The Patterns of Historical Population Movements in Europe and Some of Their Genetic Consequences

ROBERT R. SOKAL,[1]* NEAL L. ODEN,[2] MICHAEL S. ROSENBERG,[1] AND DONNA DIGIOVANNI[1]
[1]*Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, New York 11794–5245*
[2]*The EMMES Corporation, 11325 Seven Locks Road, Suite 214, Potomac, Maryland 20854*

ABSTRACT   Population movements of 891 ethnic units in Europe over the past 4,200 years, and the correlations of these movements with modern genetic distances were investigated on a one-degree-square grid of the continent. There is significant spatial pattern in movements from sources, to targets, and overall. Patterns change significantly over time. Patterns of sources and targets differ significantly. Modern movements are more numerous than ancient movements. Movements on the periphery of Europe are few in number and are concentrated in direction, while Central European movements are numerous and unconcentrated in direction. Modern genetic distance is negatively correlated with the amount of population exchange between localities. Regional genetic variance is positively correlated with number of movements into, but not out of, areas. The findings are interpreted in the context of European ethnohistory and population biology. Am. J. Hum. Biol. 9:391–404, 1997.   © 1997 Wiley-Liss, Inc.

The demographic and genetic properties of modern populations are in part dependent on the historical processes that produced these populations. An important component of these processes is population movement. A database featuring population movements in its various forms over, mostly, the last 4,200 years of European history was used to address a series of questions concerning the patterns and directions of these movements.

To this end, a European ethnohistorical database describing the movements and locations of 891 ethnic units in Europe for the past 4,200 years was assembled. This database was used to count the number of movements of ethnic units on a European grid of one-degree quadrats. Then, the patterns of these counts of movements was examined with respect to time and place. Are these movements evenly distributed over time and space, or are there preferred periods and places of activities? Which are the periods and locations of high population movements? Do some areas serve mainly as population sources whereas others serve as targets, or are some areas simultaneously high output and input areas?

Ultimately, whether this information can predict some of the genetic properties of the populations was considered, specifically, whether multiple genetic inputs into an area are noticeably correlated with the bumpiness of its gene-frequency surface and also whether genetic distances among different locations in Europe are related to the frequency of population movement between them.

In a parallel study (Sokal et al., 1996), predictions about the genetic composition of populations made from the population movement model were significantly correlated with modern genetic distances between these populations. Knowing that the model has been verified in this manner encourages the present investigations into the patterns of population movement.

Several years before the ethnohistorical database had been completely assembled,

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*Correspondence to: Robert R. Sokal, Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, NY 11794–5245.

Sokal (1991) investigated whether general trends along the lines described above could be detected. To this end, an "approximate summary database" which consisted of relatively few (420) records, subjectively chosen to represent the major migration movements in Europe was used. Rather than use exact outlines of geographic boundaries, as were employed in the present paper, the earlier work was based on presence/absence scores in 5 × 5-degree quadrats as basic units. The results of this rather coarse study support the finding that the patterns of population origin and targets differ with time and space in these populations, and that the diversity of population movements is related to the modern genetic variances of the populations. To some degree, Sokal (1991) could also predict genetic distances from population movements between locations, but more data were needed to establish unequivocal significance. The present study extends these findings considerably. Almost ten times as much information as in the previous analysis is available, and the geographic refinement is 25 times greater than before. The earlier findings can be substantiated far more decisively, and new observations are now possible.

DATA
Ethnohistorical data

The population movements recorded in this study were extracted from a European ethnohistory database assembled in our laboratory. The dataset originally consisted of 6,161 records that describe the history of 891 ethnic units. Each record bears the name of a gens or tribe (or that of an archaeological horizon in the case of prehistorical records, or of a modern nation in the case of more recent ones). The record lists the name of the language family of this unit, a point in time or a time interval when the action described in the record occurred, and the geographic location of the action. With each verbal description of a geographic source and target area in a record, an outline (or outlines) featuring digitized geographic coordinates is associated. Each record also contains an action code which describes one of the following activities of the named ethnic unit. Actions not considered movements are *location* in an area, *assimilation* by other populations, and *wandering* in the area. Actions considered movements, i.e., those that presumably engender gene flow, are *migra-*

tion (of an entire gens), *partial migration* (by part of the population only), *expansion* and *contraction* into an area, *settlement* (into a small defined area, as by colonists), *resettlement* of one ethnic unit by a more dominant one, military *conquest*, military *attack*, and *naval attack* of a coastal region. In addition there are comments on a variety of relevant matters, such as the source area of the population, reported or estimated population sizes (when available), synonyms for the gens, affiliations with other groups, etc. The reference from which the information is abstracted is also furnished.

These records were obtained between 1984 and 1986 by RRS from 191 secondary and tertiary archaeological and ethnohistorical sources and 91 historical maps. Since 1986, the data have been subjected to many checks. Spatial and temporal inconsistencies between records and duplicate information were removed, and provisions for the frequent synonymy of ethnic units was made. This resulted in condensing the 6,161 initial records into 3,459 final records. Table 1 shows a representative sampling of records to give the reader some indication of their nature. The entire ethnohistorical database can be inspected on the world wide web at *http://life.bio.sunysb.edu/ee/msr/ethno. html*.

The 3,459 records include 1,710 non-movement locations, assimilations, and wanderings. The remaining 1,749 comprise population movements distributed as follows: attacks 416; contractions 47; conquests 228; expansions 207; migrations 224; naval attacks 60; partial migrations 274; resettlements 75; settlements 218. The database starts at 2200 BC and continues to 1970 AD. However, there are 37 records, mostly of Anatolian speakers, that are earlier, some as far back as 3000 BC.

Computations were based on one-degree-square quadrats. There are 2,216 such land-based quadrats in the employed map of Europe. This scale was chosen because the digitized ethnohistorical data are detailed enough to warrant one-degree-square quadrats, as are the gene-frequency data. In the earlier approximate summary database (Sokal, 1991), 5-degree-square quadrats were employed for both ethnohistorical and genetic information. The results of the earlier study were compared with those of the present study and showed substantial agreement. This indicates that at least over the

TABLE 1. Sample records from the ethnohistorical database

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
170	9	−200	−150	A	Burgundians	G	Bornholm (Island)	L	
									Start date conservative. End date to conform to (170–13). But note that (185–10) considers Burgundians to have originated along middle Oder R.
149	10	680	#	N	Bulgars	T	Betw Isker R, Balkans & Black Sea (capital Pliska, BG).	Q	
									From S Russia (Pontic steppes nr coasts of Sea of Azov (or even the Kuban R) up to the Dnepr.) {900–374} To form Danube-Bulgarian Empire. Part of Bulgars only (Asparukh's horde; after the death of Kurt or Kuvrath).
328	5	1054	1242	N	Chudes	F	Area around N (Severnaja) Dvina & Vaga RR, N SU.	L	
									Group of early "Baltic Finns".
49	9	1055	1064	N	Uzi	T	{Betw Don & lower Danube RR} (given in reference as: Bug, Sereth, Lower Danube RR.) {900–393}		
									From area between Ural & Volga RR (given in ref as: Patxinachia, Chaxaria, Alania (transcribed from Greek). Former homeland of Pechenegi.) {49–7} Probably coexisted with the Pechenegi for a period of time.
149	37	1392	#	N	Venetians	I	Coast of Albania nr Durres (Durazzo)	S	
									From Venice.

Explanation of record fields:
(1) Reference source.
(2) Item number abstracted from reference.
(3) Start date. Dates preceded by a minus sign are BC, others are AD.
(4) End date. A "#" in this column indicates that the action took place in a single year only.
(5) An A in this column identifies approximate dates. Others, marked N, are (more or less) exact.
(6) Name of gens, tribe, people or archaeological horizon.
(7) Language family of group in column (6). F—Finnic, G—Germanic, I—Italic, T—Turkic.
(8) Target area of action. Numbers in this field refer to reference sources of this information. Other abbreviations: BG—Bulgaria, N—north, nr—near, R—River, RR—rivers, SU—Soviet Union.
(9) Type of action. L—location, M—migration, Q—partial migration, S—settlement.
(10) Source area and comments. Numbers in this field refer to reference sources of this information.
Other abbreviations: R—river, RR—rivers, S—south.

range from one to five degrees the statistics and tests employed are robust to quadrat size.

Each population movement was weighted equally as 1. So when the population in quadrat i moved to another target quadrat j this resulted in a value of 1.0 being entered in element ij of a counts matrix whose rows and columns are the source and target quadrats, respectively. In most cases, the outlines of the source and target area do not coincide exactly with the boundaries of a degree-square quadrat. In those cases, proportional contributions from and to the populations were calculated. The row and column sums are the source and target counts, respectively, for each quadrat. They are measures of the amount of population movement originating from each quadrat and also entering each quadrat.

The updating equation for the counts h_{ij} from quadrat i to quadrat j is

$$h_{ij} = h_{ij} + \frac{wa_i a_j}{T}$$

where w is the action code weight, a_i is the proportion of the ith quadrat that is land,

and T is the land area of the target outline (polygon) measured in units of one-degree-square quadrats. This formula results in source and target counts that are not in integer form. The computations (and numerous others) were carried out by means of a program called ETHNO, written by NLO.

The accuracy of the dates, outlines of areas, or language-family affiliation in the records may be in question. There is no doubt that some errors must remain in the database despite numerous checks to which the data were subjected. These errors could be in recording or transcription, or could be our misinterpretations of the historical facts. Other workers may have different interpretations for who moved, where they moved to or from, or about the nature of the movement. It would have been desirable to subject the data to independent checks by a panel of historical scholars, but this was impractical. It took 10 years from the start of data collection to the completion of the current ethnohistory database; finding a panel to collaborate might easily have doubled the preparation time. As a second-best alternative, Sokal et al. (1996) subjected the data to a series of sensitivity tests to see how errors in chronology, area description, or language-family labeling could have affected the results we obtained. Their general conclusion is that, with respect to predicting the ethnic properties of different areas, the results are quite stable and robust to simulated errors in and omissions from the ethnohistorical database. Since the basic mechanism of computing ethnohistorical affinities (as per Sokal et al., 1996) and the counts of the present study are closely related, a new series of sensitivity tests was not undertaken. It should be noted that errors in chronology and in language-family affiliation will not affect the values in the counts matrix of the present study; only errors in area descriptions or omissions from the ethnohistorical database could have such effects.

Genetic data

Several publications (Sokal, 1988; Sokal et al., 1988, 1989a, 1989b) have described in detail the gene frequencies employed in this study. A total of 93 allele or haplotype frequencies belonging to 26 genetic systems (blood group antigens, proteins, enzymes, HLA, and immunoglobulins) were employed. With some exceptions, each system corresponds to a genetic locus. The entire dataset comprises 3,481 samples from Europe, collected after 1945. Each sample is based on at least 50 individuals, but most are far more numerous. To avoid the complexities of the Caucasus, from which only very few samples are available, and to take advantage of our samples from Asia Minor, we have bounded Europe some distance west of the Urals and north of the Caspian and Caucasus, but have included all but the easternmost regions of Turkey.

Genetic distances were computed separately for each system, employing the Prevosti distance (Prevosti et al., 1975) used consistently in previous studies. These distances utilize information from all 93 allele frequencies. The dimensions of the genetic distance matrices differed since the number of samples differs for each genetic system. The number of localities ranged from a low of 34 for the Lutheran system to 870 for ABO.

METHODS AND RESULTS

Because of the multiplicity of data-analytical methods employed, each suited to answer a different question addressed to the data, the Methods and Results sections are combined. The questions are posed in order, followed by the methods employed to answer them and the results obtained.

Frequency of population movements

Source and target counts. The source counts for the entire period are shown in Figure 1. The greatest number of movements originated in the Balkans, the Pontic Steppes north of the Black Sea, with moderately high areas in much of southern and western Europe, notably France, Iberia, Italy, Greece, and Asia Minor. The areas of low source counts are in the north and east of Europe, as well as in the British Isles. The low counts are probably artificially exaggerated because these northern and eastern areas were largely unknown to historians of antiquity. Furthermore, one-degree quadrats in the north have considerably less surface area than similar quadrats in the south of Europe, and thus might be expected to harbor fewer population movements. Nevertheless, it is undoubtedly true that population densities in these northern and eastern areas were considerably lower than in central and southern Europe and the number of tribes and other ethnic units for a given area was less than in the Mediterranean
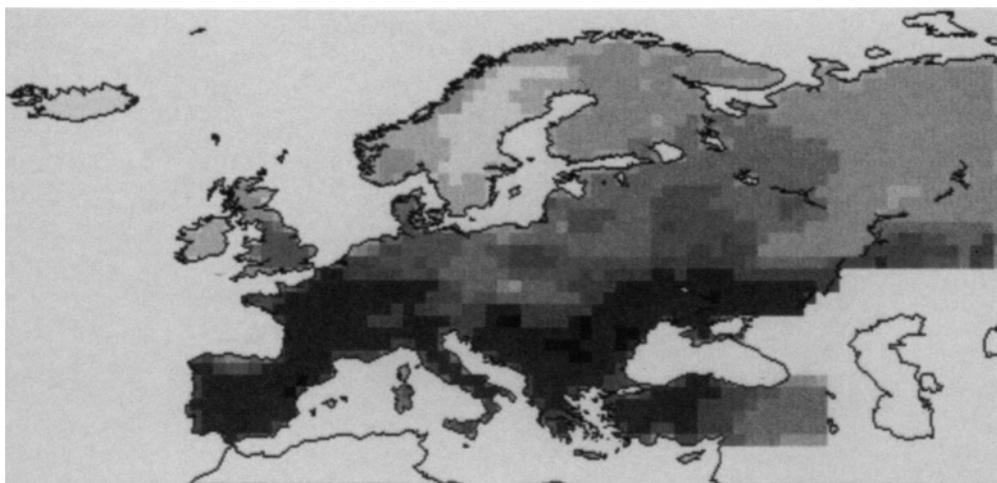
Fig. 1.   Source counts for the entire period. The shaded pixels represent magnitude of source counts in 8 classes shaded from white to darkest grey.

area. This must have resulted in fewer population movements through time.

The target counts are shown in Figure 2. The pattern is markedly different from that of the source counts. The Balkans are a well defined target area, but there are also small regions of high target counts extending into central and western Europe, as well as Northern Iberia. The pattern of the target counts is much more broken up than that of the source counts. Again, the northern regions show low counts, presumably for the same reasons already enunciated for source counts.

Hotspots. Figure 3 shows the sums of the source and target counts for the one-degree quadrats in Europe. A quadrat with a high sum would be a hotspot, i.e., one in which either or both out-movement and in-movement are high. The Balkans stand out as an area consisting of such hotspots. It is clearly a transfer place, with numerous movements into as well as out of it. Other hotspots are in Central Europe and in various scattered areas in Europe. The lowest migration activity is found in the Scandinavian peninsula.

Spatial heterogeneity. To investigate whether the regional differences in source, target, and hotspot counts reported above are significant, spatial correlograms were calculated (Sokal and Oden, 1978; Sokal, 1979). These graphs would show whether there were contiguous areas in the data that

showed similarly high or low counts. It would have been impossible to compute correlograms based on all 2,216 quadrats. They were, therefore, aggregated into 5 × 5-degree superquadrats, and the computations were done on these aggregated counts. The spatial correlograms for source, target, and hotspot counts based on great circle distances among the quadrats are shown in Figure 4. The three correlograms are very similar, indicating similar forces coming into play to create the patterns of the three types of counts. Of course, the hotspot pattern is not independent, being the sum of the other two counts. Marked positive autocorrelation is shown by all three counts up to approximately 1,500 km, confirming the regional tendencies of the variables. All but one autocorrelation coefficient is significant at $P < 0.05$ in each of the three correlograms. Using the Bonferroni method suggested by Oden (1984), all three correlograms are significant at $P < 1.0 \times 10^{-6}$. There is no question that the regional patterns of the three types of counts described earlier are highly significant.

Temporal heterogeneity. To test for heterogeneity of movement over time, the data were set up as a single vector with the 1,749 movement records in chronological order. The vector was then segmented into 9 time periods. The first time period extended for 1,000 years from −3000 BC to −2000 BC. The
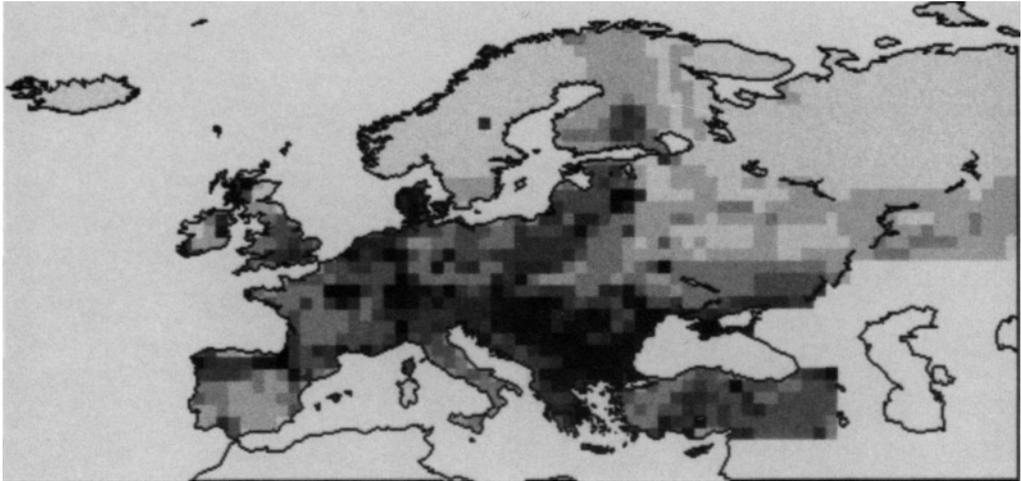
Fig. 2. Target counts for the entire period. Conventions as in Figure 1.
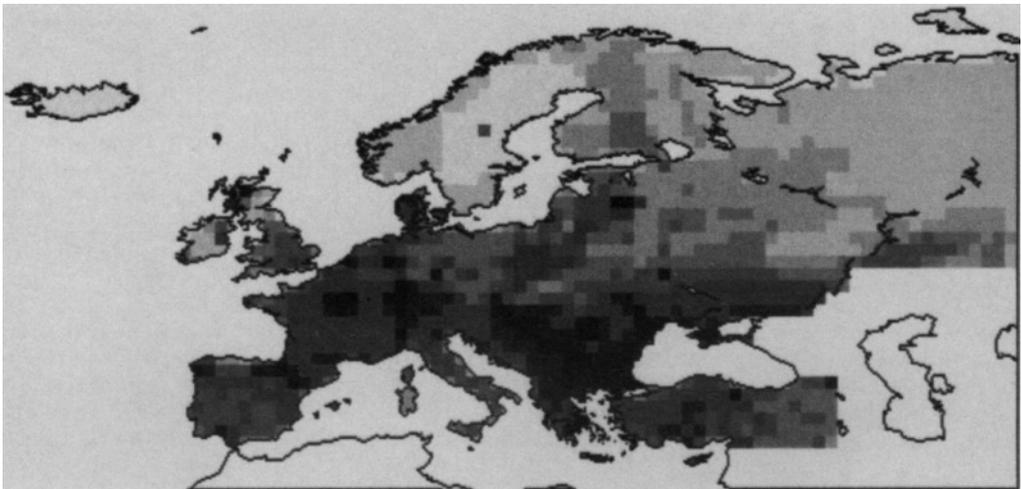

Fig. 3. Hotspot counts for the entire period. Conventions as in Figure 1.

remaining 8 periods each extended over 500 years to the present. For each record, the total source count (which equals its total target count) was entered. The count totals for each vector segment (time period) were summed, and squared, and the nine values were totalled, yielding a sum of squares test statistic. Next, records were permuted at random within the vector and the test statistic was re-calculated after each permutation had been completed. A total of 9,999 such randomizations were done and the observed sum of the squares was compared with the distribution of randomized sums of the squares. The observed sum of the squares was the highest of all the 10,000 values obtained. The null hypothesis that there was no difference in number of movements among the time periods ($P = 0.0001$) can, therefore, be rejected. The number of movements evidently changed over time. Note that this test assumes that populations move independently of each other.

Cumulative movements over time. Having shown that there was heterogeneity in the number of movements over time, the fre-
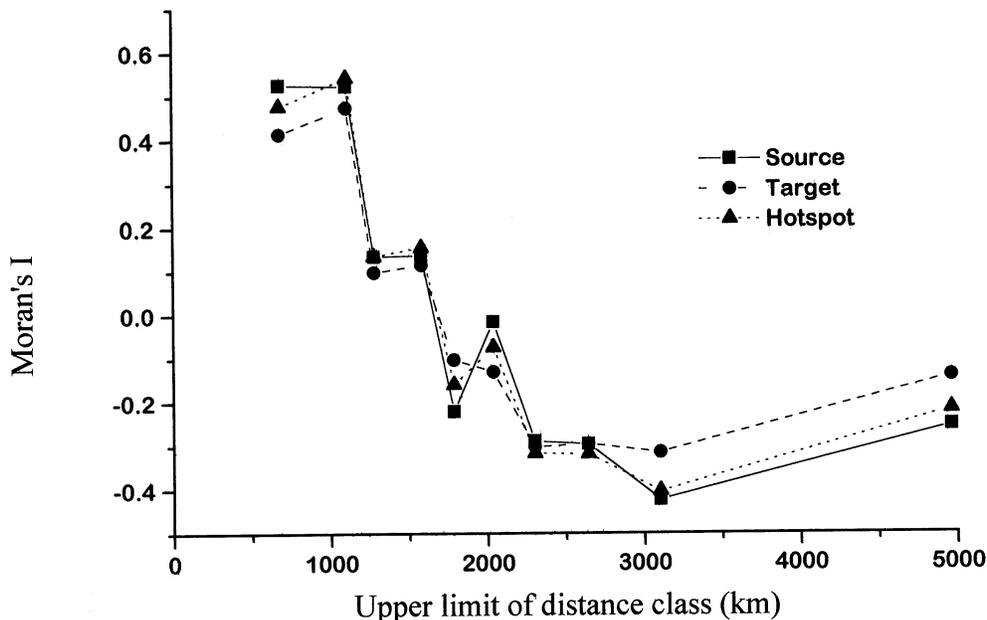
Fig. 4. Spatial correlograms for the source, target, and hotspot counts. Abscissa: distance classes in km. Ordinate: Moran's spatial autocorrelation coefficient I.

quency of movements over time was examined. To this end, the cumulative frequency of movements over the entire time period of the study was plotted. The curve is shown in Figure 5. It seems to be divided into three distinct segments. The first is a period of possibly exponential growth of movements between 3000 BC and 1 BC, followed by a linear trend between 1 AD and 1800 AD, and a very rapid increase in movements in the period since that time.

Time space interaction in counts. Since the counts were both spatially and temporally heterogeneous, it seemed possible that there could be space time interaction in these data. This was tested, separately for source, target, and hotspot counts, by creating a matrix of 9 rows for the time periods times 2,216 columns for the quadrats. Next the rows were mean-centered. The variance of the centered elements for each column was computed and the 2,216 variances were summed as the test statistic. The statistic was evaluated by randomizing the movement records across the time periods. The result of such a procedure involves numerical changes in both rows and columns. If there is a significant interaction effect, the test sum of squares should be much larger
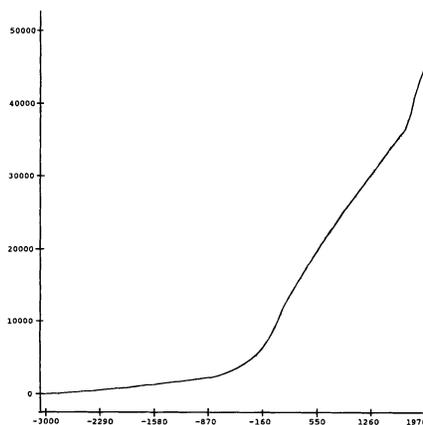

Fig. 5. Cumulative frequency of movements over the entire period. Abscissa: Dates (negative numbers are BC). Ordinate: Cumulative frequency.

than the randomized sums of squares. The result for 499 randomizations was P 0.002 for all three types of counts, indicating that there was clearly interaction in these data. Thus, differences among time periods depend on the particular group of quadrats in which the population movements occur or,

alternatively, different regions of Europe vary in their pattern of change in population movement over time.

Asymmetry of movements. It was shown earlier that the quadrats yield some hotspots, i.e., that the sum total of source counts and target counts differs for different quadrats. The question arises as to whether there is an asymmetry of response for these hotspots; are some hotspots primarily sources and others targets? To answer this question, an asymmetry test was carried out to see, given there are hotspots, whether some hotspots are typically senders and others are typically receivers, or whether the hotspots reflect generalized levels of activities that are symmetrical. The statistic for this test is the sum of the squared differences between the row and column margins of the counts matrix. Randomized versions of this statistic were generated by rerunning the ETHNO program, each time randomly flipping target and source quadrats within the movement records. If the observed statistic is much larger than that of the randomized distribution, this implies that certain quadrats are typically senders and others are typically receivers, rather than reflect a high generalized level of activity. The results show that the sum of squared differences of the observed dataset is greater than that of any of 499 randomized datasets. It was, therefore, concluded that there is statistically significant evidence for asymmetry of movements at $P = 0.002$. The quadrats differ in their in-bound and out-bound numbers of movements.

Directions of movements. A map showing magnitude, direction, and uniformity of movements was prepared (Fig. 6). This was done as follows: regions of 4×4 one-degree quadrats for the entire map were defined. For each of the 16 quadrats in these regions, equal length arrows pointing from the center of the quadrat to the 2,215 other quadrats that were possible targets for movements from the original quadrat were constructed. These arrows were weighted by the number of movements to the target quadrat. All of the arrows for all 16 quadrats of a region were translated to the center of the region; then each arrow was replaced by a point at the tip of the arrow. The points were weighted by the number of movements and then the center of gravity of all these points was calculated. This resulted in a single point that became the tip of a new arrow

(shown as a line segment in Figure 6) originating in the center of the region. This shows the direction of movement for that region. A circle in the center, whose diameter was proportional to the total number of movements coming out of the 16 quadrats was drawn. This is the magnitude of movements emanating from that region. The direction of the line segment gives the average direction of movement. The length of the line segment is a measure of uniformity (or concentration) of direction. The shortest lines (effectively invisible in Figure 6) indicate lack of uniformity of direction of movement. The longer the line, the more uniform the direction of the movements of the 16 quadrats.

Figure 6 shows very clear patterns. Movements from northern and eastern Russia were quite uniform in a westerly and southwesterly direction, whereas movements from Scandinavia tended in a southeasterly direction. In Central Europe and in the Balkans, there was much population movement in various directions. The magnitude of the movement is shown by large circles, the lack of a uniform direction by the short line segments attached to the circles. Movements from Asia Minor were largely in a westerly direction. There is an evident negative correlation between concentration and magnitude. This is due to the fact that peripheral quadrats experience mostly one (therefore, low magnitude, concentrated) movement, while central quadrats experience many (therefore, high magnitude, unconcentrated) movements. Note that there is a bias in this figure for the peripheral regions. The direction of the line segments is necessarily toward the center, since movements beyond Europe were not recorded in this European ethnohistorical database. If such a study were to be extended to include Asia and/or Africa, there would undoubtedly be centrifugal movements from peripheral areas of Europe to these added regions. Thus the concentration of movement directions shown in Figure 6 would be diminished and the average direction would not be so markedly centripetal.

Genetic distances versus gene flow

Can the ancient population movements be related to modern genetic structure? It would be ideal, of course, to be able to relate these movements to ancient genetic structure, to which they should be more clearly
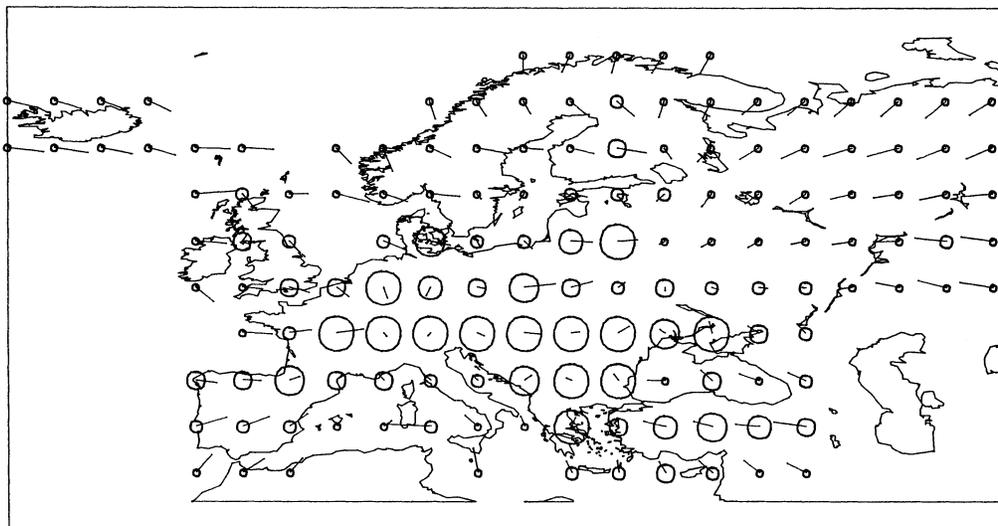
Fig. 6. Directions, magnitude and homogeneity of historical population movements in Europe. A single symbol represents the average of every sixteen (4 4) one-degree-square quadrats. Centered in the middle of this larger quadrat is a circle whose diameter is proportional to average magnitude (frequency) of movements. Issuing from the circle is a line segment which points in the average direction of the movements. The length of the line segment is proportional to the uniformity (concentration) of the movement directions.

linked; unfortunately, genetic data for ancient populations in Europe are not available. The general underlying assumption is that population movements between geographic regions in Europe led to gene flow between these regions and that the number of population movements between a pair of quadrats in our study is directly proportional to the amount of gene flow between them. As a measure of gene flow, the average of the reciprocal population counts between each pair of quadrats ij was calculated. This quantity was computed for all pairs of quadrats and assembled in a matrix representing cumulative gene flow. From this matrix, gene flow measures were obtained between any pair of localities for which genetic distances based on any one system were available. When a genetic distance represented two geographically close localities located in the same one-degree quadrat, they were assigned an arbitrary gene flow measure of 3 near the upper tail of the observed distribution of gene flow measures. In this way, we prepared matching matrices of gene flow measures, genetic distances, and geographic (great circle) distances, whose dimensions

varied for each genetic system according to the number of localities. The data were then analyzed by the Smouse-Long-Sokal three-matrix procedure (Smouse et al., 1986) and pairwise correlations of genetics with gene flow, as well as partial correlations of genetics with gene flow, geographic distance kept constant were calculated. The significance of these correlations was tested by Monte Carlo permutational methods based on 499 permutations.

Table 2 shows the results of the pairwise and partial correlations. All but one of the pairwise correlations are negative, as would be predicted for a correlation between genetic distance and gene flow. Sixteen of the 26 are significant at P 0.05. The average correlation over all systems is –0.0704. By Fisher's method for combining probabilities (Sokal and Rohlf, 1995), the overall P-value of the null hypothesis of no association between genetic distance and gene flow is vanishingly small, P 5.43 10^{-15}. The partial correlations, while significant, are not as markedly so. Only 5 of the systems are individually significant, all of them negative, as predicted. The average partial correlation is

TABLE 2. Correlations between genetic distances (GEN) and a measure of gene flow (GF). Geographic distances (GEO)
are held constant on the right

Genetic system	r(GEN,GF)	P	r(GEN,GF.GEO)	P
1.1 ABO	−0.1431	0.008	−0.0425	0.002
1.2 ABO	−0.0873	0.002	−0.0104	0.338
2.5 MN	−0.0369	0.018	−0.0283	0.002
2.7 MN	−0.0682	0.038	−0.0022	0.508
3.1 P	−0.0408	0.030	−0.0240	0.008
4.1 RHESUS	−0.0564	0.188	−0.0125	0.712
4.13 RHESUS	−0.0444	0.014	0.0089	0.358
4.19 RHESUS	−0.1362	0.004	−0.1291	0.004
5.1 LUTH	−0.0542	0.048	−0.0622	0.032
6.1 KELL	−0.0401	0.194	0.0030	0.652
6.3 KELL	−0.0659	0.068	−0.0380	0.200
7.1 ABHSE	−0.0610	0.006	0.0718	0.866
8.1 FY	−0.0492	0.008	−0.0181	0.282
36.1 HP	−0.0409	0.038	0.0234	0.810
37.1 TF	−0.0682	0.178	−0.0110	0.512
38.1 GC	−0.0092	0.306	0.0334	0.596
50.1.1 AP	−0.0808	0.116	0.0093	0.902
52 PGD	0.0390	0.848	0.0802	0.922
53 PGM1	−0.1016	0.002	0.0086	0.638
56 AK	−0.0468	0.062	0.0234	0.878
63 ADA	−0.0751	0.006	0.0152	0.562
65 TASTER	−0.0224	0.198	0.0107	0.512
100 HLA-A	−0.2223	0.002	−0.0615	0.098
101-102 HLA-B	−0.2212	0.002	−0.0564	0.150
200 GM 1,2,5	−0.0414	0.268	0.1210	0.950
201 INV (KM)	−0.0559	0.026	0.0588	0.824
mean r value or combined P	−0.0704	5.432×10^{-15}	−0.0011	0.003

−0.0011 and the combined *P*-value is 0.003. Apparently much of the significance of the pairwise correlation is accounted for by geographic distance. Clearly, the smaller the geographic distance between two quadrats, the more population movements and hence gene flow, between these quadrats. Geographic distance can account for a large proportion of the correlation. Nevertheless, for some systems there is a clear effect of the variation in gene flow when geographic distance is held constant.

Fractionated, as well as cumulative, gene flow matrices were also calculated for the nine time periods. The results are shown in summary form in Table 3. Average pairwise correlation is invariably negative as predicted and highly significant by Fisher's method of combining probabilities (all cases $P < 3 \times 10^{-7}$). However, the partial correlations are not significant for the fractionated results and become significant only by 1500 AD for the cumulative results. That is, a clear relation between ancient population movements in a time period and modern genetic distances cannot be demonstrated when geographic distances are held constant. There is a general tendency for in-

creased significance of partial correlations for the cumulative results as later periods are approached so that more recent population movements seem to affect the genetic distance more than more ancient ones.

Genetic variance and counts

Finally, we tested whether the genetic variances that are found in the present-day gene-frequency surfaces can be related to the counts of population movements resulting from the ETHNO program. For most genetic systems, single-degree quadrats were too small an area to obtain a genetic variance (because many quadrats had no genetic samples and most others had just one). Therefore, the data were aggregated into 5×5 degree quadrats by grouping 25 adjacent single-degree quadrats. Gene-frequency variances were computed in each 5×5 quadrat for each observed gene frequency and divided by $\overline{pq}$ computed separately for that quadrat to standardize them. The resulting ratios (F_{ST}'s) ranged from 0 for invariant gene frequencies, to 1 for gene frequencies whose variance matches expectations, and to greater than 1 for overdispersed gene frequencies. These ratios were then averaged

TABLE 3. *Correlations between genetic distances (GEN) and cumulative (upper table) or fractionated (lower table) measure of gene flow (GF), averaged over genetic systems. Geographic distances (GEO) are held constant on the right*

Time interval	mean r(GEN,GF)	combined P	mean r(GEN,GF.GEO)	combined P
3000 BC–2001 BC	−0.0233	2.973×10^{-7}	0.0067	0.3255
3000 BC–1501 BC	−0.0234	4.465×10^{-8}	0.0070	0.2699
3000 BC–1001 BC	−0.0232	4.911×10^{-8}	0.0080	0.2953
3000 BC–501 BC	−0.0260	1.695×10^{-9}	0.0073	0.2846
3000 BC–1 BC	−0.0324	1.377×10^{-10}	0.0071	0.1902
3000 BC–500 AD	−0.0501	2.555×10^{-13}	0.0027	0.0669
3000 BC–1000 AD	−0.0572	1.323×10^{-13}	0.0039	0.0595
3000 BC–1500 AD	−0.0634	6.349×10^{-15}	0.0020	0.0349
3000 BC–1970 AD	−0.0704	5.432×10^{-15}	−0.0011	0.0033

Time interval	mean r(GEN,GF)	combined P	mean r(GEN,GF.GEO)	combined P
3000 BC–2001 BC	−0.0233	2.973×10^{-7}	0.0067	0.3255
2000 BC–1501 BC	−0.0232	6.901×10^{-8}	0.0071	0.3156
1500 BC–1001 BC	0.0229	3.700×10^{-8}	0.0078	0.3181
1000 BC–501 BC	−0.0259	5.611×10^{-9}	0.0061	0.2142
500 BC–1 BC	−0.0297	1.177×10^{-9}	0.0066	0.2102
1 AD–500 AD	−0.0423	2.697×10^{-12}	0.0021	0.0702
501 AD–1000 AD	−0.0321	4.679×10^{-10}	0.0081	0.6274
1001 AD–1500 AD	−0.0311	9.634×10^{-12}	0.0046	0.1284
1501 AD–1970 AD	−0.0331	3.213×10^{-11}	0.0031	0.1081

over the available gene frequencies to give a single measure of variance for each quadrat. The averages were not always over the same number of gene frequencies since samples for different genetic systems came from differing locations. The source and target counts were similarly aggregated for each 5×5 degree quadrat.

The results are shown in condensed form in Table 4. The correlation of variances with target counts is twice as large as that for source counts. The correlation with source counts cannot be shown to be significant, whereas that for target counts clearly is, even when a correction for spatial autocorrelation developed by Clifford et al. (1989) is applied. It was concluded that there is a positive correlation between movements into an area and its genetic variance, but that such a relationship cannot be demonstrated for source counts, the number of movements out of an area.

The differential responses of genetic variance to counts over the nine time periods of the study were examined. The fractionated results suggest that positive and significant correlations occur for both source and target counts between 1000 BC and 1000 AD, whereas the cumulative results show positive and significant correlations for targets starting at 1 AD and for sources from 500 AD to 1000 AD. Again, a stronger effect of target counts is noted in these data.

TABLE 4. *Correlation between overall standardized gene frequency variances and source or target counts*

Type of count	Correlation	P^*
Sources	0.203	0.196
Targets	0.399	0.008

Note: *The probability values have been corrected by the method of Clifford et al. (1989) for spatial autocorrelation in the variables.

DISCUSSION
Patterns of population movements

The patterns of source and target counts shown in Figures 1 and 2 demonstrate a clear preponderance of movements in southern Europe, with low counts in the north and east. Undoubtedly, the single factor most responsible for this phenomenon is the lower population density in the northern and eastern regions of Europe. Agriculture came relatively late to these areas, if it reached there at all, and climatic and physiographic factors determined a sparser population. This in turn led to fewer ethnic units, hence less migrational activity. A contributing factor must also be the smaller area of one-degree square quadrats in northern Europe compared to one-degree quadrats in the Mediterranean area. The latter quadrats have more than twice the area of the northernmost quadrats in this study. This again makes for population diversity in the south, which in turn leads to more population movements.

A further factor making for low population movement counts in the north is the concentration of early western civilization almost entirely in the Mediterranean basin. Historians of the antique had little information about events transpiring farther north. This is reflected in the paucity of records describing northern and northeastern movements. Thus, the difference in counts is partly a natural phenomenon (lower population density) and partly an artifact (quadrat area and ancient records).

Within the southern tier of higher counts, the Balkans stand out as an area of both high source and especially high target counts. When maps for fractionated time periods were examined (not shown), the Balkans appear consistently as areas of high source and target counts, with the possible exception of the latest period, 1501 AD to 1970 AD. This prominence of the Balkans as a population transfer place is also attested to by the hotspot map (Figure 3). The Balkans appear to be the crossroads of Europe, receiving population inputs from three directions: through the Pontic Steppes north of the Black Sea, through Asia Minor south of that body of water, and from central Europe via the Danube Valley and the Iron Gate. Extensions of the high values in the Balkans can be found in the Pontic area north of the Black Sea and in Central Europe. These extensions are related to two major migrational tracks in Europe. One is the nomadic invasions of Europe from Central Asia which passed through the Pontic Steppes on their way into the Balkans and Central Europe over a period of some 2000 years; the other is the large number of Germanic migrations through late antiquity and the Middle Ages which resulted in profound changes in the ethnohistorical map of Europe.

That the patterns are real is supported by the finding of spatial heterogeneity. The patterns changed with time as demonstrated by both the temporal heterogeneity tests and the significance tests for time-space interaction. There is, therefore, statistical support for the differences in patterns over time described in the previous paragraph. Also, the frequency of movements accelerated over time. To what can this phenomenon be ascribed? Possibly this is a reflection of the increase in population density with time. Unfortunately, this hypothesis cannot be tested since inadequate estimates of density over time are available. The increase in frequency of movements could also be due to increased knowledge of such events from historical records with the passage of time. It would be difficult to construct variables for population density and intensity of historical research to test their effect on the number of movements. The directionality of movements is attested to by the asymmetry test and Figure 6.

Genetic distances and population movements

It is satisfying to discover that the cumulative effects of population movements between pairs of quadrats is significantly correlated with modern genetic distances between these quadrats. Evidently ethnohistorical events can explain modern genetic structure. This is not a surprising finding, but it is pleasing to see it demonstrated. The measure of gene flow, the average of the reciprocal population counts between each pair of quadrats, is but a rough measure of the expected resemblance between populations. The correlations it produces are very low for this reason, and also because the relationship, which is estimated in a linear fashion, is, in fact far from linear. It should also be noted that correlations between interpoint distances are smaller than correlations between data from which the interpoint distances are calculated. For example, in a simulation in which 1,000 X_i, Y_i-pairs were generated with correlation $r_{XY} = (0.1, 0.3, \text{etc.})$, r_{XY} typically exceeded the correlation between interpoint distances $|X_i - X_j|$ and $|Y_i - Y_j|$, of all pairs of points $(i \neq j)$ by anywhere from 40% to 420%. Nevertheless, the pairwise correlation between genetic distances and population movements is highly significant overall, and even the partial correlations with geography held constant are significant by conventional criteria. A much better explanation of the genetic distances is given in a parallel paper (Sokal et al., 1996) in which the ethnic composition of the moving and of the recipient populations are estimated which leads to measures of ethnohistoric affinities between populations. These are then used to predict the same genetic distances that were analyzed in this paper. The correlations are substantially higher, as are even the partial correlations with geography held constant.

These results can be compared with that of the earlier approximate study (Sokal, 1991) in which partial correlations between genetics and gene flow, geography con-

stant, were entirely nonsignificant. In this study (Table 2), Fisher's combined probability for the partial correlations is strongly significant at $P = 0.003$. It appears that the more extensive data of the present study have clarified the earlier picture. Unlike the earlier study, correlations during later time periods of the study were lower than the earlier ones.

Note that the correlations are so much lower in this study than in the earlier approximate study by Sokal (1991). If two data sets are spatially autocorrelated, the correlation observed between them may appear to be enhanced by spatially aggregating the observations in each data set. Current work reports observations on one-degree-square quadrats, while the previous work reports more highly aggregated observations on 5-degree-square quadrats.

Genetic variances and population movements

The findings of the present study are more clear cut than those of the earlier work by Sokal (1991). In that approximate study, correlation between the source and target counts and genetic variance were found, but the correlation of source counts was higher than that of target counts and more individual systems were significant for source counts than for target counts. One would have predicted the opposite relationship. Genetic variances should be greater in areas which receive more numerous (and presumably diverse) inflows. The present, more extensive data, follow this prediction, and, in fact, the only relationship that is significant is that between target counts and genetic variances. Again, it appears as though the more extensive database has clarified the relationships.

There are corollaries of this relationship. The more movements that there are into an area, the more likely it is that populations speaking languages in different families will be among the incoming populations. These populations typically are genetically different and their introduction will lead to an increase in genetic variance of the populations. Sokal et al. (1988) showed that 5×5-degree quadrats in Europe that were crossed by one or more language boundaries had greater genetic variances than quadrats that were not crossed, and Sokal (1991) found that the correlation of target counts with the number of modern languages found in a quadrat was significant, the correlation with

target counts being higher than that with source counts. Thus, there appears to be indirect evidence that movements lead to multiple modern languages, which is reflected by the increase in the genetic variance of the area.

CONCLUSIONS

For well-studied regions, such as Europe, it is possible to assemble a set of ethnohistorical records describing population movements. This assemblage can be analyzed for patterns of movements in space and trends over time. It is possible to develop nonstandard statistical tests that examine the significance of the patterns and trends. The dataset can then be used to make predictions about modern genetic patterns. In turn, these predictions can be tested.

A contrasting approach which has been used extensively (see Cavalli-Sforza et al., 1994, for numerous examples) is to study and characterize patterns of genetic variation in a collection of samples. Then the historical or archaeological records are examined for the event or events that can explain the observed pattern. There is some danger inherent to this approach. One can usually find some event that is concordant with the observed pattern, and there is no certainty that it is in fact the process that explains the pattern. Generally, there have been no statistical tests to associate the historical event with the genetic pattern.

The present approach first constructs a collection of items of information about historical population movements. From their aggregate, measures that predict genetic patterns, are developed and the relationship between the predicted and observed patterns are tested. Currently, whether this scheme works for subsets of records, such as for a specific ethnic group or for a set of populations originating from a given area, it is being tested. Ultimately, it would be desirable to be able to test for the effects of single records. However, the structure of the test may not be sufficiently sensitive to pick up such detail.

ACKNOWLEDGMENTS

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