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Abstract - Spatio-temporal patterns of living organisms have been the object of numerous developments in the recent years. Analysis of these patterns in large mammals require to study the distribution over very large areas, that is usually beyond the capabilities of scientists. We tried to explore an approach to spatial patterns at a regional scale in France for several ungulates, considering species that could have been of interest as prey for prehistoric man. Original data came from hunting results collected at a relatively high resolution (Commune, *i.e.* c. 15 km² in average), much better than extant Atlases. Distribution of wild boar, red deer and roe deer was examined for an area of 69,000 km² (12.6% of the surface area of France). Red deer are distributed in clusters of 400 to 3,000 km² with some isolated records in between. Roe deer show a gradient in number, from the mediterranean zone (absent) to the western part of the region (high density). Wild boar are irregularly scattered in the agroecosystems, but widespread and abundant in most areas with more than 25% forest. Relationships with forest cover is very strong in wild boar, strong in red deer, and low in roe deer. Population dynamics have been studied in detail in wild boar over an area of 30,000 km². This area appears as divided in zones differing by density and stability of the population, size of home ranges and dispersal rate. There is a continuous flow of individuals migrating between zones. They are the main contributors to population changes in low-density areas. In contrast, population changes in high-density areas do not depend on dispersal but probably on changes in birth rate. We conclude with some proposals to use this knowledge in a prehistoric context.

Résumé - **Caractéristiques spatiales dans les populations de grands mammifères.** Les patrons spatio-temporels des organismes vivants ont fait l'objet de nombreux développements dans les années récentes. L'analyse de ces patrons chez les grands mammifères requiert d'étudier les distributions sur de très grandes surfaces, ce qui est généralement au-delà des possibilités des chercheurs. Nous avons essayé une approche des patrons spatiaux, à l'échelle régionale en France, pour plusieurs ongulés, en considérant des espèces qui ont pu avoir un intérêt comme proie pour l'homme préhistorique. Les données originales proviennent des résultats de chasse avec une assez haute résolution (la commune, soit environ 15 km² en moyenne), bien meilleure que tous les Atlas existants. La distribution du sanglier, du cerf élaphe et du chevreuil a été examinée dans une région couvrant 69000 km² (12.6% de la surface de la France). Le cerf est distribué en amas de 400 à 3,000 km² avec quelques données isolées entre eux. Le chevreuil montre un gradient numérique depuis la Méditerranée (où il est absent) jusqu'à la partie Ouest de la région (haute densité). Le sanglier est irrégulièrement disséminé dans les agrosystèmes, mais répandu et abondant dans les zones avec plus de 25% de boisement. Les relations avec le couvert forestier sont très fortes pour le sanglier, fortes pour le cerf, atténuées pour le chevreuil. La dynamique des populations de sanglier a été analysée en détail pour une région de 30,000 km². Cette région apparaît divisée en zones différant par la densité et la stabilité de la population, la taille des domaines vitaux et le taux de dispersion. Il y a un flux continu d'individus migrant entre zones. Ce sont eux qui contribuent le plus aux changements de population dans les zones à faible densité, alors que les changements dans les zones à forte densité ne dépendent pas de la dispersion mais probablement des variations de la natalité. Nous concluons par des propositions pour utiliser ces connaissances dans un contexte préhistorique.

Key-words: Large mammals, Spatio-temporal patterns, Populations.

Mots clés: Grands mammifères, Patrons spatio-temporels, Populations.

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1. Introduction

Although publications on spatial organisation in mammals are exceedingly numerous,

those considering the mechanisms at work at a large geographical scale (and not limited to the distribution areas of the species) are scarce.

Consequently, there are relatively few reliable data to test new spatio-temporal models (see Bascompte & Solé, 1995 and 1998 for a discussion of spatio-temporal modelling). Population biologists have proposed different models of spatial organisation. A relatively simple classification of distribution patterns over the entire geographic range of a species consists of three categories, namely: *i.* isolated populations (the range is divided into separate "islands" without any exchange between them); *ii.* metapopulations (the range is divided into distinct subpopulations, with exchanges between them, and a certain rate of extinction and immigration; the classical example is that of a species distributed on a continent and adjacent islands); *iii.* continuous populations (the range is continuously, even though heterogeneously, occupied, without local extinctions). In this classification, source-sink systems are included in continuous populations. Metapopulation models may depend on initial definitions (Gotelli & Kelley, 1993), and the border line between meta- and continuous populations is sometimes fuzzy. Exploitation of large animals by man has long been a problem of spatial interactions between predator and prey. What we know of the ancient distribution of hunters' populations suggest that they searched for prey on very large areas, within a radius of 50 km at least. Understanding hunter-prey relationships in the past may benefit from a good knowledge of the distributional rules in present populations of big game, at the same large spatial scale.

Unfortunately, most studies addressing the spatio-temporal dynamics of animal populations suffer from the too small surface area encompassed by the field work, simply because the extent of this work is limited by material constraints. The main constraints are due to the fact that the only approach to evaluate population numbers, birth or death rates, and dispersal, consists of time-consuming and expensive techniques such as capture-marking, standardized observations, and telemetry. Consequently, it is rare that demo-

graphic processes can be examined over a significant area, as required. Large game species in Europe (namely ungulates of the families *Cervidae* and *Bovidae*) are an exception to this failure, at least in some countries, owing to the comprehensive recording of animals killed by hunters and accidents, with a relatively high accuracy, over the entire area of the country. In the present paper, we take an example from French ungulates. After giving the outline of the distribution of eight species, we present a thorough analysis of the patterns observed in the three main species with emphasis on population modelling in Wild boar, *Sus scrofa*. In conclusion, we examine how these results can help to understand the distribution of animals, men, and exploitation of animals by men during the Stone Ages.

2. Material and methods

We used as a first source the book "Atlas des Mammifères sauvages de France" (Fayard, 1984) which gives distributional maps of the presence/absence of each species in a rectangular grid of 0.4 grade (longitude) by 0.2 grade (latitude), *i.e.* approximately 28 by 22 km (616 km²). A more detailed regional analysis was then made using hunting results (courtesy of Office national de la Chasse, the Service National du Patrimoine Naturel, and the Fédérations Départementales de Chasseurs). These results were obtained for each administrative unit (Commune), and analysed for a large region in the southern part of France, covering 69,000 km² (Fig. 1). Over this area, the average surface of a Commune is *ca* 15 km², *i.e.* a resolution 40 times greater than in the French Atlas. Hunting results consist of total numbers of animals killed per Commune, for three species: Red deer *Cervus elaphus*, Roe deer *Capreolus capreolus* and Wild boar *Sus scrofa*. There is a shooting plan for Red deer and Roe deer, *i.e.* the number of individuals to be shot is prescribed by commissioners before the shooting season. There is no shooting plan for Wild boar, but the extent of the shooting season, and the number of

hunting days per week, can be modified to take account of apparent trends of population decrease or increase. For all three species, numbers killed per km² were used to roughly classify the population into two or three classes of abundance.

To explore the mechanisms involved in the dynamics of Wild boar populations, we used the results of mark-and-release studies (Spitz, *et al*, 1984) made in seven different sites distributed over a control area of 30,000 km². Recovery of tagged animals by hunters was facilitated by information delivered by hunting administrations and newspapers. Dispersal was analysed through the distribution of distances between trapping site and recovery site (Janeau & Spitz, 1990). Mortality rate was calculated using the general panel of methods developed by Cormack (1970) and Lebreton (1977) then applied to Wild boar (Gaillard, 1987; Spitz, 1989). Proportion shot in the living population was estimated by the same way and provided an estimate of the population total number. Total number present before or after shooting season was also estimated

through an iterative method based on the analysis of game bag (Badia *et al.*, 1991).

Analysis of distribution maps was performed using an ARC-INFO® compatible vector-raster GIS (ALLIANCE ®). Vector data concerning administrative units came from database published by Institut Géographique National. Data on landscape and land cover were found in the General Agriculture Census (Ministère de l'Agriculture) and in a Corine Land Cover (Corine, 1992) database. Analysis of relationships with habitat was performed using usual statistics in SPSS®, and multivariate analysis and segmentation of binary tree in SPAD®.

Latin names of animals are those used in Wilson & Reeder (1993), except for mouflon which is still controversial, and english names are those commonly used (see also Mitchell-Jones *et al.*, 1999).

3. Results

3.1. General features at low resolution. There are eight species of ungulates living in free-ranging conditions in France. The French Atlas shows various patterns of distribution.

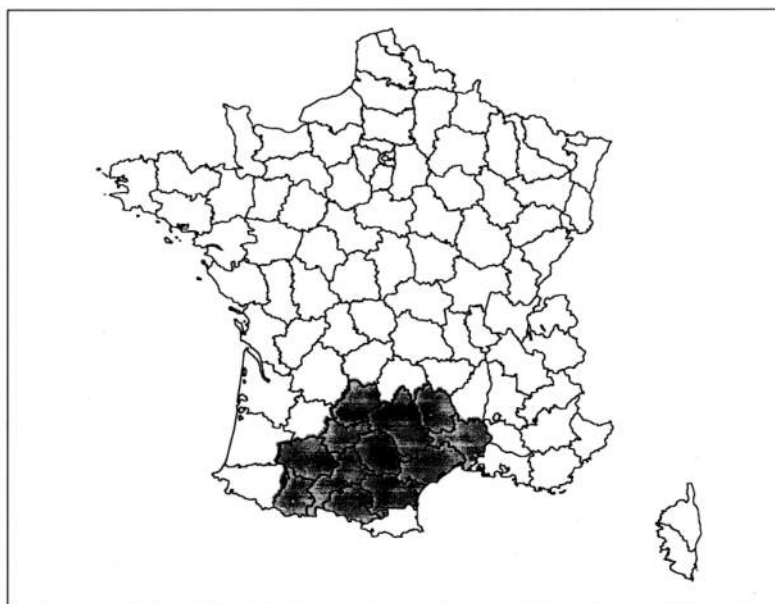


Fig. 1 - Map of France divided in Départements. Shaded: the study area (12 Départements covering 69.000 km²).

i. Subcontinuous distribution is observed in Roe deer and Wild boar. For both species, observed gaps are large enough (more than 50 km) to be true gaps in their range. These gaps can be explained by historical reasons: these are areas still unoccupied after a phase of expansion. For Roe deer, in addition, the southern limit of the species (corresponding to the transition between mediterranean and non-mediterranean climate) is observed in France, and is visible on the map. ii. Subcontinuous restricted distribution is characteristic of the three mountain ungulates: Alpine chamois *Rupicapra rupicapra*, Southern chamois *Rupicapra pyrenaica* and alpine ibex *Capra ibex*. Each of these species has a range limited to a mountain massif or (for chamois) a group of massifs without any significant gap. However these patterns conceal quite different situations. Southern chamois has a really continuous distribution over the Pyrénées. The distribution of chamois is quasi-continuous over the Jura-Alps complex, but populations in Vosges and Cantal were recently introduced and are still isolated. Ibex populations originated from artificial restocking plus very few natural colonisations, but all populations now seem potentially interconnected. iii. Separate clusters is the situation observed in Red deer. Formerly (beginning of the 20th century) restricted to a few private or state hunting estates, all in the northern half of the country, this species was the object of numerous restocking operations in various regions, in mountains and lowlands, and recently exhibited natural expansion in many regions. As a result, the French Atlas shows a constellation of large and small clusters, but it is impossible at this scale to define whether the larger units are really continuous or not, and whether some of the smaller units are definitely (or not at all) connected with others. Mediterranean mouflon *Ovis musimon* is another species distributed in separate clusters on the continent. All clusters result from artificial restocking in the last decades, most of them not at all connected with other

populations, even at short distance. Fallow deer *Dama dama* is the extreme instance of this kind of distribution: there are only two or three small populations, inhabiting eastern France, undoubtedly considered as autonomous.

3.2. General features of the distribution of Red deer and Wild boar at high resolution

All representations are given using a map of 12 Départements of southern France, covering 69,000 km². Fig. 1 shows the location of this area in France.

i. *Red deer* (Fig 2) Current distribution is shown in presence-absence, relative to percent of forest cover. Hatched areas are those covered with more than 35% forest. Presence of red deer in a Commune is presented as a black dot. Most points of presence are in Communes with more than 35% forest. Obvious relation between presence of red deer and forest cover is confirmed by very high Chi-square values (2 x 2 table of frequencies, chi-square=240.59 when fixing the lower limit of "forested" at 25% of forest cover, 269.894 for 30% and 287.941 for 35%, DDL= 1 in all cases). Fig. 2 shows that Red deer is currently distributed in clusters, each spread over 400 km² to 3,000 km². Isolated reports may correspond to expansion movements from the main clusters. Map in Fig. 2 shows that the main red deer clusters are often located at the limit of less wooded areas, or overlap them.

ii. *Roe deer* (Fig 3) As seen for the national distribution of the species, the range of roe deer reaches its southern limit in the studied area. The detailed map shows no point of presence in the mediterranean lowlands, and in a part of the cultivated lowlands farther west. Although many signs of colonisation of this part of the region exist, populations are still too scarce to be submitted to the shooting plan. Large local differences in kill index are observed with a tendency to an increase to the West. In the westernmost part of the study area (where the populations seem to be the highest) the distribution is yet quite heterogeneous. Correlation between kill index and

forest cover is low (linear regression gives adjusted $R^2 = 0.016$). It is more informative to say that 77% of Communes with no roe deer have less than 35% forest. In the cross table of roe deer (presence-absence) and forest cover (2 classes), Chi-square = 104.916 when fixing the lower limit of "forested" at 35% of forest cover, 141.744 for 30% and 179.792 for 25%.

iii. *Wild boar* (Fig. 4) Wild boar are widespread in the study area. Apparent gaps in the distribution seem correlated with very high altitudes in the Pyrénées, and with cultivated lowlands. When introducing two levels of abundance, zero excluded, (0 to 0.9 individuals shot per km² and more than 0.9/km²), large and small clusters appear, interconnected by a great number of isolated points at the higher level. A majority of Communes with more than 0.9/km² (82%) appear included in the areas with more than 25% forest (the cross tabulation gives Chi-square = 529.076). In contrast,

Communes with no wild boar have a less strong relation with forest cover (36% are Communes with more than 25% forest).

3.3. Preliminary conclusions

Even for the more widespread species (Wild boar), the distribution appear discontinuous, as proved by the high proportion of Communes with "absence" located in apparently favourable environment (forest). All three species, in fact, show features characteristic of expanding populations, even though each of them is at a different stage of expansion. Red deer is still distributed in semi-isolated nuclei, with a few signs of expansion from certain ones, and interconnection between others. All three species have a strong link with the percentage of forest in the landscape, either because their presence (Red deer) or their higher densities (Wild boar) are mostly limited to high percentage of forest, or because their absence (roe deer) is mostly limited to low percentage of forest.

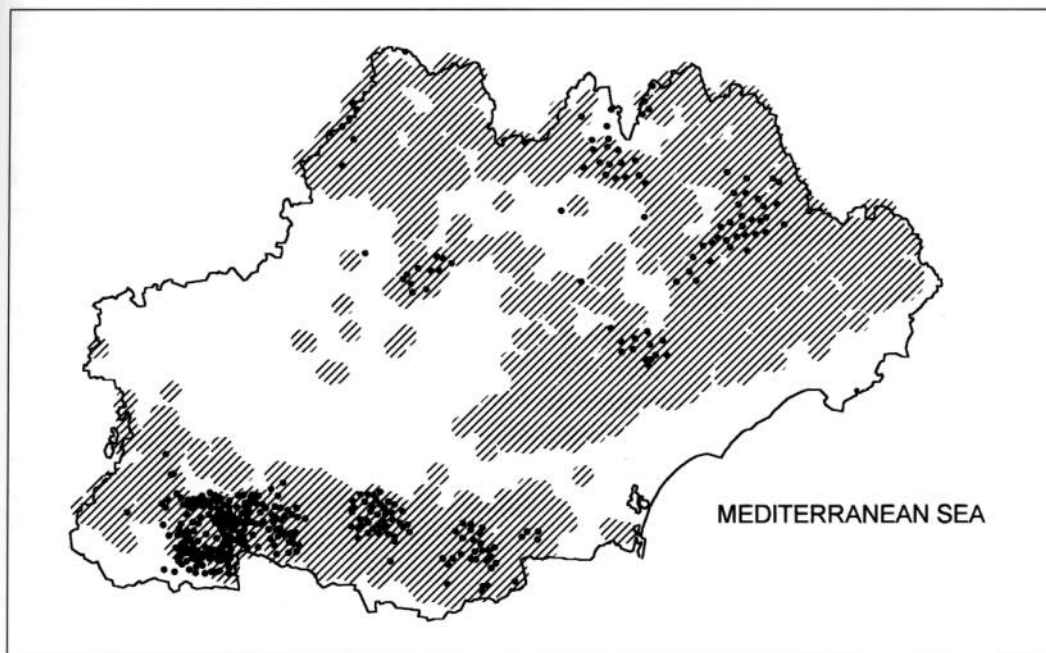


Fig. 2 - Distribution of Red deer in the study area. Hatched: more than 35% forest. Dots: communes with presence of Red deer. Scale is approximately 1/2,000,000.

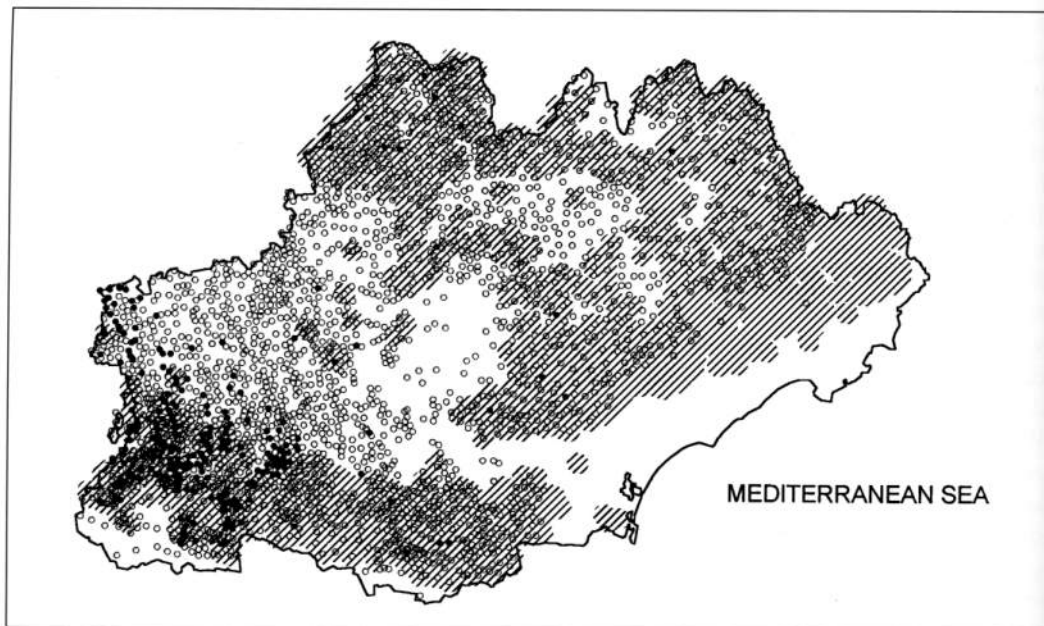


Fig. 3 - Distribution of Roe deer in the study area. Hatched: more than 35% forest. Open circles: roe deer present, less than 1.25 killed per km². Black dots: roe deer present, more than 1.25 killed per km². Scale is approximately 1/2,000,000.

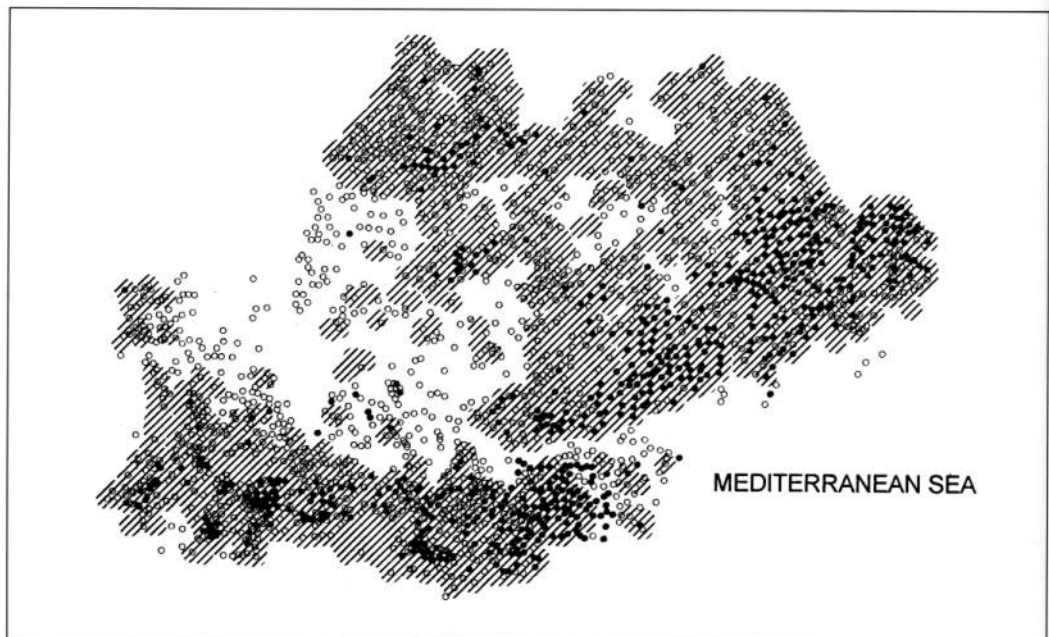


Fig. 4 - Distribution of Wild boar in the study area. Hatched: more than 25% forest. Open circles: less than 1.0 killed per km². Black dots: more than 1.0 killed per km². Scale is approximately 1/2,000,000.

4. Population dynamics of Wild boar at a regional level

Interpretation of the distribution map of Wild boar should take account of the spatial organisation of individuals. Numerous studies (see specific articles and reviews in Spitz *et al.* 1992 and Macchi *et al.* 1995) show that wild boar are distributed in nuclei based on one or several adult females, living there with their young of the last generation. A tentative approach to the spatial organisation of a population of wild boar was made in an area of 30000 km² (Fig. 5). The respective ranges of different nuclei tend to overlap more and more when population density gets higher.

Consequently, we considered three levels of abundance based on kill density. At less than 0.2 boars killed per km² (level 1), nuclei are unstable (risk of extinction) and well apart from each other. Between 0.2 and 1/km² (level 2), nuclei are stable and closer from each other but still apart. Above 1/km² (level 3), nuclei are more or less overlapping by their peripheral zone. Fig. 5 shows the extent of the areas corresponding to each level, and the observed dispersal from seven

capture points. From Spitz and Valet (1991) we extracted the average values of population density and long distance dispersal (recoveries at more than 20 km) given in table 1.

This table shows that, in our reference area, the greatest number of long-distance dispersers is produced by areas of level 3, though their dispersal rate is the lowest. Fig. 5 shows that very few long-distance dispersers were killed in areas of low density (2) compared to medium density (8) and high density (14). However this distribution is not very different from an expected distribution where proportions would be those observed for the total number after hunting (Table 2: 1, 4 and 19 respectively; Chi-square=6.32, df=2, P close to 0.05). Thus everything works as if long-distance dispersers were distributed in proportion of the density of the receiving population. With the assumption that colonisers would be distributed in the proportions observed in the recoveries, table 2 shows that the potential colonisers issued from long-distance dispersal represent half the resulting population in areas of level 1, and much less in other areas.

Tab. 1 - Estimation of long-distance dispersers from areas at different levels of population density of wild boar.

Area	Density (after hunting)	Long-distance dispersal rate	Total area (Km ²)	Total number (after hunting)	Total dispersers
Level 1	0.08/km ²	0.50	5,000	400	200
Level 2	0.50/km ²	0.20	10,900	5,450	1,090
Level 3	3.00/km ²	0.05	8,200	24,600	1,230

Tab. 2 - Participation of long-distance dispersers into the resulting population in each area.

Area	Total number (after hunting and dispersal)	Potential colonisers	Proportion of colonisers in resulting population
Level 1	200	200	50%
Level 2	4,360	830	16%
Level 3	23,370	1,490	6%

Large changes in numbers have been observed in areas of level 3 during the last two decades, whereas changes in areas of level 1 were very limited (Spitz & Valet, 1991). During the minimum phases, all the areas currently in levels 2 and 3 were at level 1, but this did not change

hunting data are available, the distribution in space of even the commonest species of large herbivores has been far from uniform. All species are first limited to a particular geographical range, then, within this range, show strong irregularities in their distribution.

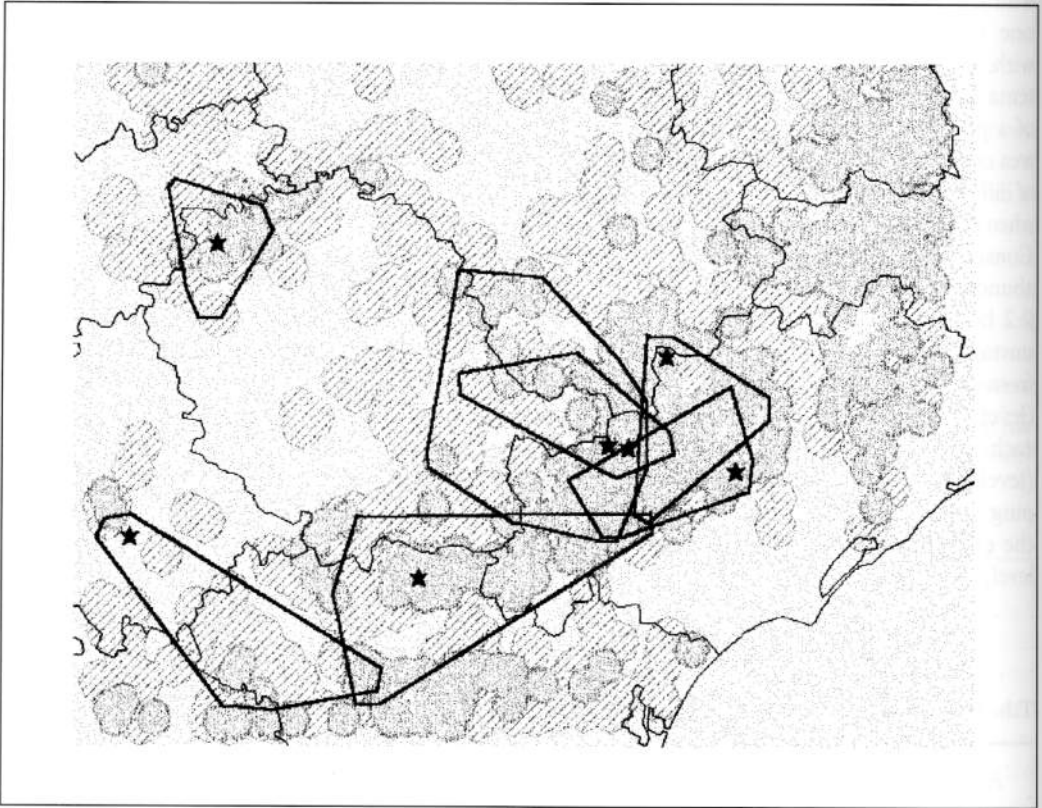


Fig. 5. Organisation of Wild boar populations and dispersal. White: populations of level 1. Hatched: populations of level 2. Shaded: populations of level 3. Polygons: area of dispersal from each of the seven marking sites (black stars). Scale is approximately 1/1,000,000.

greatly the number of potential colonisers (1910 vs 2320), thus ensuring a relative "stability" of the immigration flow. All these features encourage to test the corresponding long-term data with a metapopulation model.

5. Conclusion. Perspectives to the study of the palaeo-environment of man

During recent periods for which faunistic and

A part of these irregularities depends obviously of environmental factors, as shown for the distribution of densities of wild boar or the occurrence of red deer. Another part is linked with the recent history of each species: all large herbivores in France have a distribution that reflects recent events of restocking, colonisation or extinction. Another part could correspond

to self-organising distributional patterns. In the case of wild boar, if forest cover or landscape are the main factors that fix the carrying capacity of an area, a thorough analysis of demographic data show that this spatial structure seems to result from a metapopulation functioning, maintained mainly by dispersal, whereas changes in birth rate and survival might be responsible of the long-term changes observed in the more populated areas (that can contain 80% of the total population), thereby ruling the dynamics of the total number.

We have no reason to believe that populations of big game were more uniformly distributed in prehistoric times. Moreover, what we know of the plant cover and climate in Europe during the past 20,000 years suggests that paleolithic hunters tribes confronted very contrasting situations (and very different from the present) at a relatively small geographical scale. In fact glacial and postglacial climatic oscillations have occurred at about the same temporal scale as that necessary for the development of complex biocoenoses (a few centuries).

Consequently our territory, during this period, has been a changing patchwork of contrasting land covers, complicated by relief and variable extension of inlandis. Some of the potential prey were seasonally migrating, others were restricted to rare habitats, others lived in scattered flocks... The situation was very far from an ideal immutable wilderness, as opposed to the present landscape entirely rebuilt by modern Man. All these considerations militate for spatio-temporal patterns of big game populations as complicated and variable in the past as now.

Can prehistoric remains inform us on the distribution of ungulate species? If these remains are fragments of the entire body of large species, we can assume that they were located in the hunting ground or just beside. In contrast, selected fragments can suggest transportation of venison, but even in this case, nomadic tribes would have no reason to transport it too far. A relatively simple classification of remains (probably transported, probably not transported; species probably

hunted in flocks; species probably hunted on local movement or migration route; species probably snared or trapped; species probably hunted in very specific environment) could be used to draw several different maps of the potential distribution of the species hunted by prehistoric men. For instance, it would be interesting to compare a map of presence/absence of a species with a map of mass-kill of the same species. The main difficulty could come from the very large range of dates for which these remains are reported.

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