ha). Those declines were observed at sites with high proportion of grassland only.

The ROMPA hypothesis of Lidicker (1995) refers to the ratio of optimal to marginal patch area and hence expresses the proportion of optimal habitat in a landscape for a target species. ROMPA may influence the probability of arvicolid population densities undergoing multiannual cycles. If optimal habitats are scarce (low ROMPA), then the landscape matrix serves as a large dispersal sink, and population densities are very stable and small. At very high ratios, rodent densities are also either stable but relatively large, or they exhibit annual cycles, depending on differences in quality between optimal and marginal habitats (Ostfeld, 1992). At intermediate ROMPA, multiannual rodent population cycles are more likely (Lidicker, 1995). If grassland is referred to as optimal habitat for grassland species, the results obtained in this study seemed consistent with this hypothesis. High amplitude of *M. arvalis* and *A. terrestris* population fluctuations with sharp declines were likely to be observed at sites of intermediate ROMPA only: at Sancey (ROMPA is 33 %) for *M. arvalis* only (proportion of permanent grassland to farmland lower than 85 %) and at Le Souillot (ROMPA is 51 %) for the two species. Populations were stable at sites of low ROMPA: Chemin (17 %) and Mouthe (22 %).

SYNCHRONY BETWEEN RODENT POPULATIONS

Sancey and Le Souillot are the study sites where higher mean biomasses of grassland rodents, as well as strong fluctuations, were recorded. Furthermore, there

is a large disproportion between the populations biomasses of hedgerow rodents and of grassland rodents: average biomasses of *M. arvalis* are 51 times and 17 times higher than hedgerow rodents at Sancey and Le Souillot respectively. This contrast between hedgerows and adjacent biotope has previously been shown at Le Souillot (Giraudoux *et al.*, 1994) and in Poland (Ryszkowski, 1982).

These particular conditions are therefore favourable to test the hypothesis that similar body-sized rodent populations are synchronized (Andersson & Erlinge, 1977; Korpimäki, 1986). Giraudoux *et al.* (1994) have shown that over a time span of 8 years, the population dynamics of *Clethrionomys glareolus*, (and to a lesser extent of *Apodemus flavicollis*) was synchronous with the population dynamics of *Microtus arvalis*. In the present study, the population of *M. arvalis* at Sancey was synchronous with the populations of hedgerow rodents (a too short time span for the present study could prevent synchronic patterns from being clearly detected at Le Souillot). Moreover, the three large declines and low density periods of *M. arvalis* observed at Sancey and Le Souillot were concomitant with the declines of hedgerow rodents. No pattern of this type was observed at Chemin.

CONCLUSION

These results point out a distinction between two kinds of ecological systems: stable where biomasses of rodents were relatively low (Chemin and Mouthe); unstable with high amplitudes of fluctuation of grassland rodents, phases of very low biomass, and synchronous declines of the rodent community (Sancey and Le Souillot). In this latter system, the prey-resources for predators were highly unstable. This kind of influence of landscape composition on the patterns of rodent population dynamics is likely to determine how the predator community works (functional and numerical responses).

Remarkably, stable patterns of density variations occurred in the two places where the percentage of grassland was lower, and instability occurred with higher percentage. This illustrates two disturbance patterns in prey-resource variations: in landscapes of high percentage of permanent grassland, predators must respond to stochastic crashes of abundant prey-resources, while in landscapes of low percentage of permanent grassland predators must adapt to resource density regularly low. Interestingly, those landscapes can be at relatively short distance (see Fig. 1) within regional scale. At this scale, variations were asynchronous between sites (see Figs 2 and 3). One can therefore wonder if such mosaic of population dynamics patterns of rodent communities lead to large scale movements of predators and exchanges between landscape patches.

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