

Geographic distribution of consanguinity in Europe

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Summary. Average consanguinity (α) of 20 large regional or national samples derived from Roman Catholic Dispensations or state archives shows a strong negative relationship with latitude ($r = -0.738$; $P < 0.001$) which seems best explained by cultural-historical factors. Isolates show no such pattern and are more variable in their inbreeding levels. Two-way analysis of variance shows the sample division by population size to be significant, the division by geography to be not significant, with no significant interaction between the two factors. In a one-way analysis of variance only the mainstream samples showed significant geographic differences ($P < 0.001$). There is no such geographic association in Japan which has greater cultural and historical homogeneity. The clinal patterning in average consanguinity may bias frequency estimates of rare alleles, including genetic disorders.

1. Introduction

Western Europe is said to form a distinct demographic region, characterized by late age at marriage and high celibacy rates, termed the European marriage pattern (Hajnal 1965). If this is correct, Europe may be conveniently treated as a single region for purposes of genetic analysis. To examine this claim the geographic patterning of inbreeding levels on European populations was investigated, using published estimates of consanguinity for 20 samples falling within the limits of Hajnal's (1965) Western European marriage region.

2. Materials and methods

Average consanguinity (Wright 1921, Bernstein 1930, Wright 1951) was estimated as:

$$\alpha = \sum p_i F_i$$

where p_i equals the frequency of consanguineous marriages which would result in offspring with inbreeding coefficient F_i . No attempt was made to include matings more distant than second cousins ($F = 1/64$) or to add generational depth to the sample data.

Most data on inbreeding in Europe derive from the requirement of the Roman Catholic Church for dispensation to marry close relations (Moroni 1961, Serra 1961). The data from Belgium, France, Italy, Sardinia, Spain, Czechoslovakia and Ireland (Eire and the North) are from diocesan dispensations, while data from The Netherlands were derived from state archives (Polman 1951, in Cavalli-Sforza and Bodmer 1971) and those for the UK from medical surveys (Bell 1940, Kilpatrick, Mathers and Stevenson 1955) which follow political boundaries.

The mainstream data relate to the first half of this century, although several samples include some marriages contracted at the end of the nineteenth century. The latest data from each region are used because of considerable secular change in inbreeding rates (Roberts 1975, Pettener 1981, 1985).

Because of the special constraints on marriage patterns (Roberts 1975, Jorde 1980), socially, geographically or genetically isolated populations are treated separately. Data

for isolates almost always derive from pedigrees and would include more than one generation, and higher values of α would be expected. They are therefore not strictly comparable to the data for mainstream populations but may be at least compared amongst themselves.

To quantify the distribution of inbreeding in Europe, latitude of study site (or national or regional capital if study site was not designated) was compared with the value of α normalized for use in parametric analysis to 1_n ($\alpha \times 10^{-4}$), calculating the linear regression coefficient and Pearson's coefficient of correlation to estimate change of average inbreeding levels with geographical distance. A two-way analysis of variance was also performed on the sample, dividing it by size of sampled region (mainstream v. isolate) and geographical zone (Southern Romance-speaking v. Northern), and a one-way analysis of variance separately on mainstream and isolate populations, again subdividing by geographical region.

3. Results

For the samples utilized, table 1 indicates their origin, latitude, year(s) in which the data were collected, average sample consanguinity (α) as far as second cousins, nature of sample, data source, and reference. The mainstream sample size is assumed to be very large. Similar information for the isolate populations is summarized in table 2.

For the mainstream populations, the linear regression of 1_n average population consanguinity $\times 10^{-4}$ (Y) on latitude (X) is:

$$Y = 9.504 - 0.613 X \text{ (SD} = 0.599; R^2 = 0.615)$$

The simple Pearsonian coefficient of correlation is -0.784 ($P < 0.001$). These results suggest a strong negative curvilinear relationship, inbreeding being lowest in Northern Europe and highest in Southern Europe (figure 1). The levels of inbreeding range from 0.0001 in The Netherlands to 0.00221 in Spain.

For European isolate populations the relationship between latitude and inbreeding levels is not apparent. If all 15 isolates in table 2 are considered, the coefficient of correlation is very low ($r = 0.162$; $R^2 = 0.026$) between latitude and inbreeding. If the exceptionally high value for the Irish Tinkers is ignored, the correlation between the two variables is reduced to -0.111 ($R^2 = 0.012$), again not significant ($P < 0.3$). In sum, results for isolated populations suggest no demonstrable geographical pattern to compare with that found in the mainstream samples. Rather, the isolate populations appear to be more influenced by local demographic factors such as community size (Serra and Soini 1959, Relethford 1985) or mate availability (Brennan and Boyce 1980, Brennan 1981, Dyke 1984).

The two-way analysis of variance (table 3) indicates that there is a strong and significant population size component to the inbreeding level but that geographic considerations are less important. The interaction factor is very weak. If the mainstream and isolated groups are tested separately by one-way analysis of variance (table 4) the results of the regression analysis re-emerge with the mainstream populations showing a considerable geographical bias and the isolates not.

4. Discussion and conclusions

From the limited number of studies available, the mean population consanguinity increases rapidly and non-linearly from Northern to Southern Europe. No effect is implied of any environmental or geographical influence in this observation; instead, it

Table 1. Mean coefficient of inbreeding (α) in mainstream European populations.

Sample site	Latitude ($^{\circ}$ N)	Years	α	Sampling frame	Data type source	Reference
<i>Northern Groups</i>						
Netherlands	52.5	1937-1948	0.000094	National	State Archives	Polman 1951 (in Cavalli-Sforza and Bodmer 1971)
Ireland	53.4	1959-1968	0.000158	National	RC Dispensations	Masteron (1973)
Belgium	50.9	1918-1959	0.0005	National	RC Dispensations	Twisselmann (1961)
Anversa, Belgium	51.2	1926-1950	0.000292	Provincial	RC Dispensations	Deraemker (1958)
Münster, Germany	52.0	1899-1951	0.000195	Diocese	RC Dispensations	Panse and Krings 1949 (in Serra 1961)
Cologne, Germany	51.0	1893-1943	0.000303	Diocese	RC Dispensations	Mueller 1953 (in Serra 1961)
England and Wales	51.5	1925-1939	0.000263	National	Survey	Bell 1940
Tyrone and Londonderry	55.0	1954	0.000362	Provincial	Survey	Kilpatrick <i>et al.</i> (1955)
Czechoslovakia (Brno)	49.2	1930-1966	0.000275	Diocese	RC Dispensations	Zahálková and Preis (1970)
<i>Southern Groups</i>						
Finistère, France	48.3	1911-1953	0.0011	Province	RC Dispensations	Sutter and Tabah (1955)
Loir-et-Cher, France	47.7	1812-1954	0.0011	Province	RC Dispensations	Sutter and Tabah (1955)
Corsica	42.0	1926-1945	0.002360	Department	RC Dispensations	Sutter and Tabah (1948)
Yonne, France	47.8	1926-1945	0.000250	Department	RC Dispensations	Sutter and Tabah (1948)
Northern Italy (Como, Milano and Varese)	45.5	1933-1953	0.000648	Districts	RC Dispensations	Serra and Soini (1959)
Lombardy, Italy	45.6	1943-1947	0.001094	Districts	RC Dispensations	Serra and Cresseri (1959)
Reggio Emilia, Italy	44.6	1921-1963	0.001819	Diocese	RC Dispensations	Barrai and Moroni (1965)
Parma, Italy	44.8	1931-1950	0.000588	Diocese	RC Dispensations	Cavalli-Sforza (1956)
Sardinia	39.5	1965-1969	0.000771	Districts	RC Dispensations	Moroni <i>et al.</i> (1973)
Mondofedo, Spain	43.4	1922-1964	0.00221	Province	RC Dispensations	Valls Medina (1967)
Toledo Region, Spain	39.8	1900-1979	0.00176	Province	RC Dispensations	Calderon (1983)

Table 2. Mean coefficient of inbreeding (α) in European isolates.

Sample site	Latitude (°N)	Years	α	Estimated mean population size	Number of marriages	Data type source	Reference
<i>Northern Groups</i>							
Orkney Islands, Scotland	59.0	1950	0.00183			Pedigree	Roberts <i>et al.</i> (1979)
Colonsay, Scotland	56.1		0.0023	81		Pedigree	Sheets (1980)
Jura, Scotland	56.0		0.0044	74		Pedigree	Sheets (1980)
Irish Tinkers (Dublin)	53.3	1971-1975	0.03209		37	Marriages	Gmelch (1977)
Ivad, Hungary	47.5		0.00283			Pedigree	Nemeskéri and Thoma (1961)
Kippel, Switzerland	46.4	1900-1970	0.00498	450		Pedigree	Friedl and Ellis (1974)
Töbel, Switzerland	46.3	1665-1950	0.00583	600		Pedigree	Ellis and Starmer (1978)
Saas, Switzerland	46.1	1500-1950	0.00536	1817		Pedigree	Hussels (1969)
U-Jesingen (Württemberg)	48.6	1922	0.002250		204	Survey	Spindler (1922) (in Serra 1961)
Hohenzollern	48.3	1922	0.013410		117	Survey	Reutlinger (1922) (in Serra 1961)
Amnden, Switzerland	47.2	1930	0.001875		139	Pedigree	Grob (1934) (in Serra 1961)
Illgau, Switzerland	47.0	1930	0.013797		52	Pedigree	Egenter (1934) (in Serra 1961)
<i>Southern Groups</i>							
Bologna Valleys	44.5	1950-1980	0.000300		2240	RC Dispensations	Pettener (1981)
Lodigiano, Italy	45.3	1933-1956	0.000610		31005	RC Dispensations	Serra and Soini (1961)
Las Hurdes, Spain	40.3	1951-1958	0.004250		814	RC Dispensations	Valls Medina (1960) (in Serra 1961)

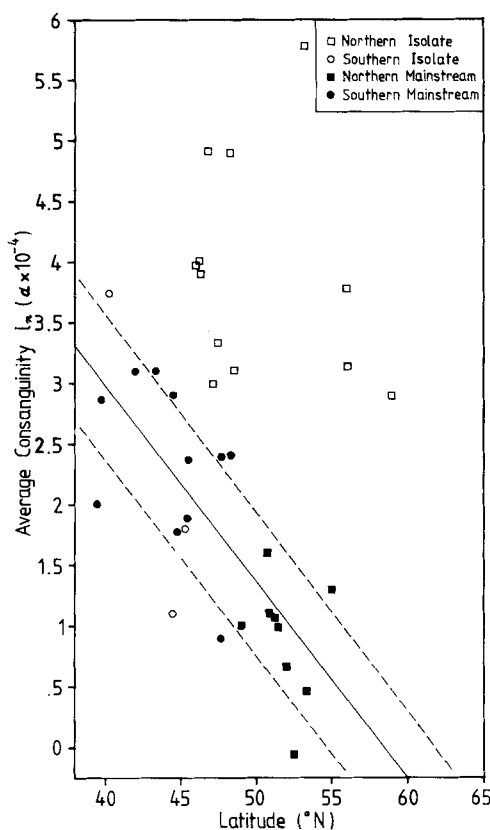


Figure 1. Distribution of latitude and average consanguinity ($1_n \alpha \times 10^{-4}$) in Western European mainstream and isolate populations.

Table 3. Two-way analysis of variation for average consanguinity, testing for affects of geographical division (North-South) and population size division (mainstream-isolate).

Source of variation	Amount of variation	d.f.	Estimated variance	Observed <i>F</i> -ratio	Significance level
Geographical location	0.0000807	1	0.0000807	2.919	NS
Population size	0.0002688	1	0.0002688	9.721	$P < 0.01$
Interaction	0.00000636	1	0.00000636	0.230	NS
Within-cell variation	0.0008573	31	0.0000277		
Total variation	0.0012132	34			

NS, Not significant

Table 4. One-way analysis of variance for mainstream and isolated populations divided between North and South Europe.

Source of variation	Amount of variation	d.f.	Estimated variance	Observed <i>F</i> -ratio	Significance level
<i>Mainstream</i>					
Among-column means	0·00000470	1	0·00000470	17·08	$P < 0·001$
Within cells	0·00000494	18	0·00000027		
Total	0·00000964	19			
<i>Isolates</i>					
Among-colum means	0·00008234	1	0·00008234	1·26	NS
Within cells	0·0008524	13	0·00006557		
Total	0·00093475	14			

NS, Not significant

points to the cultural and historical differences between these two regions. Thus the European marriage region is not homogeneous regarding mate choice.

Inbreeding was apparently quite low in the Mediterranean area through the sixteenth and seventeenth centuries (Roberts 1975, Pettener 1981, 1985), but by the nineteenth century inbreeding levels rose very high. The causes of this increase may include loss of primogenitive rights during the Napoleonic period (Moroni 1967), and an increased survival in sibships coupled with relaxation of ecclesiastical disapprobation (Pettener 1981). The most recent information from Mediterranean regions (Cavalli-Sforza and Bodmer 1971, Roberts 1975, Pettener 1981, Calderon 1983, Pettener 1985) suggests a steep decline in consanguineous unions since 1900 due to increased mobility, industrialization and other socio-economic changes. Inbreeding levels are declining in isolates as well (Sheets 1980, Brennan 1981), and the high inbreeding levels reported for groups spanning several hundred years may be biased by the non-comparability of time-periods.

Results for analysis of variance must be interpreted cautiously. With only 35 total samples, the mean cell size for the two-way analysis of variance is slightly over eight, and the southern isolate groups cell contains only three examples. Thus, the normality and homoscedasticity assumptions of the test are met with difficulty.

In contrast to the European case, average inbreeding levels in Japanese prefectures show no evidence of association ($r = 0·004$) with their estimated latitudes (Imaizumi 1971, pp. 224–225). Japan is more homogeneous both historically and culturally than Europe (Reischauer 1947, Komatsu 1962, Kennedy 1963), and this homogeneity is manifested in lack of geographic differentiation in consanguineous marriages.

Our results suggest that medical genetic studies, particularly those that entail estimation of rare recessive frequencies, may require compensating calculations if estimated frequencies are to be compared across broad geographic areas of Europe. Indeed, Romeo *et al.* (Romeo, Menozzi, Ferlini, Fadda, Di Donato, Uziel, Lucci, Capodoglio, Filla and Campanella 1983, Romeo, Bianco, Devoto, Menozzi, Mastella, Giunta, Micalizzi, Antonelli, Battistini, Santamaria, Castello, Marianelli, Marchi, Manca and Miano 1985) recently used consanguinity to estimate frequencies of rare deleterious recessive alleles in Southern Italy. Similarly, some aspects of clinal patterns in Europe may be, in part, artefacts of this regular patterning of inbreeding levels. For example, if the true frequency of a recessive allele is 0·01, virtually no error in estimation of its frequency would occur in Northern Europe, but its frequency would be overestimated by nearly 20% with α values similar to those reported for Spain (Valls Medina 1967).

Moreover, the magnitude of these inbreeding effects should be considered minimal (Hajnal 1963). Only consanguinity for one generation to the level of second cousins was examined in the present study which may lead to serious underestimation (Roberts 1969, Boyce 1983). Moreover, only marriage records for relatively large regions were used to estimate α . Full coefficients of inbreeding for the non-dispersed marriage of partners are unknown and are therefore assumed to be zero. For data from smaller local populations, the estimate of inbreeding may be expected to be appreciably greater. This too contributes to a consideration of the reported values as minimal.

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Zusammenfassung. Die durchschnittliche Konsanguinität (α) von 20 großen regionalen oder nationalen Stichproben von römisch-katholischen Dispensen oder Staatsarchiven zeigt ein stark negatives Verhältnis mit dem Längengrad ($r = -0,738$; $P < 0,001$), was am besten durch kulturgeschichtliche Faktoren erklärbar ist. Isolate zeigen kein solches Muster und sind in ihrem Inzuchtsniveau stärker variabel. Die Zweiweg-Varianzanalyse zeigt, daß die Stichprobengliederung nach Bevölkerungsgröße signifikant und die geographische Einteilung nicht signifikant ist, mit keiner signifikanten Interaktion zwischen den beiden Faktoren. In einer Einweg-Varianzanalyse zeigten nur die Hauptstichproben signifikante geographische Unterschiede ($P < 0,001$). Es gibt keine solche geographische Verknüpfung in Japan, das eine größere kulturelle und historische Homogenität hat. Das Gradientenmuster der durchschnittlichen Konsanguinität kann Frequenzschätzungen seltener Allele einschließlich genetischer Störungen verzerren.

Résumé. La consanguinité moyenne (α) de 20 grands échantillons régionaux ou nationaux déduite des dispenses catholiques romaines ou d'archives de l'Etat montre une forte relation négative avec la latitude ($r = -0,738$; $P < 0,001$) qui semble être le mieux expliquée par des facteurs historicoculturels. Les isolats ne montrent pas un tel tableau et sont plus variables dans leurs taux de consanguinité. L'analyse de variance à double entrée montre que la division de l'échantillon par effectif de la population est significative, que la division sur la base de la géographie ne l'est pas, sans interaction significative entre les deux facteurs. Dans une analyse de variance simple, seuls les échantillons principaux montraient des différences géographiques significatives ($P < 0,001$). Il n'y a pas une telle association géographique au Japon qui a une plus grande homogénéité culturelle et historique. La distribution en gradient de la consanguinité moyenne peut biaiser les estimations de la fréquence d'allèles rares, incluant des désordres génétiques.