Importance of Assessing Population Genetic Structure before Eradication of Invasive Species: Examples from Insular Norway Rat Populations

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Abstract: *Determining the inter-island migration abilities of pest species and delimiting eradication units enable more viable long-term eradication campaigns because recurrent colonization from neighboring islands is avoided. We examined the genetic structure of the invasive Norway rat (*Rattus norvegicus*) to identify gene flow between islands and delimit population units at different geographical scales. We investigated variation in eight microsatellite loci in rat populations from 18 islands, representing five archipelagos off the Brittany coast (France). Although most of the islands are isolated from each other, short genetic distances, weak* F_{ST} *values between close islands, and a high level of cross-assignment showed that individuals collected on different islands could represent a single population unit. A Bayesian clustering method also supported the existence of high levels of gene flow between some neighboring islands. Thus, the statement "one island equals one population" can be false when inter-island distances are less than a few hundred meters. Genetic studies enable the definition of island clusters among which migration may occur that should be considered eradication units. To avoid reinvasion and to minimize ecological and economic costs, rats on all islands in an eradication unit should be eradicated simultaneously. We suggest that the genetic monitoring we performed here can be applied for management of any pest.*

Key Words: assignment test, biological invasion, eradication unit, islands, microsatellite markers, population structure, *Rattus norvegicus*

Importancia de la Estimación de la Estructura Genética Poblacional Antes de la Erradicación de Especies Invasoras: Ejemplos con Poblaciones Insulares de *Rattus norvegicus*

Resumen: *La determinación de las capacidades de migración interinsular de especies plaga y la delimitación de unidades de erradicación hace posible que las campañas de erradicación sean más viables a largo plazo porque se evita la recolonización recurrente desde islas vecinas. Examinamos la estructura genética de la rata* Rattus norvegicus *para identificar el flujo de genes entre islas y delimitar unidades poblacionales en diferentes escalas geográficas. Investigamos la variación en ocho loci microsatélites en poblaciones de ratas de 18 islas, representando a cinco archipiélagos de la costa de Bretaña (Francia). Aunque la mayoría de las islas están aisladas unas de otras, las distancias genéticas cortas, los valores* F_{ST} *débiles entre islas cercanas y un alto nivel de asignación cruzada mostraron que los individuos recolectados en islas diferentes pudieran representar a una sola unidad poblacional. Un método de agrupamiento Bayesiano también sostuvo la existencia de altos niveles de flujo génico entre algunas islas cercanas. Por lo tanto, la afirmación de que "una isla equivale a una población" puede ser falsa cuando las distancias interinsulares son menores a unos cuantos cientos de metros. Los estudios genéticos permiten la definición de grupos insulares, entre los que puede ocurrir migración, y que*

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deben ser considerados como unidades de erradicación. Para evitar la reinvasión y para minimizar costos ecológicos y económicos, se debería erradicar simultáneamente a las ratas de todas las islas en una unidad de erradicación. Sugerimos que el monitoreo genético que realizamos puede ser aplicado para el manejo de cualquier plaga.

Palabras Clave: estructura poblacional, invasión biológica, islas, marcadores microsatélite, prueba de asignación, *Rattus norvegicus*, unidad de erradicación

Introduction

During the last few centuries, the rate of biological invasions has accelerated, presumably as a result of increased international trade and transport (Di Castri 1989; Mack et al. 2000; Pascal et al. 2003). Because invasive species have been identified as the second main cause of biodiversity loss after habitat destruction (Alonso et al. 2001) and the main cause of species extinctions in island ecosystems (Clout & Veitch 2002), studies of processes of colonization and control of alien populations are major topics for conservation biologists and a priority for wildlife management (D'Antonio & Kark 2002).

The Norway rat (*Rattus norvegicus*), the ship rat (*R. rattus*), and the Pacific rat (*R. exulans*) have been introduced to more than 80% of the world's islands (Atkinson 1985). The Norway rat is regarded as one of the world's 100 worst invasive alien species (Lowe et al. 2000). It is known to have caused declines or extinctions of many insular species (Atkinson 1985), including birds in Brittany (Kerbiriou et al. 2004). Moreover, the Norway rat often acts as a reservoir and vector of several pathogenic agents such as *Leptospira interrogans* (Sunbul et al. 2001) and *Salmonella enterica* (Hilton et al. 2002).

Results of many studies show that eradication of alien mammals is a powerful conservation tool for insular ecosystems, and many spectacular recoveries of threatened species have followed eradication campaigns (Towns et al. 2001; Graham & Veitch 2002; Kerbiriou et al. 2004; Pascal et al. 2005). Recent technical advances allow the eradication of the Norway rat from islands of more than 3000 ha, three orders of magnitude larger than was possible 40 years ago (Clout & Veitch 2002). Nevertheless, eradication operations typically have large economic and ecological costs. Although many eradication campaigns have succeeded, some have failed (Thorsen et al. 2000). For example, among the eradication campaigns conducted on 144 New Zealand islands, 7% failed (Courchamp et al. 2003). Thus, before an agency invests in an eradication campaign, risks and causes of eradication failure should be assessed.

On islands, one major risk of eradication failure is the ability of the target species to recolonize from neighboring islands or from the adjacent mainland. Groups of islands interconnected or geographically close enough to allow migration have been called "eradication units" (Robertson & Gemmell 2004). Such eradication units can be defined as genetically isolated units with clusters of populations that must be eradicated at the same time in order to maximize the long-term success of the operation. Identifying eradication units is not easy because migration patterns depend on multiple biological, geographical, and human factors (Russell & Clout 2004). Moreover, direct observations of migration events do not easily allow identification of routes of potential recolonization, in particular if migration events are rare. Analyzing the genetic population structure of the target species among the cluster of islands and interpreting it in terms of gene flow may provide an alternative approach to identifying eradication units.

Genetic information on Norway rat populations in the wild is scarce and generally not oriented toward population structure (Klöting et al. 1997, 2003; Voigt et al. 1997, 2000). The Norway rat is native to northern China and Mongolia. It reached Europe in the fourteenth century and spread throughout Western Europe in the eighteenth century (Vignes & Villié 1995). A previous mtDNA study of genetic variation of Norway rat populations was conducted in the insular complex of Ushant Island and the Molène Archipelago off the Brittany coast (Calmet et al. 2001). This study demonstrated that, in most cases, each population on each island was founded independently and they do not exchange migrants. Nevertheless, low levels of genetic differentiation within two pairs of islands suggested that migration events were likely.

To extend the results of Calmet et al. (2001) in more diversified insular situations, we investigated genetic variation in Norway rat populations from 18 islands in five archipelagos off the Brittany coast. Analysis of the genetic structure of these insular populations was performed using several spatial scales and led to an a posteriori discussion about successes and checks on evaluation of the eradication attempts. Our aim was to acquire information about the invasion history of the Norway rat on the Brittany islands.

Methods

Population Sampling

We collected 510 individuals from three mainland sites and 18 islands off the coast of Brittany. The sampled islands

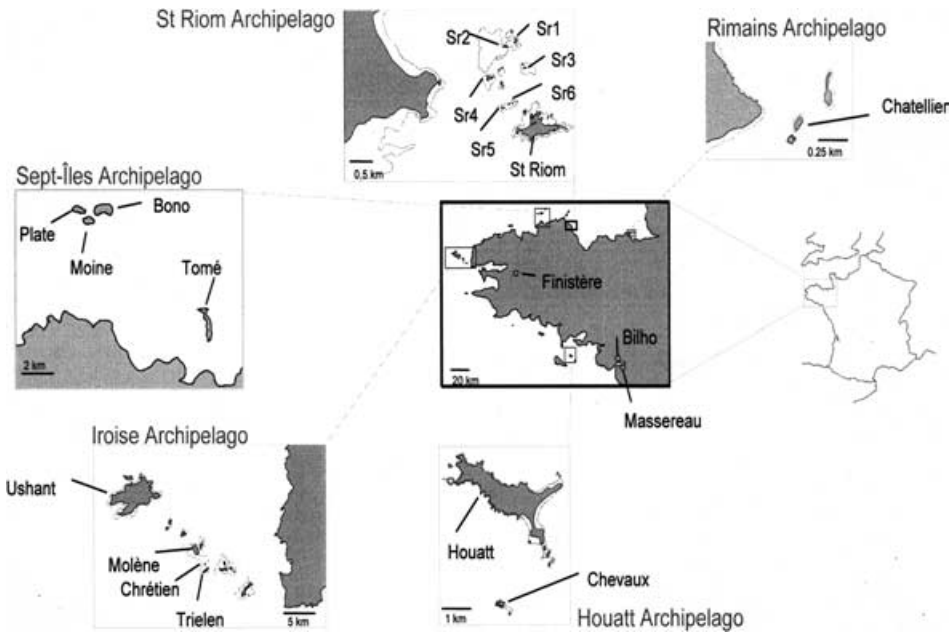

Figure 1. Map of the Brittany coast showing the five archipelagos and the mainland samples of the Norway rat. Site names are abbreviated elsewhere in the text as follows: Iroise Archipelago: Ou, Ushant Island; Mo, Molène; Tr, Trielen Island; Ic, Chrétien Island; Rimains Archipelago: Ca, Chatellier Island; Continental samples: Fi, Finistere; Bi, Bilho; Ma, Massereau; Sept-Iles Archipelago: Bo, Bono Island; Im, Moine Island; Pl, Plate Island; To, Tomé Island; St. Riom Archipelago: Sr0, St. Riom Island; Sr1 to Sr6, Islet 1 to 6; Houatt Archipelago: Ho, Houatt Island; Ch, Chevaux Island.

belong to five different archipelagos (Fig. 1). Except for the Ushant and Houatt individuals, the insular samples were collected during rat eradication attempts (Pascal et al. 1996; Kerbiriou et al. 2004; Lorvelec & Pascal 2004; Pascal & Lorvelec 2005). The strategy used for these eradications included successive trapping and poisoning. Trapping allowed the capture of more than 90% of the individuals. Including three mainland samples enabled comparison of genetic diversity between insular and mainland populations. Because the mainland samples were not collected on the coast adjacent to the islands, they were not used to identify the geographical origin of the insular population founders. Where the number of trapped animals was < 20, all individuals were analyzed, whereas only subsamples were used when this number exceeded 20 (Table 1). Norway rat phalanges were preserved in 80% alcohol and stored at 4° C before extraction of genomic DNA with the DNeasy 96 tissue kit (Qiagen, www.quiagen.com). Owing to problems of preservation, some older samples had a high percentage of missing data.

Detection of Length Polymorphism of Microsatellite Loci

To investigate genetic variation we used eight microsatellite markers previously characterized for Norway rat genome mapping (Jacob et al. 1995; D10Mit5, D11Mgh5, D13UW1, D19Mit2, D10Rat20, D7Rat13, D5Rat83, and D16Rat81). The microsatellite loci were chosen on the basis of their location on different chromosomes to avoid potential linkage. Each forward primer was labeled with fluorescent dyes before amplification by polymerase chain reaction (PCR), with an annealing temperature of 55° C and 35 cycles, except for D13UW1 and D19Mit2 (40 and 37 cycles, respectively). The PCR was performed in 10 μL volumes, containing 1μg DNA, 0.1μM of one primer labeled with 5′ fluor labels and 0.2 of the other primer, 0.2μM of each dNTP, 1 unit Taq polymerase, and 1X reaction buffer with 1.5mM $MgCl_2$. All PCR products were pooled in a single run on an ABI prism 310 capillary electrophoresis system (Applied Biosystems, Foster City, CA). Amplification size was scored using GeneScan Analysis software (Applied Biosystems, version 3.1.2).

Statistical Treatments

Analysis of Within-Population Variation

We calculated numbers of alleles for each locus and population with the program Microsatellite Analyser (MSA) 3.00 (Dieringer & Schlötterer 2002). For small populations (<20) all individuals were analyzed. Thus, for small populations, exact distributions of allele numbers were obtained and not estimated. Because other populations' sample sizes were not small, corrections for differences in sample size were useless. To be cautious, however, we computed the frequency of each allele per locus, observed heterozygosity, expected heterozygosity, and deviations from Hardy-Weinberg expectations with GENEPOP software (version 3.3, Raymond & Rousset 1995). For loci with fewer than five alleles, an exact test of Hardy-Weinberg proportions was performed. For loci with five or more alleles, we obtained an unbiased estimate of the exact probability by using the Markov chain method of Guo and Thompson (1992) for each combination of locus and population. We used sequential Bonferroni tests to

Table 1. General information and genetic diversity of the Norway rat on Brittany islands from eight microsatellite markers.[a]

Archipelago/continental area	*Island[b]/site*	*Surface (ha)*	n	A	H_e	H_o	p[c]
Insular samples							
Houatt	Chevaux	293	11	1.38	0.10	0.10	—
	Houatt	2.5	24	2.50	0.39	0.27	0.03
	$F_{ST} = 0.68$						
Iroise	Ushant	1557	20	4.00	0.56	0.47	0.003
	Molène	45.3	17	3.63	0.48	0.42	—
	Trielen	14.5	24	2.13	0.20	0.18	—
	Chrétiens	1.3	12	1.25	0.07	0.09	—
	$F_{ST} = 0.52$						
Sept-Îles	Bono	22	96	3.75	0.48	0.49	—
	Moines	9	24	3.50	0.51	0.49	—
	Plate	5	24	3.75	0.47	0.47	—
	Tomé	30	72	4.62	0.60	0.59	—
	$F_{ST} = 0.33$						
St. Riom	St. Riom	14.5	45	4.38	0.53	0.51	—
	Sr1	<1	12	2.13	0.39	0.49	—
	Sr2	<1	13	2.25	0.40	0.44	—
	Sr3	<1	7	2.25	0.42	0.56	—
	Sr4	<1	23	3.38	0.46	0.51	—
	Sr5	<1	5	2.38	0.41	0.43	—
	Sr6	<1	8	2.88	0.46	0.48	—
	$F_{ST} = 0.09$						
Rimains	Chatellier	1.5	32	4.50	0.63	0.64	0.005
Overall insular	$F_{ST} = 0.41$						
Continental samples							
Finistère	—	—	24	8.63	0.77	0.70	**
mouth of the Loire River	Massereau	—	7	5.63	0.75	0.85	-
	Bilho	—	17	5.63	0.69	0.63	**

[a] *Key:* n, *number of rats genotyped;* A, *mean number of alleles among loci;* H_e *and* H_o, *expected and observed heterozygosity, respectively.*
[b] *The* F_{ST} *values have been calculated among islands within each archipelago and among all islands.*
[c] *Hardy-Weinberg equilibrium global test (-, not significant; **, highly significant).*

compute the critical significance levels for simultaneous statistical tests (Rice 1989). Genotypic associations between all pairs of loci were tested for each sample with Fisher's test on R × C contingency tables in GENEPOP 3.3.

Analysis of Population Structure

The F_{IS}, F_{ST}, and F_{IT} parameters were estimated following Weir and Cockerham (1984). We tested the significance level of the F_{ST} value for each population pair by calculating the p value of the F_{ST} estimate. We conducted all these calculations with MSA 3.00 and determined significance levels by making 10,000 permutations of genotypes among groups. A pair-wise matrix of Cavalli-Sforza and Edwards chord distance (Cavalli-Sforza & Edwards 1967) was obtained with MSA, and a dendrogram was constructed using the neighbor-joining method (Saitou & Nei 1987). We estimated node support with 1000 bootstrap replicates in the software package PHYLIP 3.5c (Felsenstein 1989).

To assess the structure of insular populations, we performed an analysis of molecular variance (AMOVA) with Arlequin 2.001 software (Schneider et al. 2000). Genetic variation was partitioned into three levels: within islands, among islands within archipelago, and among archipelagos.

The number and the geographical limits of the insular populations were inferred using two different assignment tests. We considered only individuals successfully typed for more than four loci (i.e., more than 50% of the genotypic information). With this exception, both tests were applied to the whole data set. First, the fully Bayesian clustering method implemented in Structure (version 2.1, Pritchard et al. 2000) was used to determine the most likely number (K) of population units. The program was run five times for each value of K from 1 to 18 (i.e., the number of islands). For each value of K, the run with the highest likelihood was retained. We used the model with admixture and the correlated frequencies option. No information on population origin of the individuals was used. After some preliminary tests of the convergence time needed for the Monte-Carlo Markov Chain, a burn-in period of 100,000 steps followed by 500,000 steps was chosen. Once the number of population units K was estimated, the proportion of membership of each island (e.g., the proportion of genome sampled on it) in each cluster was calculated.

We also explored population structure (GENECLASS software, version 1.0.02, Cornuet et al. 1999). These assignment and exclusion methods, originally used to identify the geographic origin of an unknown individual (Eldridge et al. 2001; Manel et al. 2002), can also be used as accurate tools for understanding real-time population structure and spatial dynamics (Paetkau et al. 1995; Kyle & Strobeck 2001; Cegelski et al. 2003). The assignment test estimates the likelihood of the multilocus genotype of a given individual originating from one of a set of putative source populations and determines its most probable origin. We also computed the cross-assignment percentage, defined as the percentage of individuals assigned to an island other than the one on which they were sampled.

A complementary statistical approach involves performing an exclusion test (Cornuet et al. 1999), that is, calculating the probability that a population is the origin of each individual, with a given threshold. We chose a threshold of 0.05 and obtained the rejection probability by simulating 10,000 individuals from allelic frequencies. Although the previous assignment test indicates only the "most likely origin" of an individual, the exclusion test allows (1) statistical rejection of all the populations if the "real origin" has not been sampled and (2) identification of the populations that cannot be statistically rejected as origin of an individual even if they are not the most likely.

We chose the Bayesian method, first proposed by Rannala and Mountain (1997), because Cornuet et al. (1999) showed with various simulated data sets that it was the most accurate of the three available in GENECLASS. To compute the allelic frequencies in each population, we used the "leave one out" option.

Finally, we used two tests of the relation between the geographic distance and the level of differentiation between islands. First, a Mantel test was conducted (Mantel 1967) comparing the matrix of log-transformed geographic distances between all the islands (shortest distance coast to coast) to the pair-wise F_{ST} matrix with Genetix software (version 4.05, Belkhir et al. 1996–2004). Second, because only intra-archipelago comparisons are relevant regarding short-distance migration, the significance level of the Pearson correlation coefficient for all intra-archipelago pairs of islands was also calculated.

Results

Within-Population Genetic Diversity

The tests for linkage disequilibrium were not significant. Thus, we assumed the microsatellite loci were independent for all statistical treatments. All eight loci were polymorphic in at least one population. The total number of alleles per locus ranged from 9 to 25 and the mean observed heterozygosity per population ranged from 0.09 to 0.85 (Table 1). The mean number of alleles over all loci was significantly larger for the mainland samples (from 5.63 to 8.63) than for insular samples (from 1.25 to 4.62) when they were compared with a Wilcoxon signed rank test ($p = 0.035$). Global departure from Hardy-Weinberg equilibrium was observed on Ushant, Chatellier, and Houatt islands and on the mainland. These global tests, however, are only supported by zero to two loci in separate tests after sequential Bonferroni corrections.

Population Structure Analysis

The analyses of molecular variance showed that the within-island level explained 90.18% of the total genetic variance, whereas the among-islands-within-archipelago and among-archipelago components explained, respectively, 4.89% and 4.93%. The variance components among archipelago, among islands within archipelago, and within islands were 0.025, 0.024, and 0.454, respectively. The three hierarchical levels of the analysis were significant. The F_{ST} values calculated between all pairs of insular populations were significant for all pair-wise comparisons except between most islands of the St. Riom Archipelago. These analyses revealed a high level of population structure within as well as between archipelagos. Most islands are highly differentiated from each other, even within an archipelago. Indeed, Houatt and Chevaux islands in the Houatt Archipelago, Molène and Ushant islands from the Iroise Archipelago, Tomé Island from the Sept-Iles Archipelago, and Chatelliers Island from the Rimains Archipelago were all separated from all other samples by high genetic distances (Fig. 2). All individuals from this set of islands, except one from Tomé Island, were assigned to the island where they were trapped by GENECLASS (Table 2). Other islands, even in the same archipelago, were rejected as possible origins (data not shown). Each sample was identified as a single population by clustering methods, by the program Structure, when K increased (Table 3).

In three cases there was little or no population structure. First, among the islands of the Iroise Archipelago, short genetic distances separated Trielen and Chrétien islands, and in the neighbor-joining tree (Fig. 2) their grouping was supported by a bootstrap value of 99%. Moreover, although the cross-assignment percentage between these two islands was low (Table 2), most individuals could not be statistically rejected from both islands by exclusion tests (data not shown). The clustering methods grouped these two islands together even for $K = 10$ (Table 3).

Second, on the distance tree Sept-Iles Archipelago islands (except Tomé Island) are close to each other, and their grouping was supported by a bootstrap value of 95%. When we exclude Tomé Island from the archipelago, the global archipelago F_{ST} decreased from 0.33 to 0.07 and the within-archipelago cross-assignment percentage increased from 11.9% to 17.7%. The exclusion test revealed that few individuals from each island were excluded from

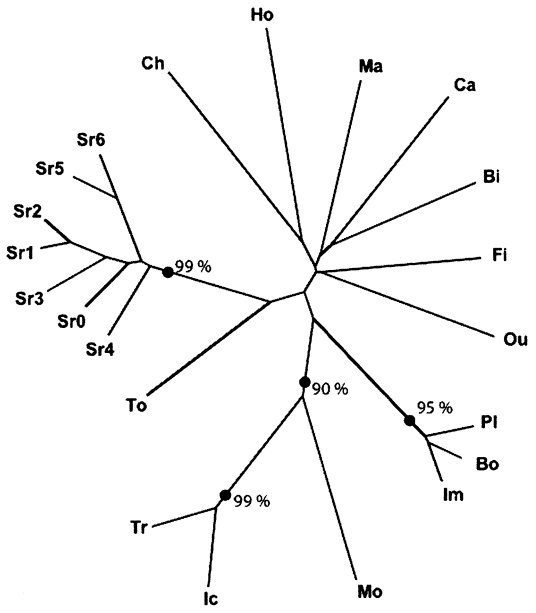

Figure 2. Neighbor-joining tree of insular and mainland populations of Norway rat. Nodes supported by bootstrap values greater than 80% are indicated. Abbreviations defined in Fig. 1 legend.

the other islands. Moreover, the three islands shared all their alleles. A clustering process grouped them in one cluster for $K = 7$, but a split that did not correspond to the islands' geography was obtained with higher K values.

Finally, no structure was observed among the islands of the St. Riom Archipelago. The F_{ST} value for this archipelago was very low (0.09). The short genetic distances between these islands were supported in the dendrogram by a bootstrap value of 99%. The cross-assignment percentage within this archipelago was 36.4%, and the exclusion test showed that all islands of this archipelago are possible origins for each individual. The individuals of St. Riom islands were grouped in the same cluster for all tested values of K.

The Spearman correlation coefficient calculated between intra-archipelago geographic distances and F_{ST} was significant. The Mantel test conducted on the whole inter-island distance matrix was also highly significant.

Discussion

From Genetic Structure to Gene Flow

One of the critical issues in interpreting the distribution of genetic variation among populations is that shared polymorphism, and hence genetic proximity, can be due to either a shared origin or ongoing gene flow. For the purpose of eradication projects, it is critical to distinguish between these two sources of genetic similarity because ongoing gene flow with neighboring islands could lead to project failure because of recolonization. Another misleading situation that is critical to detect in eradication projects is the existence of low and/or recent gene flow between populations that have previously diverged and, thus, cannot be interpreted as totally isolated from each other.

Nevertheless, unintentional introductions or invasions of mammals on islands generally involve few individuals (Kilpatrick 1981; Berry 1986). During population foundation, random sampling effects can lead to an immediate burst of differentiation (Mayr 1954; Berry 1983). Detecting such founder effects depends on the variability of the genetic marker used. Indeed, if the markers were highly polymorphic in the source population, two independent samplings of one or a few individuals could lead to an instantaneous, strong genetic differentiation between two populations founded independently. The differentiation is then accentuated by genetic drift over time and may, apart from differences in gene frequencies, also involve the existence of private alleles (e.g., alleles present on only one island). In such situations, even low or recent exchange between populations located on different islands should be detected (Slatkin 1985). In the case of important founder effects and when we use polymorphic markers as microsatellites, the detection of a genetic proximity between two populations should be interpreted as ongoing gene flow.

Population Genetics and Colonization Dynamics

The interpretation of the structure of genetic variability in terms of population founding and migration events was congruent with information about colonization history and geography. Most islands are geographically completely isolated, and thus the genetic distance between populations on separate islands is usually large. For all these isolated islands, all the individuals were assigned without ambiguity to the island where they have been trapped. A clustering method indicated that each of these islands contained a single biological population. Moreover, the level of intrapopulation variability was lower than in mainland populations, which indicated both small population size and probable bottleneck effects during the founder event. These results are in accordance with the well-established theoretical relationship between population bottlenecks and loss of genetic variation (Wright 1931; Nei et al. 1975; Chakraborty & Nei 1977).

For example, the Norway rat was first reported on Trielen Island following a shipwreck in 1912. The very low genetic diversity of the population eradicated on this island in 1996 can be interpreted as resulting from a very limited number of founders from this shipwreck (the extreme would be a single pregnant female). This island is geographically highly isolated from other islands of the Iroise Archipelago except Chrétien Island, to which it

Table 2. Results of the Norway rat island assignment test with GENECLASS (Belkhir et al. 2004).[a]

			Continental			*Insular*																
Location		n	*Fi*	*Ma*	*Bi*	*Ch*	*Ho*	*Mo*	*Ou*	*Tr*	*Ic*	*Bo*	*Im*	*Pl*	*To*	*Sr0*	*Sr1*	*Sr2*	*Sr3*	*Sr4*	*Sr5*	*Sr6*	*Ca*
Continental	Finistère	24	23[b]																				1
	Massereau	7	1	6[b]																			
	Bilho	16		1	15[b]																		
Houatt	Chevaux	24				24[b]																	
	Houatt	10					10[b]																
Cross-assignment = 0%																							
Iroise	Molène	14						14[b]															
	Ushant	18							18[b]														
	Triélen	22								19[b]	3												
	Chrétien	9									9[b]												
Cross-assignment = 4.7%																							
Sept-Iles	Bono	83										72[b]	3	8									
	Moine	23										3	16[b]	4									
	Plate	24										2	3	19[b]									
	Tomé	72												1	71[b]								
Cross-assignment = 11.9%																							
St. Riom	St. Riom	38														29[b]	1	1	1	4		2	
	Sr1	2																1		1			
	Sr2	6														1	1	3[b]	1				
	Sr3	3														2					1		
	Sr4	15														2		1		11[b]	1		
	Sr5	5																		1	2[b]	2	
	Sr6	8														3					1	4[b]	
Cross-assignment = 36.4%																							
Rimains	Chatellier	32																					32[b]

[a] *For each sampling location (horizontally), the number of individuals assigned to each population is indicated (*n *is the sample size). Framed are the intra-archipelago assignments (i.e., individuals assigned to an island belonging to the archipelago they have been sampled in). The percentage of cross-assignments for each archipelago is indicated under location. Location abbreviations are given in Fig. 1 caption.*

[b] *Number of individuals assigned to the island where they have been sampled.*

Table 3. Results of Bayesian clustering analysis (in STRUCTURE) for values of *K* from 7 to 10 (Pritchard et al. 2000).*

		K			
Archipelago	*Island*	*7*	*8*	*9*	*10*
Houatt	Chevaux	1	1	1	1
	Houatt	1	1	2	2
Iroise	Ushant	2	2	3	3
	Molène	3	3	4	4
	Trielen	3	3	4	5
	Chrétien	3	3	4	5
Sept-Iles	Bono	4	4 & 5	5 & 6	6 & 7
	Plate	4	4 & 5	5 & 6	6 & 7
	Moine	4	4 & 5	5 & 6	6 & 7
	Tomé	5	6	7	8
St. Riom	St. Riom	6	7	8	9
	Sr1	6	7	8	9
	Sr2	6	7	8	9
	Sr3	6	7	8	9
	Sr4	6	7	8	9
	Sr5	6	7	8	9
	Sr6	6	7	8	9
Rimains	Chatelliers	7	8	9	10

**Populations of Norway rat on islands with the same number are clustered. Clusters are arbitrarily numbered from 1 to* K.

is partially connected at low tide. All the other islands of the Iroise Archipelago are genetically highly divergent and show many private alleles, which allows the establishment of a genetic signature for each island. It is likely, as noted by Calmet et al. (2001), that *R. norvegicus* populations on each island correspond to independent colonization events.

Another situation is found in the Sept-Iles Archipelago. Populations on all islands (except Tomé) are genetically close, as would be expected from the short geographical distances. The analyses of the genetic structure suggest at least two founding events and no subsequent genetic exchanges between Tomé and the three others islands. Finally, the Houatt Archipelago reveals yet another situation: The rat population on Chevaux Island exhibits reduced genetic diversity compared with the population on Houatt Island. Most alleles present in the former are also present in the latter. These results support the hypothesis of a step-by-step colonization, first on Houatt Island and then on Chevaux Island. This last case can be interpreted as a shared origin with an absence of current gene flow. Historical data support this hypothesis. During the nineteenth century, the farmers on Houatt brought their cattle to Chevaux Island and back once a year and may then have mediated the transfer of Norway rat specimens between the islands.

From Gene Flow to Eradication Strategies

Evidences of migration between islands can be revealed by studyinig genetic structure. In our study, such signatures of rat movements result from insular systems exhibiting short inter-island distances. This is exemplified in the St. Riom Archipelago, the three adjacent islands in the Sept-Iles Archipelago, and the islands Trielen and Chrétien of the Iroise Archipelago. Only homogenization by regular migration events can generate such genetic similarities. Although our study did not allow the determination of a distance threshold below which migration between islands would be expected, less than a few hundred meters does not seem enough to prevent migration. Such information suggests particular eradication strategies. For isolated islands (e.g., islands without other islands or mainland within a few kilometers), it is reasonable to focus the eradication on the chosen island only. Conversely, when islands are connected by consistent gene flow, eradication should include whole groups of islands simultaneously. Geographical evidence is not sufficient to determine the eradication scale, particularly when information about the colonization ability of the target species is scarce. To minimize failure risks, reduce eradication cost and environmental impact, and avoid eradication on scales larger than necessary, indirect methods with genetic markers should be a preliminary step in the management process. Such genetic monitoring could be extended to any pest species for which a clear direct measure of gene flow is not available.

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