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Habitat isolation and genetic divergence of bank vole populations

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In a previous study (Paillat and Butet 1996), we demonstrated that bank vole, *Clethrionomys glareolus* (Schreber, 1780) populations in agricultural landscapes exhibited signs of extinction in relation to the size and the connectivity of hedge fragments as already shown in small woodlots by Apeldoorn et al. (1992). These processes could have effects on the genetic structure of populations and may enable identification of landscape parameters that control their dynamics. This has already been studied in several small mammal populations (Merriam et al. 1989; Bauchau and Le Boulengé 1991; Kozakiewicz and Konopka 1991; Hanski and Kuitunen 1986; Gebczynski and Ratkiewicz 1998) and we carried out preliminary investigations to test if such an effect can occur at the landscape scale from populations of different isolation context.

Bank voles were collected by live trapping in April 1996 at three stations of the Mont-Saint-Michel Bay (north Brittany, France) and were analysed by using enzymatic and epigenetic methods. The first station (BOC) is a woodlot (0.65 ha) within a dense hedge network landscape ("bocage") providing good conditions for dispersal of bank voles. The two other stations (POLD A and POLD B) are hedges situated in an adjacent intensive agricultural landscape on reclaimed areas ("polders"). They are small linear woody elements (0.11 and 0.17 ha), 3 km away from each other, and weakly connected with other woody elements of the network. Eight voles were collected in a woodlot situated 55 km away from the study area as a control sample for enzymatic study.

Homogenates of either liver, kidney, and heart of 30 bank voles (10 from each station) were assayed using horizontal starch-gel electrophoresis. Fourteen enzyme systems were chosen for screening (locus and EC number): (ADH; 1.1.1.1), (GPD; 1.1.1.49), (IDH; 1.1.1.42), (MDH; 1.1.1.37), (PGD; 1.1.1.44), (LDH; 1.1.1.27), (ME; 1.1.1.40), (SOD; 1.15.1.1), (PGM; 2.7.5.1), (AAT; 2.6.1.1), (ADA; 3.5.4.4), (ALP; 3.1.3.1), (ES; 3.1.1.1), (GPI; 5.3.1.9).

On the basis of Otto (1978), Sikorski and Bernshtein (1984), and Vasil'ev et al. (1996), the frequency of 11 uni- and bilateral non-metric traits (binary) were scored from 53 bank vole skulls (21 from BOC, 20 from POLD A and 12 from POLD B) (Fig. 1, Tab. 1). These traits are not correlated to each other and with age or sex of voles.

Epigenetic differentiation was assessed by calculating the mean measure of divergence (MMD) between each pair of populations as described in detail by Sjøvold (1977). Statistical significance of differences between populations was observed when the value of MMD was greater than double of the standard deviation of MMD. The measure of uniqueness (MU) was also calculated for each population, as the sum of all MMD used in comparing the population. For each population and in each skull variant the inter-indivi-

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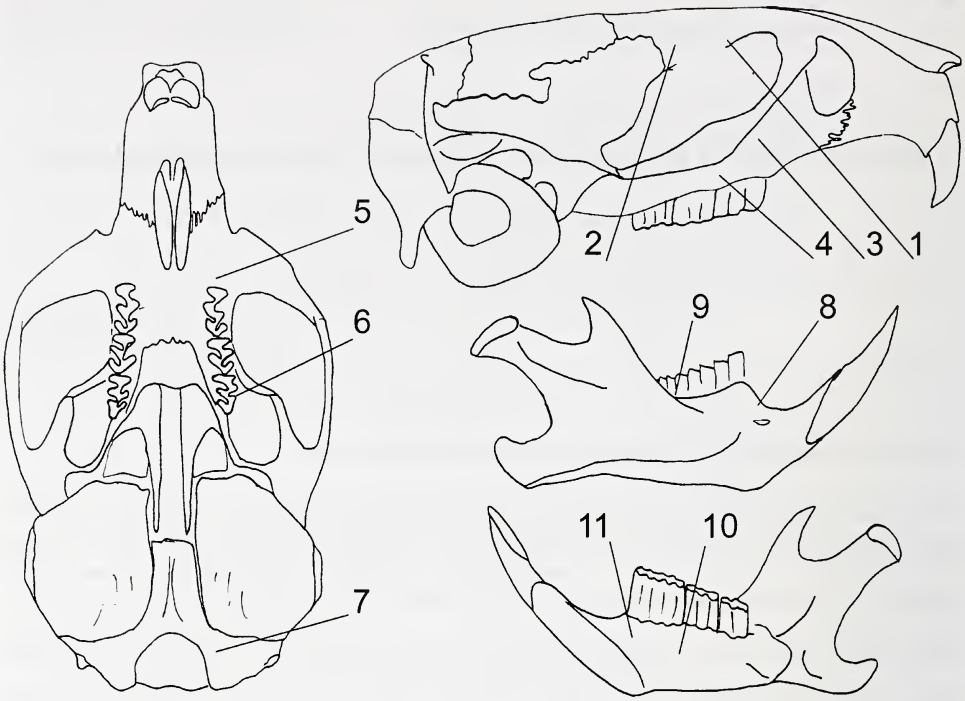

Fig. 1. Location of the 11 non-metrics traits scored in the bank vole skulls (number legends are detailed in table 1).

Table 1. Percentage frequencies of the 11 skull variants analysed (n = sample size).

Skull variants	Populations		
	BOC n = 21	POLD A n = 20	POLD B n = 12
1. Anterofrontal foramen double	71.1	45.1	58.1
2. Frontal foramen double	12.6	10.7	5.6
3. Foramen maxillare II present	66.4	91.7	78.3
4. Foramen maxillare III present	66.4	54.9	90.4
5. Foramen maxillare I present	45.3	18.1	33.8
6. Fourth M^3 buccal angle present	33.7	10.7	10.0
7. Foramen hypoglossi double	47.7	23.0	33.8
8. Foramen mentale II present	50.0	30.4	54.0
9. Dentary foramen present	52.3	67.2	82.3
10. Internal foramen mentale III present	73.4	47.5	78.3
11. Internal foramen mentale I present	28.9	25.5	17.7

dual variation was calculated as the standard deviation of the dichotomized character state values. The mean over the standard deviations of all variants (IV) served as an index of population-specific inter-individual variability (Hartl et al. 1993).

A total of 26 presumptive loci was identified by the electrophoretic study. All the loci were monomorphic and we neither observed variation in the gene loci of individuals of the three bank vole populations studied nor in the "control" group. Only epigenetic ana-

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Table 2. Phenetic distances (MMD) between populations and populations uniqueness (MU). Standard deviations of MMD are given in parentheses.

	POLD A	POLD B	MU
BOC	0.145* (0.0218)	0.0916* (0.0257)	0.2366
POLD A		0.1156* (0.0261)	0.2606
POLD B			0.2072

* = statistically significant divergence

lysis revealed differences. Observation of the matrix of phenetic distances between corresponding pairs of populations always showed significant differences between populations and the three measures of uniqueness were approximately similar (Tab. 2).

The distribution of skull variant frequencies in table 1 differed clearly from one population to another. Thus, the percentage of skull variant frequencies for frequency interval [40–60] were 36.4, 27.3, and 18.2 in BOC, POLD A, and POLD B respectively while they were 9.1, 36.4, and 45.5 for intervals [0–20] and [80–100]. These results indicate highly variable traits in the woodlot population from the bocage, whereas the two polder populations show more fixed traits. In the same way, IV values were higher in the bocage ($\bar{x} = 0.48$) than in the polder ($\bar{x} = 0.41$ and 0.42) (Krustal-Wallis Test, $P < 0.05$).

Fluctuation of heterozygosity can be linked to season and/or age, degradation, and patchiness of the forest communities (Fedyk and Gebczynski 1980; Leitner and Hartl 1988; Gebczynski et al. 1993; Gebczynski and Ratkiewicz 1998). Genetic divergences among bank vole populations over short geographic distances were observed by Leitner and Hartl (1988). However, in our fine-scale study, a total loss of heterozygosity was found both in samples and "control" groups. The small sample size (although consistent with population size) and the number of loci (although polymorphic in other studies), are perhaps partly responsible of the low heterozygosity obtained (Nei 1978), but we think that electrophoretic methods are probably inefficient to distinguish biochemical variation at our study scale.

The results with epigenetic techniques are in line with other fine scale studies on bank voles (Kozakiewicz and Konopka 1991; Sikorski and Bernshtein 1984). The three populations are genetically distinct and the analysis of the distribution of skull variant frequencies and IV values suggest that isolated populations from hedges have lost variability of their characters. Connectivity favours trait variability by promoting "rescue effects", favouring interpatch dispersal and reducing amplitude of fluctuation (Farhig and Merriam 1985; Henein and Merriam 1990). Inversely, like Kozakiewicz and Konopka (1991), we conclude that bank vole populations inhabiting small isolated habitats are subject to severe falls of density and extinction/recolonisation processes leading to the fixing of traits through "bottleneck" and founder effects.

Relationships between biochemical genetic and epigenetic variability are not clear (Hartl et al. 1993) but, in our fine-scale study, the epigenetic method appears better adapted to reveal intragenetic variation in patchy populations which can be tied to connectivity in the landscape.

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