Landscape Ecology vol. 11 no. 5 pp 279–288 (1996)
SPB Academic Publishing bv, Amsterdam

Effect of landscape structure on Common Vole (*Microtus arvalis*) distribution and abundance at several space scales

P. Delattre[1], P. Giraudoux[2], J. Baudry[3], J.P. Quéré[1] and E. Fichet[1]
[1]*Université Montpellier II, Ecoéthologie, CC64, 34095 Montpellier cedex 05, France;* [2]*Université de Bourgogne, Ecologie, BP 138, 21004 Dijon cedex, France;* [3]*INRA-SAD, 65 rue de St Brieuc, 35042 Rennes cedex, France*

Keywords: landscape structure, fluctuation, population dynamics, *Microtus arvalis*

Abstract

This paper aims to answer the following question: are the fluctuations of abundance of Common Vole (*Microtus arvalis*) specific to different types of landscapes? The research was carried out in landscapes where grassland was dominant. The sampling method was based upon a partition in both landscape types and landscape units. Tracking of vole indices was used to evaluate their relative abundance. Six landscape transects were sampled during two successive years. Results show that population variation and diffusion of demographic states are closely related to landscape types. The possible causes of this are discussed. The landscape units can be used as global variables to assess outbreak risk and landscape design can be used to prevent them.

1. Introduction

The relationships between landscape structure and species distribution is a major question in landscape ecology. Early studies dealt with easily identified features such as forest island or wooded corridors (Johnson *et al.* 1992; Kozakiewicz 1993). In this context, small mammals have often been used as models (Fahrig and Merriam 1985; Geuse and Bauchau 1985; Merriam 1990; Barry *et al.* 1990; Apeldoorn *et al.* 1992; Douglass *et al.* 1992; Lidicker *et al.* 1992; Szacki *et al.* 1993, among others). However, because of the choice of these landscape features there is a bias towards the studies of forest species (Rose and Birney 1985). In contrast 'openfield species' of small mammals have mainly been the subject of population biology studies (Krebs and Myers 1974). A review of regional studies of the Common Vole, *Microtus arvalis*, has shown that population fluctuations and outbreaks are closely correlated to land use patterns (Delattre *et al.* 1992). The dominance of permanent grassland and the decrease in cultivated fields and forests favours population outbreaks. This means that landscape composition determine *M. arvalis* population dynamics. This regional study also suggests one more hypothesis: landscape structure should affect population diffusion and population dynamics. Dispersion should be facilitated in highly connected landscapes, that are dominated by grassland, while it should be slowed down in heterogeneous landscapes. Lidicker (1988) showed that such a dispersal system can determine the features of rodent population dynamics (ROMPA hypothesis). In this paper the term diffusion is taken to mean spreading out after Forman and Godron (1986). This spreading out of high vole densities may originate both in vole movements and/or in fluctuations of factors which control population density.

This paper aims to address the following question: are the fluctuations of abundance of the Common Vole (*Microtus arvalis*) specific to different types of landscapes? It also aims to discuss the possible causes of landscape determinism in the control of vole populations.

2. Materials and methods

2.1. Study site

The study site (18,000 ha) is situated in the French Jura, west of the city of Pontarlier (district of Levier, Doubs, latitude: 45°58' N, longitude: 6°10' E), the altitude is between 700 to 900 m.

One of the main difficulties in ecological studies when dealing with population dynamics is to place observations in a context that is inclusive enough to look at these dynamics outwardly, from the boundaries of the phenomenon under study (Lidicker 1988). Therefore, this study was conducted on two perception levels.

The first level corresponds to broad space scales involving the general visual characters of landscape (= landscape type). There are four landscape types:

1) 'hedgerow network'; associated with woodlots, pastures and meadows;

2) 'openfield'; mainly meadows;

3) 'forest'; partly an old growth forest (1/3 of the area) and partly a forest resulting from recent land abandonment, either by secondary succession or by plantation, mainly of spruces (*Picea sp.*). In the latter case, the forest mosaic is mixed with farmland (meadows). This spatial pattern increases the connectedness of the forest with the hedgerow network; forest peninsulas in farmland, as well as meadows in forests, are numerous.

4) 'village' and the surrounding areas, up to 200 m from houses. Habitat is grouped and the network of roads and farm lanes is well developed.

The second perception level was defined at a smaller scale, by using more detailed and objective landscape elements (= landscape units).

The 'landscape units' are 500 × 500 m cells from a grid georeferenced to the Lambert zone II system. An estimate of the abundance of landscape elements was made from the maps of the Institut Géographique National (IGN, the French National Geographic Institute) at the 1/25,000 scale. Abundance indices are: 0 = absent, 1 = scarce, 2 = average, 3 = frequent, 4 = covers the whole cell. Landscape elements are: forest, woodlot, hedgerow, openfield, wetland, village. The degree of presence of these various landscape elements (hedgerow, woods ...) was recorded in the 728 cells of a grid. A correspondence analysis on the matrix 'landscape elements × cells', followed by a hierarchical classification have led us to identify sixteen patterns of landscape units. Software were MacMul, GraphMul (Thioulouse 1989) and Anaconda (MIS, Besançon). The classification was used to make a map (Fig. 1) which was the spatial reference for vole sampling.

2.2. Sampling methods for the Common Vole

A method to estimate the abundance of the Common Vole (*M. arvalis*) has been developed by using surface indices. Vole indices such as burrow entrances, runways and droppings, have been compared with density estimates based on line trapping of voles in the same habitats. Results have shown a strong correlation to the number of sampling intervals where droppings are present (Delattre *et al.* 1990). Dropping counts may therefore be used to monitor population fluctuations of the Common Vole over large areas. They provide an index method and also offers the definite advantage of being suitable to space and time scales otherwise incompatible with estimates from trap lines. There is no possibility of confusing the droppings of the Common Vole with that of other grassland species. The Common Vole only cohabits with the Water Vole (*Arvicola terrestris*), the droppings of which are 3 to 4 times larger and are generally laid down in burrows. Therefore the index method is easy to carry out and allows distribution maps to be made from wide transects around areas of several km^2 within a very short time span.

Sampling was carried out every spring, before the reproduction period and in autumn, at the end of the reproductive season. From April 1991 to October 1992 four sampling series were carried out along six transects, each of them from 3 to 8 km long. This represents about 30 km for each season. Along each transect, the presence-absence of vole droppings within every ten paces is noted. The transects start from a village and continue to the next one, always going through at least four of the sixteen landscape units. Habitat types (meadows, field, hedgerow and so on) are described along the

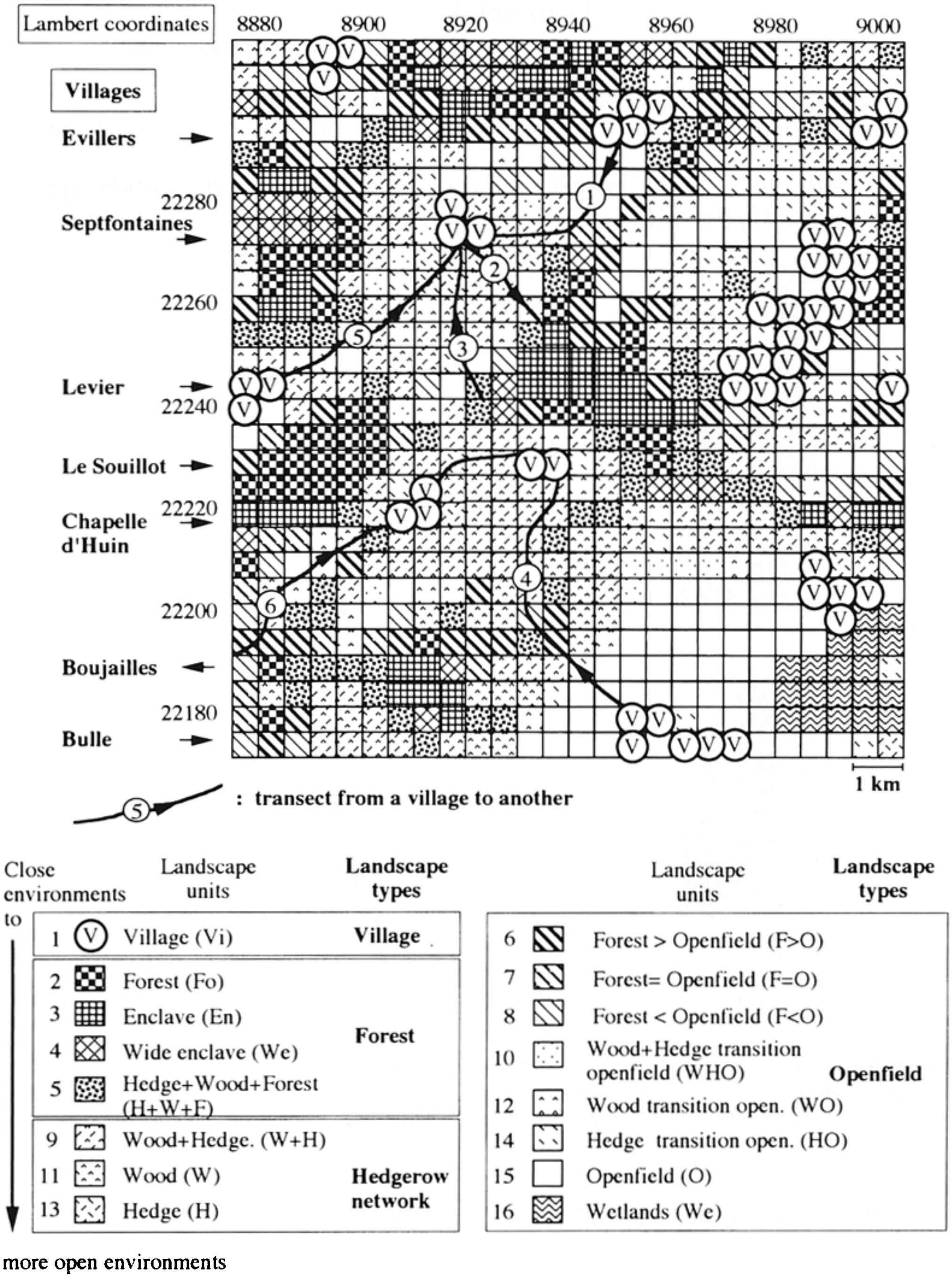

Fig. 1. Map of the study area (18,200 ha). Landscape units (25 ha) were classified according to dominant landscape features (see text). Correspondence analysis led to 16 separate landscape units. Six transects, numbered 1 to 6, were sampled each spring and each autumn.

transect. A data base (4th Dimension TM) is used to manage data and to calculate indices regarding landscape units and parcels. The abundance index is the number of 10 pace intervals where vole faeces are present. It can be expressed in two ways: frequency (number of positive intervals per 100 intervals) and a length percentage (length of positive intervals divided by a given transect length).

For two successive years we have analysed i) the differences in vole abundance between landscape

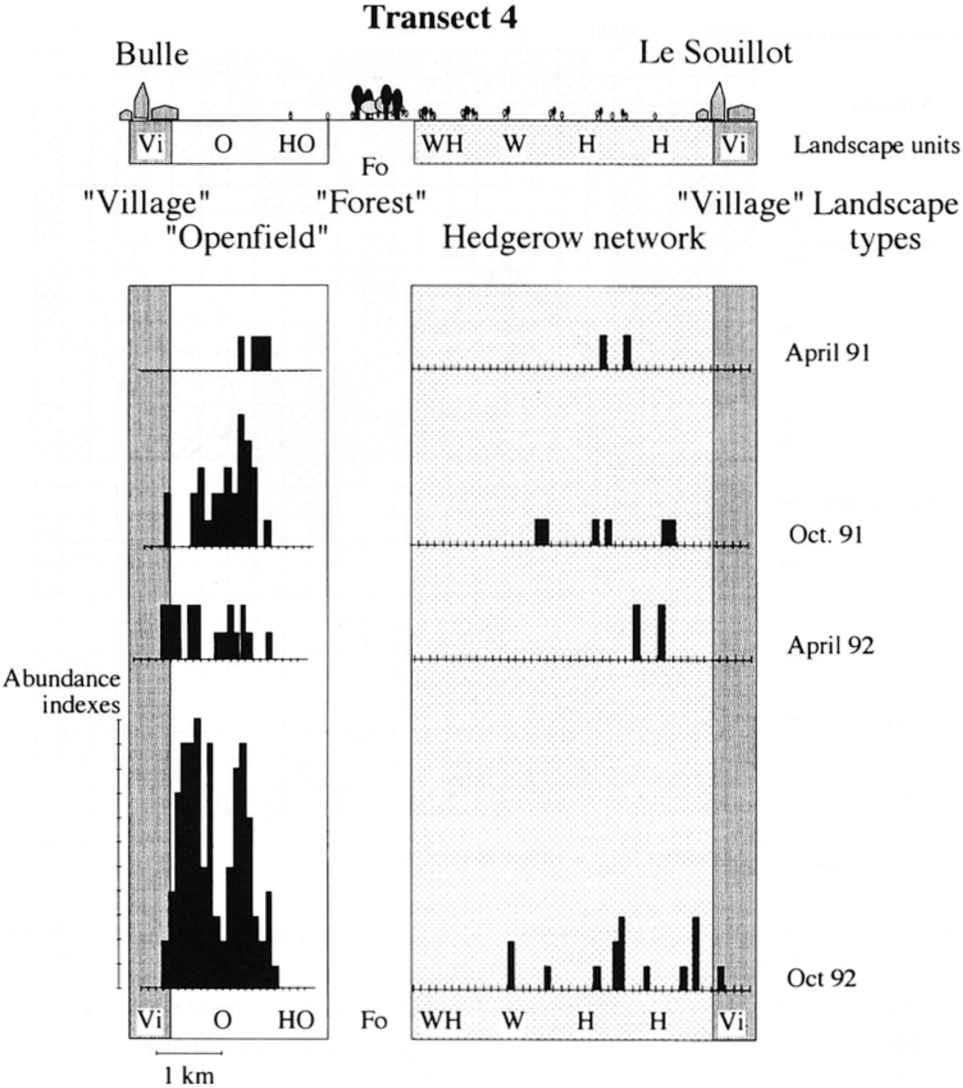

Fig. 2. Common Vole population dynamics and landscape types (transect 4, Bulle, Le Souillot). Transects were drawn in two parts to make comparison easier: the left part shows the landscape types 'village-openfields', the right part shows the landscape types 'hedgerow network-village'. The abundance index is the transect length where vole colonies are present divided by the total transect length.

types at given times, ii) changes in abundance within and between landscape types. Abundance changes were analysed at a single spatial level, the study site at two resolution scales; landscape type and landscape unit. Population diffusion was analysed at two spatial levels: the study site (at the landscape type scale) and landscape types (at the landscape unit scale).

3. Results

3.1. Population changes

3.1.1. Comparisons between landscape types

Figure 2 presents one example of the variations of vole abundance along a transect through various landscape types. The transect starts in a village, goes through an openfield, a forest and a hedgerow network, before reaching the next village.

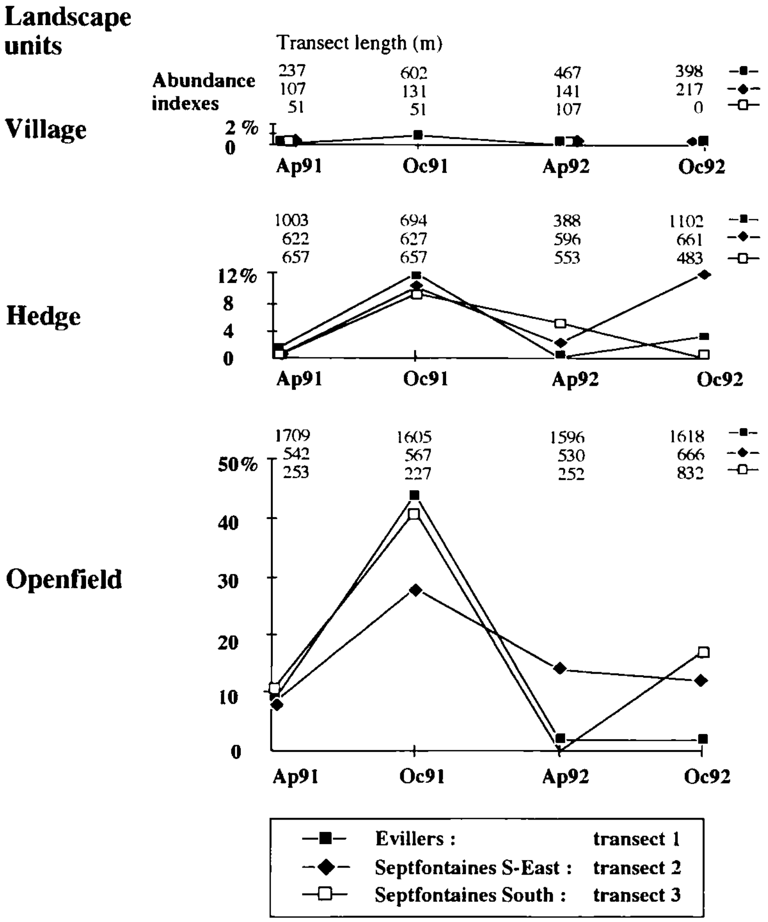

Fig. 3. Abundance variation of Common Vole population in the landscape units crossed by transects 1, 2 and 3. The above numbers are the transect lengths.

Table 1. Abundance index variations in the landscape types (transect 4; Bulle). The two numbers between brackets are respectively the length of positive intervals and the length of transect,.

Landscape type	April 91	October 91	April 92	October 92
Openfield	1,2 (19/1592)	16,8 (257/1531)	10,5 (153/1464)	62,8 (840/1337)
Hedgerow network	2,1 (39/1826)	2,2 (52/2385)	2,2 (48/2172)	8,2 (171/2067)
Village	0 (0/1360)	0 (0/165)	2,3 (19/841)	3,0 (27/911)

In the village, population abundances were low: 0 to 3% of positive intervals (1+) throughout the years (Table 1). During the reproductive season (April to October), the increase in population size remained moderate (maximum increase in abundance index is 50%). Around the village of Bulle, a 200 to 300 m length remained free of voles for the two years despite several hundred individuals per ha in the adjacent openfields. In the openfields, population density increased drastically according to the distance from the village.

In the hedgerow network, vole abundance was low in spring (2% 1+) and went up to 2 to 8% 1+ in autumn. The abundance index increase six-fold during the reproductive period in 1992 and fourteen-fold in 1991.

In the openfields and in autumn, abundance indices were seven times higher in the nearest hedgerow network and, when different from zero, twenty times higher than near the villages.

3.1.2. Comparisons between landscape units

We compared the abundance index within the three

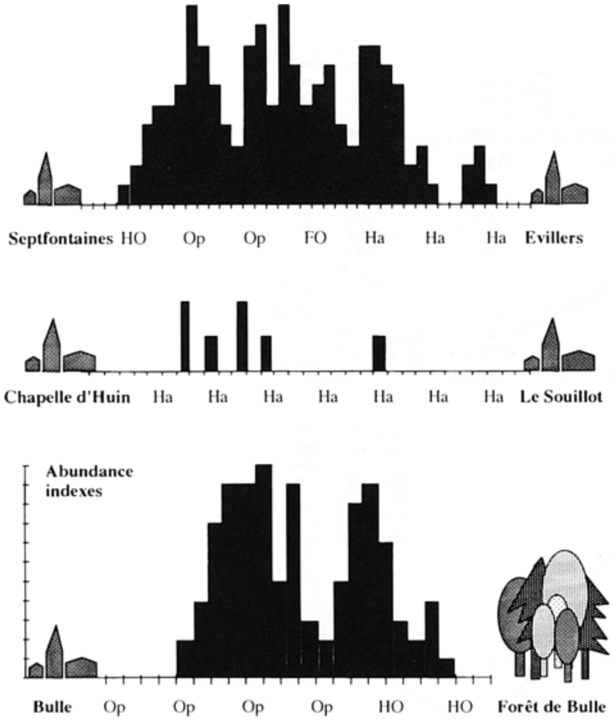

Fig. 4a. Abundance variation of Common Vole colonies in autumn and distance to the village (= 'village effect').

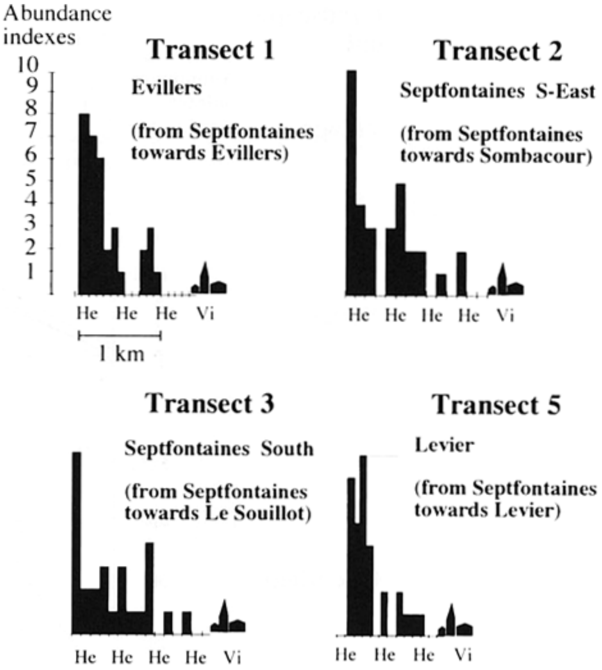

Fig. 4b. Autumn vole density gradients taken from transects radiating in four directions from Septfontaines village.

most abundant landscape types, at the scale of each landscape unit. These units are 'village', 'hedgerow' and 'openfield'. The analysis was done for transects 1, 2 and 3 whose populations exhibited synchronous variations of abundance. The results (Fig. 3) emphasize the existence of a very important depressive effect on vole density in village units (indice less than 2%; Fig. 3a) and an important one in 'hedgerow' (indice < 12%; Fig. 3b), when compared to indices from openfield units (mainly > 10%; Fig. 3c).

A comparison between all village units shows that the depressive effect, first observed around Bulle, was present everywhere (Fig. 4a). Whatever the direction of a transect from a village (*e.g.*, Septfontaines; Fig. 4b), a 100 to 400 m wide strip remained almost empty of voles during the two year study. There was a gradient of increasing vole density, the further one went from each village.

3.2. Population diffusion

3.2.1. At the landscape type level

Within the landscape type 'openfield' and during the peak period of abundance, all available habitats were colonized after each reproductive period. This means that changes in population density were important and vole diffusion very rapid. Within landscape type 'hedgerow network' diffusion was more limited during the peak period of abundance. Two examples, drawn from transects 3 and 6, illustrate the phenomenon of diffusion within the two landscape types (Fig. 5). During a single reproductive season, starting from an isolated spring population, almost all the openfield area was colonized and reached high vole densities. Within hedgerow network and with similar spring populations densities this colonization process did not occur during summer and autumn.

3.2.2. At the study site level

At this level the analysis was made from the landscape type 'openfield' (Fig. 6a). These units showed high variations in vole abundance which

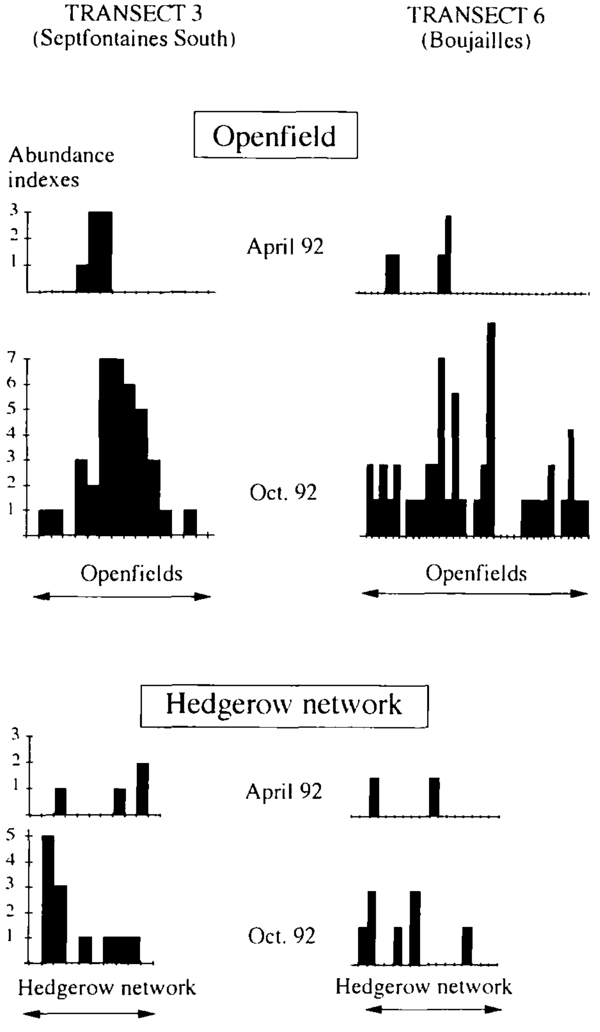

Fig. 5. Diffusion of high densities in openfield and hedgerow network during the Common Vole reproductive seasons.

may indicate significant differences between subpopulations.

On transect 1, 2 and 3, population densities were already high (10% 1+) as early as April 1991, when the study started. A phase of high abundance built up rapidly during the summer (20 to 45 1+) but came to end during 1992. Along transects 4, 5 and 6, population levels were low in April 1991 and remained so until April 1992 (0 to 15% 1+). The high abundance phase occurred during the summer 1992 in transect 4 the distance of which was the shortest from transects 1-2-3. The high abundance phase only started during the autumn in transects 5 and 6. At the study site level, a one year delay was observed between the appearance of peaks of abundance in the zone 1 (transects 1-2-3) as compared to transect 4 (Fig. 6b). The delay exceeded one year between transect 1-2-3 and transects 5-6.

4. Discussion

At landscape type scales ('openfield', 'hedgerow network', 'village') important differences in population dynamics are recorded. Three kinds of dynamics can be distinguished. The first, in village, is characterised by long periods of extinction and otherwise low population levels. The second, in hedgerow network, showed brief periods of local extinction and limited changes in population levels. The third, in openfield, exhibited high population density variations from year to year and a lasting peak of high abundance.

On a finer scale (landscape units), the low population densities that are associated with villages, persist as they do in landscape unit 'hedgerow'.

Therefore landscape units and landscape types can be considered as 'global variables' which give information on the range of the variations of vole density. They can be used to evaluate damage risks and to provide information for population management.

Population diffusion can be studied at two scales; i) within landscape types, it is the recolonisation of various habitats from local sources, ii) at the level of the whole study site, the movement of population peaks is shown at the landscape unit scale.

Within openfields, colonization of empty habitats is rapid during the reproductive period, while it is slow in hedgerow network and almost non existant in villages.

At the site level, a movement of peak density from zone to zone appears within the two year period. This movement is similar to the epicentric diffusion phenomenon reported by Finerty (1980) for the movement of abundance peaks of prey and predators. It also brings to mind the diffusion of populations on large regional scales noted for *Clethrionomys glareolus* (Teivainen 1979) and *Arvicola terrestris* (Giraudoux *et al.* 1990).

On the regional scale, Delattre *et al.* (1992) reported differences in population dynamics (called

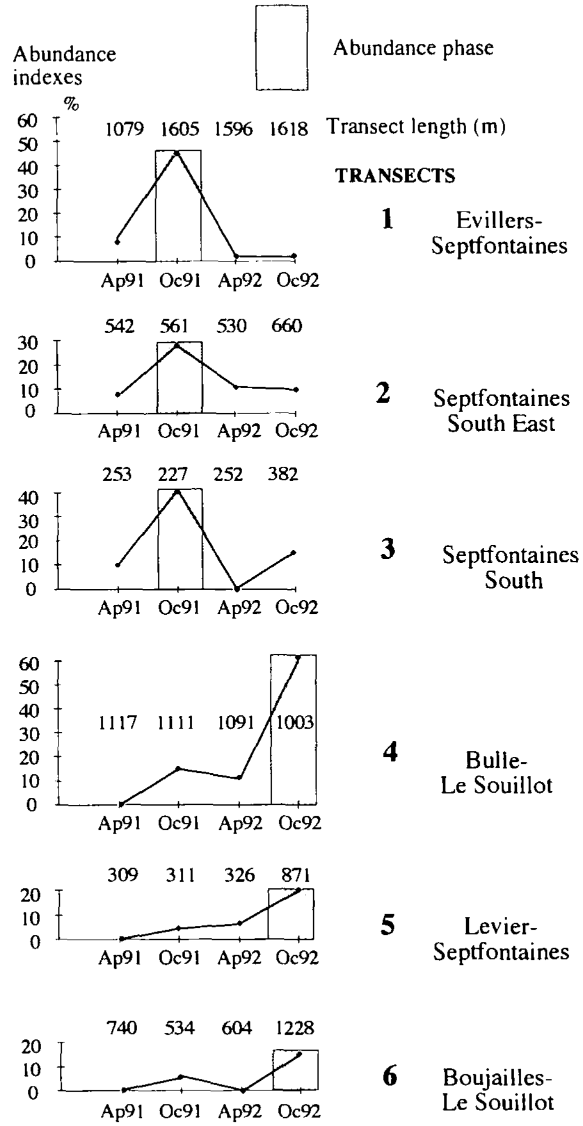

Fig. 6a. Population variations in the openfield landscape types of the six transects. The above numbers are the transect lengths (m).

types of population functioning) between landscapes with different types of permanent grassland cover. In our site (sector scale) grassland is essentially the sole type of cover, however three types of population functioning can be related to different landscape structures ('village', 'hedgerow network', 'openfield'). Thus fractal geometry may be useful to describe population dynamics, particularly in modelling.

The variations in population density, the recolonization of habitats and the diffusion of demographic states are correlated to spatial structures. Our hypothesis is that these phenomena are not the direct result of the control of the different structures *per se*, but of ecological processes constrained by spatial structures (Baudry 1989). The factors which might help to explain the fluctuations are: firstly, temporal differences between local population variations refute the theory that climatic factors are the cause of population variations, as climate influence is at a regional scale; secondly, large differences in duration and size of population variations observed during the peak phase in neighbouring populations cannot be perpetuated or explained by intrinsic factors. Moreover it has been shown that a trend to synchronicity exists between population density variations of small rodents of both grasslands (*M. arvalis*) and woodlands (*C. glareolus*) in systems where the biomass of grassland rodents is dominant (Giraudoux *et al.* 1994). This supports the idea that rodent population dynamics are driven by extrinsic factors.

Consequently essentially external and non-climatic factors should be considered to explain simultaneously the spatial and temporal variations observed. The only factors which are not eliminated are therefore predation, parasitism and disease. For instance in the 'Village' a possible interpretation of spatiotemporal patterns of rodent populations is the effect of domestic cats which are very numerous around villages (Erlinge *et al.* 1983; Hansson 1988; Giraudoux 1991). Hedgerow networks are generally characterised by a great diversity of habitats, which are favourable to a rich predator community (*i.e.*, foxes, wild cats, raptors ...) and particularly to generalist predators (Andersson and Erlinge 1977). Inversely, openfields are less frequented by generalist predators (Loman 1991) and are more favourable to specialist predators (stoat, weasel ...) whose destabilizing effect on rodent population is well documented (Hanski *et al.* 1991; Heikkilä *et al.* 1994; Henttonen *et al.* 1987). In our case, landscape may be the filter of prey/predator relationships and thus may indirectly control rodent population dynamics.

5. Conclusion

Landscape structure appears to be an important constraint upon diffusion and population outbreaks

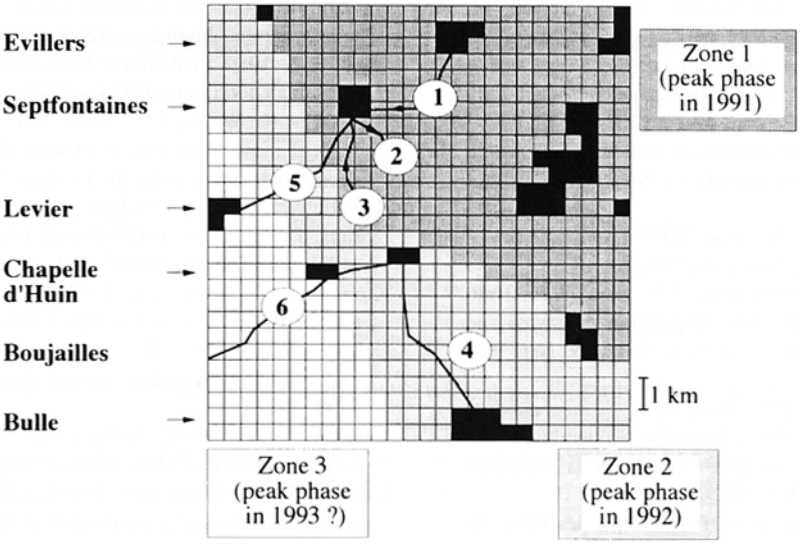

Fig. 6b. Moves of high density peaks in the study site.

(Johnson *et al.* 1992). This study opens new ways to analyse small mammal populations within a given landscape. Index methods to estimate rodent distribution and density at landscape scale may provide a good descriptive framework to support studies on source/dispersal sink systems (Lidicker 1985; Gaines *et al.* 1992) and on predation (Hanski 1987; Hansson 1989). Indeed these studies must always be perceived in an inclusive context (higher levels of organization and wider space time scale) which give sense to local studies.

We can indeed point out the importance of developing new tools to investigate species distribution over large areas in order to develop ecological studies at landscape level.

Acknowledgements

This work was supported i) by the Ministry of Environment as part of the research programme 'Déprise agricole', ii) by INRA (French National Agricultural Research Institute), as part of the 'AGROTECH program' and iii) by the Regional Council of Franche-Comté since 1992, as part of the contract 'Rodents and rural planning'. This is a paper of the network 'Population and Landscape' and of the Institute of Evolution of Montpellier (N° 96–111).

References

Andersson, M. and Erlinge, S. 1977. Influence of predation on rodent populations. Oikos 29(3): 591–597.

Apeldoorn, R.C., Oostenbrink, W.T., Van Winden, A. and Zee, F.F. 1992. Effects of habitat fragmentation on the Bank Vole, *Clethrionomys glareolus*, in an agricultural landscape. Oikos 65: 265–274.

Barry, R.E.J., Heft, A.A. and Baummer, T.E. 1990. Spatial relationships of syntopic White-footed Mice, *Peromyscus leucopus*, Deer Mice, *P. maniculatus*, and Red-backed Voles, *Clethrionomys gapperi*. Canadian Field Naturalist 104(3): 387–393.

Baudry, J. 1989. Interactions between agricultural and ecological systems at the landscape level. Agriculture, Ecosystems and Environment 27: 119–130.

Delattre, P., Giraudoux, P., Damange, J.P. and Quere, J.P. 1990. Recherche d'un indicateur de la cinétique démographique des populations du Campagnol des champs (*Microtus arvalis*). Revue Ecologie (Terre et Vie) 45: 375–384.

Delattre, P., Giraudoux, P., Baudry, J., Musard, P., Toussaint, M., Truchetet, D., Stahl, P., Poule, M.L., Artois, M., Damange, J.P. and Quere, J.P. 1992. Land use patterns and types of Common Vole (*Microtus arvalis*) population kinetics. Agriculture, Ecosystems and Environment 39: 153–169.

Douglass, R.J., Douglass, K.S. and Rossi, L. 1992. Ecological distribution of Bank Voles and Wood Mice in disturbed habitats: preliminary results. Acta Theriologica 37(4): 359–370.

Edwards, W.R. and Clark, W.R. 1988. Ecological dependency: the concept and its implications for research and management. Trans. 53 rd N.A. Wildl. & Nat. Res. Conf. SS2: 115–125.

Erlinge, S., Goransson, G., Hogstedt, G., Liberg, O., Loman, J., Nillson, I., Nillson, T., Von Schantz, T. and Sylven, M. 1983. Predation as a regulating factor on small rodent populations in southern Sweden. Oikos 40(1): 36–52.

Fahrig, L. and Merriam, G. 1985. Habitat patch connectivity and population survival. Ecology 66(6): 1762–1768.

Finerty, J.P. (Ed.) 1980. The population ecology of cycles in small mammals. Yale University Press, New Haven & London, 234 pp.

Forman, R.T.T. and Godron, M. (Eds.) 1986. Landscape ecology. John Wiley and Sons, New York, 619 pp.

Gaines, M.S., Foster, J., Diffendorfer, J.E., Sera, W.E., Holt, R.D. and Robinson, G.R. 1992. Population processes and biological diversity. Trans. 57th N.A. Wildl. & Nat. Res. Conf. 252–262.

Geuse, P. and Bauchau, V. 1985. *Apodemus sylvaticus* (Rodentia: Muridae) et *Clethrionomys glareolus* (Rodentia: Microtidae): compétition ou coexistence? Annales de la Société de Zoologie Belge 115(2): 211–220.

Giraudoux, P. 1991. Utilisation de l'espace par les hôtes du ténia multiloculaire (*Echinococcus multilocularis*): conséquences épidémiologiques. Thèse de Doctorat, Dijon, 106 pp.

Giraudoux, P., Michelat, D. and Habert, M. 1990. La Chouette effraie (*Tyto alba*) est-elle un bon modèle d'étude en dynamique de population? Alauda 58(1): 17–20.

Giraudoux, P., Delattre, P., Quere, J.P. and Damange, J.P. 1994. Distribution and kinetics of rodent populations in a region under agricultural land abandonment. Acta Œcologia 15(4): 385–400.

Hanski, I. 1987. Populations of small mammals cycle – Unless they don't. Trends in Ecology and Evolution 2(3): 55–57.

Hanski, I., Hansson, L. and Henttonen, H. 1987. Specialist predators, generalist predators, and the microtine rodent cycle. Journal of Animal Ecology 60: 353–367.

Heikkilä, J., Below, A. and Hanski, I. 1994. Synchronous dynamics of microtine rodent populations on islands in Lake Inari in northern Fennoscandia: evidence for regulation by mustelid predators. Oikos 70: 245–252.

Henttonen, H., Oksanen, T., Jortikka, H. and Haukisalmi, V. 1987. How much do weasels shape microtine cycles in northern Fennoscandia taiga? Oikos 50: 353–365.

Hansson, L. 1988. The domestic cat as a possible modifier of vole dynamics. Mammalia 52(2): 159–164.

Hansson, L. 1989. Predation in heterogeneous landscapes: how to evaluate total impact? Oikos 54(1): 117–119.

Johnson, A.R., Wiens, J.A., Milne, B.T. and Crist, T.O. 1992. Animal movements and population dynamics in heterogeneous landscape. Landscape Ecology 7(1): 63–75.

Kozakiewicz, M. 1993. Habitat isolation and ecological barriers. The effect on small mammal populations and communities. Acta Theriologica 38(1): 1–30.

Krebs, C.J. and Myers, J.H. 1974. Population cycles in small mammals. Advances in Ecological Research 8: 267–399.

Lidicker, W.Z.J. 1985. Population structuring as a factor in understanding microtine cycles. Acta Zoologica Fennica 173: 23–27.

Lidicker, W.Z.J. 1988. Solving the enigma of microtine 'cycles'. Journal of Mammalogy 69(2): 225–235.

Lidicker, W.Z.J., Wolff, J.O., Lidicker, L.N. and Smith, M.H. 1992. Utilization of a habitat mosaic by cotton rats during a population decline. Landscape Ecology 6(4): 259–268.

Loman, J. 1991. Small mammal and raptor densities in habitat islands: area effect in a south Swedish agricultural landscape. Landscape Ecology 5(3): 183–189.

Merriam, G. 1990. Ecological processes in the time and space of farmland mosaics. *In* Changing Landscapes: An Ecological Perspective. pp. 121–133. Edited by I.S. Zonneweld and T.T. Forman. Springer-Verlag, New York.

Rose, R.K. and Birney, E.C. 1985. Community ecology. *In* Biology of New World Microtus. Special Publication N° 8, pp. 310–339. Edited by R.H. Tamarin. The American Society of Mammalogists, Shippensburg, Pennsylvania.

Szacki, J., Babinska-Werka, J. and Liro, A. 1993. The influence of landscape spatial structure on small mammal movements. Acta Theriologica 38(2): 113–123.

Teivainen, T. 1979. Vole damage to forest tree seedlings in reforested areas and fields in Finland in the years 1973–1976. Folia Forestalia 387: 23 pp.

Thioulouse, J. 1989. Statistical analysis and graphical display of multivariate data on the Macintosh. Computer Applications in the Biosciences 5: 287–293.